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Eyprepocnemis alacris alacris (Serville) — biology and functional morphology of the foregut in relation to feeding (Orthoptera: Acrididae)

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Abstract. Biological studies on *Eyprepocnemis alacris alacris* (Serville) confirm the existence of only five instars unlike as in the allied species *Eyprepocnemis capitata* (Miller) and two subspecies of *Eyprepocnemis plorans* (Chorp.), viz., *E. plorans meridionalis* Uvarov and *E. plorans ornatipus* (Walker) in which six, seven or eight instar cycles are evident. The number of instars of *Eyprepocnemis alacris alacris* is always constant, being five in both sexes as against seven in males and eight in females of *E. plorans meridionalis*. Ovipositional behaviour of *E. alacris alacris* involves probing and selection of oviposition site, usually associated with damp soil with tender grass having less silica content, very essential for the early instars. Eggs with reticulate chorionic sculpture arranged in rows are always laid in pods, the eggs being confined only to the bottom third, while a foamy secretion fills up the rest of the pod, including the spaces between the eggs. The incubation period is 17–18 days, the post-embryonic development lasting 105–115 days for females and 95–115 days for males. Changes involved in the foregut armature during post-embryonic development correlated with the degree of silica content of grasses have been discussed.

Keywords. *Eyprepocnemis alacris alacris* (Serville) ; oviposition ; egg-pod ; foregut armature ; functional morphology.

1. Introduction

Seasonal periodicity as well as the duration of the post-embryonic development of acridids in ecologically different areas appear to exhibit a correlation with the annual cycles of weather and vegetation. Interpretation of such correlations involves a proper assessment of the details pertaining to the life cycles of these phytophagous insects. Major contributions in this regard are by Richard and Waloff (1954) on some British Acridids, and on other species of grasshoppers by Alexander and Hilliard (1964), Alwarez-Sanchez (1964), Antoniou (1968, 1970, 1973), Antoniou and Hunter Jones (1956), Ba Angood (1976), Barnes (1963), Burleson (1974), Descamps (1962), Gerold (1961), Hafez and Ibrahim (1958), Hunter Jones (1967a), Iyiola (1970), and Kok (1971). Very few Indian species of grasshoppers, viz., *Colemania sphenarioides* Bol. (Coleman 1911), *Hieroglyphus banian* Fabr. (Coleman and Kannan 1911), *Gesonula punctifrons* Stal. (Kapur and Dutta 1952), *Parahieroglyphus bilineatus*, *Aularches punctatus* Drury (Katiyar 1955, 1956), *Spathosternum prasiniferum* Walk. (Iqbal and Aziz 1975), *Hieroglyphus nigrorepletus* Bol. (Roonwal 1945, 1976) and *Chrotogonus trachypterus trachypterus* (Blanch.) (Parihar and Pal 1978) have been investigated. The genus, *Eyprepocnemis* has an extensive geographical distribution in the Mediterranean area, Northern and tropical Africa and Southern Asia. Some species like *E. plorans* (Chop.) and *E. noxius* Dirsh have attained a pest status in Egypt and Sudan (Joyce 1952) and a knowledge of the biology of other species of *Eyprepocnemis* would enable us in devising proper control measures. Available information on the biological aspects relates to *Eyprepocnemis capitata* (Miller) (Antoniou and Hunter Jones 1956), *E. plorans ornatipus* (Antoniou 1968), *E. plorans meridionalis* Uvarov, and *E. alacris impicra* Uv. (Mahto 1977), as well as on the food preferences, mandibular morphology of instars and adults, and growth in terms of weight, length and eye-stripe number in *E. alacris alacris* (Muralirangan 1978; Muralirangan and Ananthakrishnan 1977a). More detailed observations on the biology of *E. alacris alacris* are presented along with information on changes in the functional morphology of the foregut in relation to feeding.

2. Materials and methods

E. alacris alacris was collected principally from Guinea grass fields (figure 1) in and around Madras and reared in the laboratory modifying the technique of Hunter Jones (1967) as under.

Wooden cages with glass front (110 cm wide, 30 cm long and 40 cm high) with two sliding walls (0·3 mm thick) provided three compartments and when a large cage was needed, the sliding walls were removed. A small trap door on the top facilitated handling of hoppers and food materials. Some twigs were placed to provide sufficient grip during moulting and for basking. Without these, the mortality rate of the early instars was high, confirming the observations of Hunter Jones (1961). To the floor of the cage was fixed the egg laying tube 7·5 × 2·5 cm and alternatively 5–7·5 cm deep garden soil was provided in the wooden boxes (6 × 4 inches).

Nymphs were generally reared in cylindrical glass jars (23 cm/10 cm), though handling of early hoppers and cleaning were easy when lamp chimneys were used. Artificial light (25 W) was provided when there was a fall in the day temperature below 28° C, as also for instars between 8 a.m. and 5 p.m. to reduce the mortality rate. Care was also taken to feed the early instars with tender grass leaves. Water was provided within the cage in a dish for the instars (Gangwere 1961). Whenever hold-fasts for tubes were not available, the soil was kept in a tray and kept moist for laying the egg-pods, as the insect did not oviposit in dry soil.

Figure 1. *Panicum maximum* field.

3. Observations

The commonest species in and around Madras is *E. alacris alacris* feeding on *Panicum maximum*, *Oryza sativa*, and on other fodder grasses and plants (Muralirangan 1978). Breeding is confined to the irrigated fields of *Panicum maximum* and very few adults were collected in the months of June–July (2–4 adults for every 5 sweeps in a sweeping net), they being abundant in August–October, immediately after the rains (15–20 adults and larvae for every 5 sweeps), and gradually diminishing in December–January (5–6 adults for every 5 sweeps). In the laboratory a culture was maintained throughout, except in summer. *E. alacris alacris* has a five-instar life cycle unlike *E. capitata*, *E. plorans meridionalis*, and *E. plorans ornatipus*, which have a seven- or eight-instar life cycle. Kaufmann (1965) observed that *Zonocerus variegatus* took 1–2 months more to complete the life cycle when bred in smaller cages. However, in the present investigation, cages of sizes ranging from 23 × 15×23 cm to 110×30×40 cm were used without such differences in the duration of instars.

3.1. *Oviposition*

Adequate soil (5–7·5 cm deep) was kept either in a wooden tray or in plastic tubes (7·5 × 2·5 cm) placed on the floor of the cage and the insect oviposited only in the moist soil maintained at 28°–30° C. At 31° C they failed to oviposit.

3.2. *Oviposition behaviour*

During oviposition, the insect tapped the ground with the apex of the abdomen and felt the ground with its antennae and palps, as observed in *Locusta* (Kennedy 1949) and after exploring and choosing a suitable substratum, the females burrowed a hole within 6 min (though occasionally the females dug several times before actually ovipositing). The probing behaviour lasted 15–20 min and within 1–3 hr the process of egg laying was completed, depending on the temperature and moisture. Egg laying was not affected by the density of the insects in this species against that of *Schistocerca paranensis* (Brum.) reared in the laboratory (Hunter Jones 1967). When moist sand was kept in the tray/tube, no eggs were deposited though the female might dig a hole. In the field the egg-pods were laid only in damp soil with freshly growing grasses in the bunds. This selection of ovipositional sites appeared to fulfil the feeding requirements of the early instars, which preferred only a tender grass blade. While laying the egg-pod, the insects ignored any disturbance around though they were very sensitive while digging (Clarke 1965). *E. alacris alacris* always laid pods singly after which the abdomen was withdrawn and the females moved away without covering the top of the pod with soil particles as observed in *Schistocerca* (Popov 1959) and other species of grasshoppers.

3.3. *Egg-pod structure*

The egg-pod was generally straight, though at times slightly curved and measuring 3·5–5·7 cm long and 0·6–0·8 cm wide. The eggs occupy only a third of the pod, the rest being filled with a light brown/dull white foamy mass, secreted by the accessory glands of the oviduct (figure 2). The secretion hardens on release, to which the soil particles adhere.

The time taken for the release of the pod and the withdrawal of the abdomen by a sudden leap, as a result of the jerk of the hindfemur, was about 23–40 minutes.

The eggs in the pod were arranged at an angle, the micropylar end facing upwards. Each pod contained 28–47 eggs, arranged in rows, each row containing on an average 8 eggs. The eggs were long, with a circular micropylar cap, measuring $4\cdot99 \pm 0\cdot0066 - 0\cdot563 \pm 0\cdot0028$ mm in length and $0\cdot112 \pm 0\cdot0045$–$0\cdot170 \pm 0\cdot0075$ mm in width. The chorionic sculpture was clearly reticulate and had a double-walled appearance.

3.4. *Incubation period*

Under the normal temperature of 28° C embryonic development took place and the eggs hatched within 17–18 days. All the eggs hatched within 30 minutes (from the hatching of the first egg) and the egg mortality was below 10% in the laboratory. The provisional cuticle, which was shed as the nymph emerged, had a shrivelled appearance and was seen scattered around the exit hole of the egg-pod on the ground. Immediately after hatching, the hoppers were pale yellowish and within 30 min they turned brown.

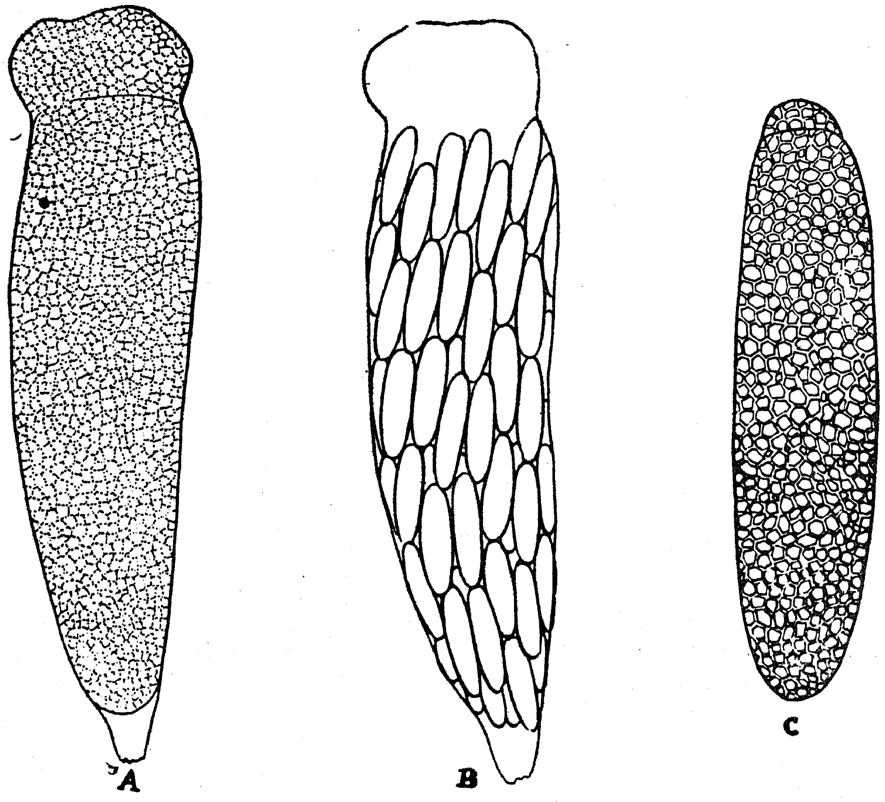

Figure 2. *E. alacris alacris*: **A.** Full egg-pod. **B.** L.S. of the pod. **C.** Chorion sculpture.

3.5. *Nymphal development*

The number of instars was constantly five in both sexes in contrast to 6, 7, and 8 instars of *E. capitata* (Antoniou and Hunter Jones 1956) and 7 in males and 7–8 in females of *E. plorans meridionalis* (Jago 1963). In *Nomadacris septemfasciata* and *Schistocerca gregaria* (Albrecht 1955; Roonwal 1947) there appears to be no 'type' differences in the development and in the number of instars in *E. alacris alacris*. No change in the number of instars was observed in *E. alacris alacris* even when it was bred in smaller cages, in contrast to *Zonocerus variegatus* (Kaufmann 1965).

The average durations of the I–V instars were 11–19; 15–17; 17–19; 24–26 and 20–22 days respectively for females and 11–19; 15–17; 17–19; 24–26 and 17–19 days for males.

3.6. *Adult*

The adults live on an average for 65 days. The total time taken to complete the development is 95–105 days for males and 105–115 days for females. During its lifetime each female lays 4 egg-pods on an average.

The development of adults includes two important but different physiological processes, *viz.*, general growth and the growth of the reproductive organs (Uvarov 1977). Muralirangan and Ananthakrishnan (1978) have shown that in *E. alacris alacris*, the weight increase from instar to instar varies irregularly but the adult weight is in accordance with the hatching weight. The female reaches 90 times the weight of the I instar while it is 75·3 times in the males. Among the adults, during the pre-reproductive period, which is 8–10 days, the weight increases steadily until it reaches the basic weight (basic weight is the weight of a matured uncopulated adult) and during the reproductive period the weight fluctuates around the basic weight. The weight during the pre-reproductive period increases until a maximum of 1·1 times the basic weight is reached, representing the mature weight. On oviposition the weight decreases. It is observed that the ovarial maturation sets in more or less after the attainment of the basic weight. The increase in the weight during pre-reproductive period is generally owing to the growth of the insect, while the increase during maturation period is correlated with the development of the reproductive organs (figure 3).

When the insects were reared in isolation, the weight of the male increased to 1·4 times the emergence weight, fluctuating between 323 and 398 mg and the maturation period also doubled from 4–5 days to 10–11 days. Similarly, unmated females took 21–22 days (14–15 days in mated females) to reach the maturation weight and on dissection it was observed that the ovaries had not properly developed in 14–15 days, suggesting that normal development took place only in the presence of the opposite sex. It was also observed that the total span of life of a mated male was shorter than that of the unmated male, while this was not seen in females.

3.7. *Brief description of the instars*

3.7a. *Instar I*: Head brownish. The first stripe of the eye was just being formed along the anterior side of the eye with the pigments scattered through-

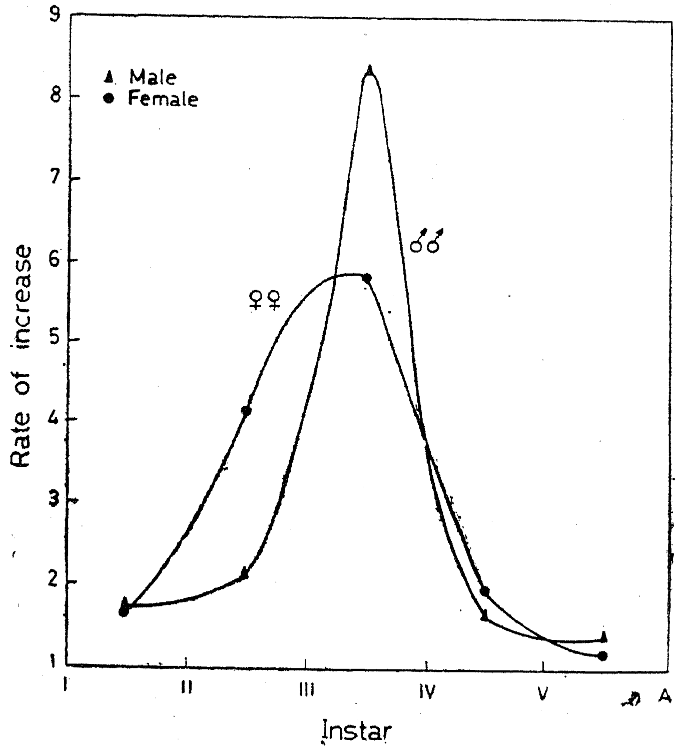

Figure 3. Graph showing the rate of growth in weight in *E. alacris alacris.*

out. Antenna with 12 segments ; 8th the largest giving the antenna a club-shaped appearance. Prothorax almost concolourous with head. Hind femora (3·3 mm long) with two brownish streaks in the basal half and with 10 pairs of black-tipped spines. Abdomen brown. Total body length 6 mm.

Sexual differentiation in instars with regard to the terminal abdominal segment is evident in *Locusta* (Dirsh 1950) and *E. plorans meridionalis* (Jago 1963). The upper ovipositor valve was small, triangular, with round ends. The lower valve was comparatively small. Subgenital plates were with a parabolic apex, covering only the base.

3.7b. *Instar II* : Head dark brown. Antenna with 20 segments, basal half of the antennae yellowish brown and club-shaped as in I instar. Eyes with two vertical stripes on the anterior side. Prothorax almost concolourous with the head. Hind femora (4 mm long) with two brownish streaks in the basal half as in the I instar and with 10 pairs of black-tipped spines. Abdomen brown. Total body length 6·43 mm.

Upper ovipositor valve long, the round base with an inverted ' U '-shaped excision. Lower valve small. Apex of the subgenital plate rounded.

3.7c. *Instar III*: Vertex and the median aspect of the head without the brownish stripe and hence head uniformly yellowish brown. Eyes with three vertical stripes. Pronotum uniformly pale brown even on the dorsum. Wing rudiments very small, concolourous with the abdomen. Hind femora (6·8 mm long in females and 5·0 mm long in males) brownish yellow, with a black longitudinal streak. Tibiae yellowish brown with two dark bands near base and 10 pairs of black-tipped spines. First five abdominal segments darker than the rest. Total body length 12·2 mm in females and 11·2 mm in males.

Upper ovipositor valves large, with rounded apices; lower valves slightly smaller than the upper. Subgenital plates with apex rounded, more or less as long as paraprocts.

3.7d. *Instar IV*: Vertex of the head light brown, but much paler while extending to occiput, being prominent only laterally. Eyes with four vertical stripes. Antenna with 24 segments, 1–2 yellow, 3–7 brownish yellow, the rest brown. Scape larger and wider than the rest. Other segments almost subequal except the 4th which is slightly shorter. Segments cylindrical, parallel-sided, slightly longer than wide. Pronotum with a brownish stripe on the vertex extending over the dorsum as a broad, velvetty stripe, with brownish yellow along the lateral aspects. Hind femora (12·6 mm long in females and 12·0 mm long in males) brownish yellow, with a black longitudinal streak along the inner and outer surfaces. Tibiae yellowish. The dark bands of the tibiae very pale and not distinct and with 10 pairs of black-tipped spines. Tarsi yellowish brown. Abdomen greenish brown, paler ventrally. Total body length of female 21 mm and that of male 19·5 mm.

Right and left ovipositor valves separated along middle, upper slightly longer than the paraprocts. Subgenital plate broad and slightly smaller than the paraprocts.

3.7e. *Instar V*: Vertex of the head light brown, extending uniformly upto clypeus but widening laterally while extending to occiput. Eyes with five vertical stripes. Antenna with 25 segments, 1–6 yellowish brown, the rest brown scape larger and wider than the rest : other segments almost subequal. Pronotum with a brown stripe on the vertex of the head extending medially over the dorsum as a broad, velvetty black stripe ; the lateral aspects brownish-yellow. Wing rudiments yellow from costal margin to anterior thirds, the rest brown. Hind femora (17·3 mm long in females and 12·7 mm long in males) brownish yellow, darker towards apex and with a black longitudinal streak, extending along the anterior 2/3 of the inner and outer surfaces. Tibiae yellowish-brown with traces of crimson at apex and with two dark bands near base; dorso-lateral angles with 10 black-tipped spines. Tarsi brownish. Abdomen greenish-brown, paler ventrally. Total body length of females 26·6 mm and 21·6 mm in males.

Upper ovipositor valve) longer than the paraprocts while the lower valve is equally long. Subgenital plate parabolic and slightly smaller than paraprocts.

Total body length of adult female 36·6 mm and that of adult male 26·6 mm and hind femora length of female 20·5 mm (male 15·3 mm).

3.8. *Foregut armature changes in some instars during post-embryonic development*

Though the nature of the foregut armature of the adult of *E. alacris alacris* was described earlier (Muralirangan and Ananthakrishnan 1974) and the last two nymphal stages were absent, it is necessary to find out the structural changes involved in the foregut armature and their possible correlation with the food preference of the instars.

During the postembryonic development of *E. alacris alacris* there is a clear evidence of a change in the structure of Zone II and Zone IV (figure 4), while Zone I and Zone III do not seem to exhibit any definite change. In Zone II of the IV instar, there are only 1–2 rows of teeth, measuring about 11·1 μ with only 16 teeth in 223 RL (Ridge length), while in the fifth instar, the number of rows of teeth of Zone II increases to 1–4, measuring 11·1–22·2 μ long with 23 teeth in 223 RL. In Zone IV of the fourth instar, the vertical ridges are only 27 but are smooth except for the presence of some small, round, feebly chitinised areas while the same zone in V instar shows about 57 vertical ridges which are not smooth. They exhibit some crossconnections between the vertical ridges and, under high magnification, they appear pitted. When the V instar moults to adult, the vertical ridges of Zone IV develop scale-like highly chitinised areas which carry a group of pointed and chitinised teeth. Zone II in adults is well developed with 5 ridges carrying strong, chitinised teeth measuring 13·0–22·2 μ long and compactly arranged (20 teeth in 223 RL) (Muralirangan and Ananthakrishnan 1974). Muralirangan and Ananthakrishnan (1977a) have shown that the preferential feeding of *E. alacris alacris* is due to the morphological adaptations of the gut. The early instars are not able to feed on well-grown *Panicum maximum*, which has a high silica content (4·6%) because of the absence of the well-developed gut armature, and so they die if grass with less silica (2·5%) is not available. From the later stages onwards, viz., III, IV and V instars, they are able to feed on the tough grass of *Panicum maximum* because of the well-developed armature and this helps the insect to consume more food from III instar onwards which accounts for the high rate of increase in weight from II to III (Muralirangan and Ananthakrishnan 1977a). Similar changes in the post-

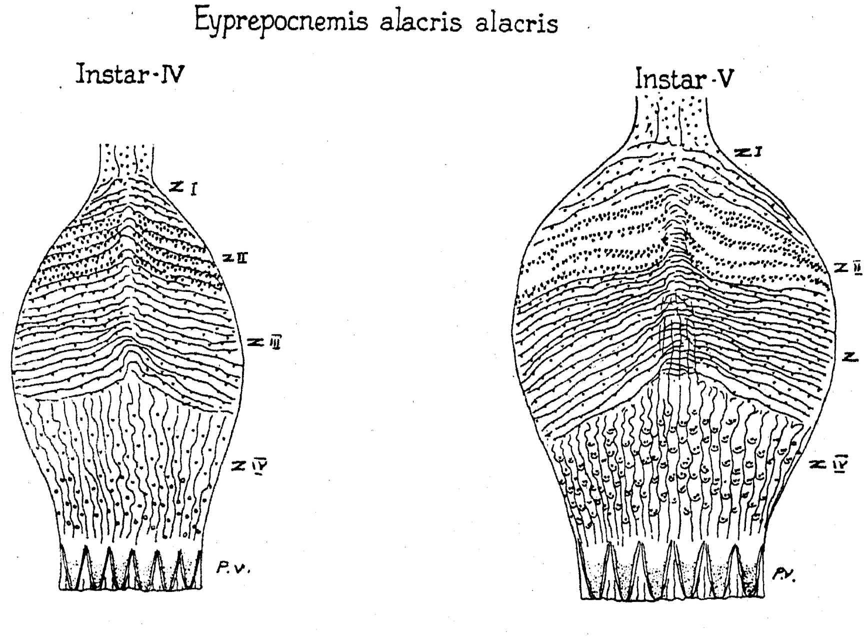

Figure 4. Foregut structure in instars of *E. alacris alacris*.

embryonic development of the mandible of *E. alacris alacris* have already been investigated by Muralirangan (1978).

4. Discussion

Food plants indirectly affect the choice of egg-laying sites, by reducing the movement/mobility of the females during feeding and *E. alacris alacris* were observed to lay their pods only near regularly irrigated areas (moisture being an important factor for development). It is also easier to make a hole in wet soil than in dry soil and in places with a fresh growth of grasses. This confirms the view of Zakharov (1930, 1950), who laid stress on vegetation as a factor in the choice of egg-laying sites in *Locusta migratoria migratorioides* and his data indicated that the choice of oviposition site depends on the feeding habits of the predominantly graminivorous species. In *E. alacris alacris* the choice of oviposition depended on the availability of tender leaves of *Panicum maximum* to facilitate feeding of early hoppers which were not able to process high silicated grasses. While laying the pods, the females of *E. alacris alacris* abandoned many holes without egg laying. This behaviour might be due to some physical obstruction or instinct hygiene (Nikol'skii 1925) but in the present study; the tray containing the soil was carefully prepared without any pebbles and, in another, clean soil was provoided for oviposition. This suggests that it may not be a factor for abandoning and it might be an instinct which had developed even before the female was ready to lay the egg or it might also be a behaviour to test the physical and chemical nature of the soil (Zakharov 1930, 1950). The studies made here show that only on certain occasions, it was noted that the female laid the eggs in the first digging itself. Hence it may be concluded that it might be an instinct that develops even before the ovary is ready to release the eggs. It was also noted that while the female was laying the pod, it was not disturbed easily but those which were digging were more sensitive, as suggested by Clarke (1965).

E. alacris alacris has a bivoltine cycle as seen in *Tylotropodius gracilippus* (Chapman 1962a), in which there are two periods of increase in the percentage of mature females and both the periods coincide with the rainfall. Similar observations have been made in *E. alacris alacris* as well and the generations that follow each other have clear intervals especially in summer and no individuals were collected during this season.

The life histories of *E. capitata* and *E. plorans meridionalis*, which were studied earlier (Antoniou and Hunter Jones 1956; Jago 1963), show 6, 7 and 8 instar life cycles in the former and 7 in males and 7–8 in females in the latter. However, *E. alacris alacris* constantly has a 5-instar life cycle for both the sexes, and in addition it does not exhibit any 'type' differences in development as suggested for *Nomadacris* (Albrecht 1955) and *Schistocerca* (Roonwal 1947). In *E. alacris alacris* the duration of each nymphal stage remains more or less the same in both sexes upto the IV instar and differences exist only in the V instar between the male and the female, suggesting that the ovarian development is accelerated, thus requiring a few more days to complete the development than the males. This confirms the observations of Muralirangan and Ananthakrishnan (1977a), and the weight of the ovary, body weight as well as the rate of increase, show high values. It is also reported by Kaufmann (1965) that *Zonocerus variegatus*, reared in larger cages, takes 7 months to complete the life cycle, the life cycle being completed in 8–9 months (when reared in smaller cages). In this study *E. alacris alacris* were reared in different cages, varying in size, and all completed the development in the normal period, suggesting that the cage size cannot be a factor in determining the duration of instars. Probably, if bred in smaller cages, overcrowding may have some influence on ovarian maturation.

While determining the number of instars, Jago (1963) used the additional eye-stripe character and proved the presence of an intercalary instar in *E. plorans meridionalis*. In determining the intercalary instar, other characters such as the rotation of wing rudiment, and linear measurements of some parts were used. Antoniou and Hunter Jones (1956) depended only on the eye-stripe character. However, *E. alacris alacris* has only a 5-instar life cycle which is confirmed by the definite number of eye-stripes, which increases at the rate of one stripe for every moult resulting in 6 eye stripes in the adult of both the sexes (Muralirangan 1977).

That the characteristic black, velvetty stripe on the pronotum becomes evident only after III or even the IV instar. Apart from this and some colour changes, there was no difference except for the progressive growth of different parts of the body. In *Acrida* Hafez and Ibrahim (1958) have reported that the supra-anal plate becomes elongate in instars, subsequently becoming reduced in adults. Such a feature is not evident in *E. alacris alacris.*

Changes in the mandibular (Muralirangan 1978) and foregut structure were evident during post-embryonic development of *E. alacris alacris*. In the I and II instars the incisors are long and sharp, which gradually become flat on aging probably due to the friction with silica containing grasses (Muralirangan 1978). The foregut of IV and V instars revealed that the number of rows of teeth in Zone II and Zone IV increased from IV instar to V instar, in addition to the increase in the number, chitinisation, size and the number of vertical ridges of Zone IV and in the presence or absence of scale-like chitinised areas. This indicates that the food preference in *E. alacris alacris* mainly depends on such morphological correlates.

Williams (1954) suggested a correlation between the degree of specialisation of the mandible with the foregut armature. The more the mandible is developed, the less is the specialisation of the foregut. The present observations on the foregut structure and the mandible do not lend support to the above view. The foregut of acridids examined had a well-developed armature with equally developed chitinised mandibles. As suggested by Isely (1944), Williams (1954), Gangwere (1966), Muralirangan and Ananthakrishnan (1977a), and Muralirangan (1980) there appears to be some correlation between the specialisation of the foregut armature and the mandibular structure with the choice and nature of food and its feeding habits.

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