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Biology of the African Earwig, *Euborellia cincticollis* (Gerstaecker), in California and Comparative Notes on *Euborellia annulipes* (Lucas)

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Field-collected females of the African earwig produced and brooded up to 8 clutches of eggs. The total number of eggs produced at 72°–80°F averaged 83.7 with a range of 15–175. The average period of time from egg to adult was 128.5 days. Eggs completed embryogenesis only at 100 per cent RH and increased in weight and dimension during this period. Five nymphal instars (rarely four or six) occurred at 72°–80°F. Six or seven instars completed development at 90°–92°F. Only wingless individuals occurred at 72°–80°F while at 80°–85°F and 90°–92°F wingless, brachypterous and winged forms were produced. Light traps revealed that earwig flights occurred between July 14 and September 26 from sunset to about 10 P.M.

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Biology of the African Earwig, *Euborellia cincticollis* (Gerstaecker) in California and Comparative Notes on *Euborellia annulipes* (Lucas)[1]

INTRODUCTION

THE AFRICAN EARWIG, *Euborellia cincticollis,* is a relatively new insect to California. It received little attention until it was found to damage seedlings and mature fruit of Persian and cantaloupe muskmelons. Since its introduction into California, *E. cincticollis* has spread from the extreme southern part of the state to the northern part of the Central Valley. It apparently was introduced into California from Africa in 1946.

When this study was started, little information was available concerning the biology and habits of *cincticollis,* even in its native home of Africa. Ting (1951) gave a brief summary on the observations that had been made on *cincticollis* in California. He compared several of its morphological features with the closely related species, *E. annulipes* (the ring-legged earwig). Some works on the biology of *E. annulipes* were of value in this study (notably Klostermeyer, 1942; Neiswander, 1944; and Bharadwaj, 1966).

This study aims to provide basic information on the life history and habits of the African earwig both in the laboratory and in the field. It is hoped that some of this information may be useful if control should become necessary. We compare some of the morphological and biological characteristics of *annulipes* with *cincticollis* because both species occur in California and their similarity could lead to confusion in identification.

TAXONOMY AND DESCRIPTION

According to Popham (1965), the African earwig was transferred from the family Labiduridae to the subfamily Carcinophorinae, family Carcinophoridae. Some confusion existing among early workers about the identification of this earwig is caused by its being a polymorphic species with respect to the wings, meso-, and metanotum.

The species was first described from The Cameroons, Africa, by Gerstaecker (1883) who proposed the name *Brachylabis cincticollis.* The original series described by Gerstaecker had abbreviated tegmina and were wingless (Rehn, 1924). Kirby (1891) described some fully alate specimens from Gambia, Africa, as *Psalis picina.* Later authors (Burr, 1909b; Rehn, 1924) were of the opinion that Kirby's series rightly belonged to the same species as that originally described by Gerstaecker. Burr

[1] Submitted February 19, 1971.

considered the alate material of Kirby to be merely the mature form of the abreviated-tegmined specimens first described by Gerstaecker but Rehn disputed this, stating that Gerstaecker's material evidently was based on adults and the species was dimorphic.

Bormans (1900) worked on this group and placed *Brachylabis cincticollis* in the genus *Anisolabis*. At that time he did not include *Psalis picina* Kirby with *Anisolabis cincticollis*.

Burr (1909a) placed *Anisolabis cincticollis* into the genus *Psalis*. Because Burr considered *Psalis picina* to be synonymous with *Psalis cincticollis,* he included it in his list of synonymy (Burr, 1909b). Later work by Burr (1914) led to a consideration of variable characters in Dermaptera including alary dimorphism. Hence, in 1915 he revised the Psalidae and based the new groupings primarily on the shape of the metaparameres. Burr (1915) placed *Psalis cincticollis* in *Euborellia.* The designation for *Euborellia cincticollis* by Burr in 1915 has remained to the present. The synonymy for the African earwig may be summarized as follows:

Euborellia cincticollis (Gerstaecker)

Brachylabis cincticollis Gerstaecker, 1883, Mitth. Ver. Vorpomm. **14**:44. (Cameroons, Africa).

Psalis picina Kirby, 1891, Linn. Soc. Lond. **23**:516. (Gambia, Africa).

Anisolabis cincticollis, Bormans, 1900, Tierreich, Forf. p. 43, no. 1.

Psalis cincticollis, Burr, 1909a, Ann. Nat. Hist. **3**(ser. 8):255, 257.

Euborellia cincticollis, Burr, 1915, Jour. Roy. Microsc. Soc. **35**:544.

Adult (figures 1–7). Specimens examined from California and Arizona were somewhat different than those originally described by Gerstaecker (as cited by Rehn, 1924). The type material had the tegmina obliquely concavo-truncate distad and not more than one-half as long as in fully alate specimens; also, the metanota of Gerstaecker's specimens were obtuse-angulate, emarginate at the caudal margins and wingless.

Several types of alary polymorphism were found in this study. They were: (1) wingless, mesonotum and metanotum without developments; (2) winged, mesonotum with normal tegmina and metanotum with full wings; and (3) brachypterous. Three types of brachyptery have been observed: (1) mesonotum with small tegmina, metanotum without wings; (2) mesonotum without tegmina, metanotum with wing rudiments; and (3) mesonotum with small tegmina, metanotum with wing rudiments. The first type of brachyptery was described from the original series in Africa and a similar type is found occasionally in California, although the degree of abbreviation of the tegmina may differ. The second type is the most common form of brachyptery in California and was first noted by Ting (1951). The third type was limited to a single specimen from California.

Another species in California, *Euborellia annulipes* (Lucas), is similar to the African earwig. It has occasionally been reported as being winged (Hincks, 1947; Burr, 1915; Zimmerman, 1948), but Gurney (1950) believed that at least some of these reports were in error, since no winged forms were found by him or others who subsequently worked with this species. He stated that winged specimens must "be most unusual" (i.e. rare). No winged forms of *annulipes* have been reported from California.

The most common earwig found in California is *Forficula auricularia* Linnaeus. Its lobed second tarsal segment readily separates it from members of *Euborellia* whose second tarsal segment is cylindrical.

The African earwig has the following characteristics (Ting, 1951) applying to all mature forms whether wingless, brachypterous, or winged (except where one form is specifically indicated):

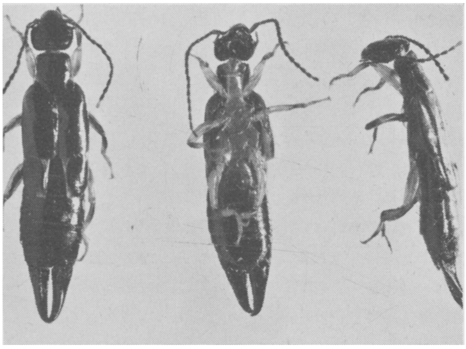


Fig. 1. Winged form of *E. cincticollis*, adult females.

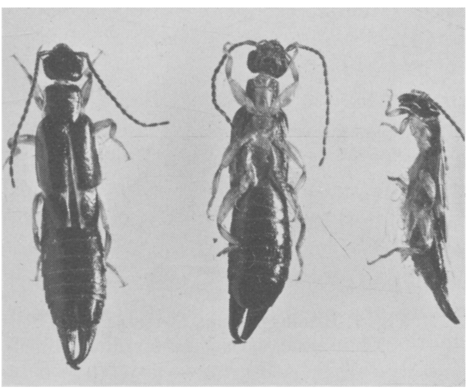


Fig. 2. Winged form of *E. cincticollis*, adult males.

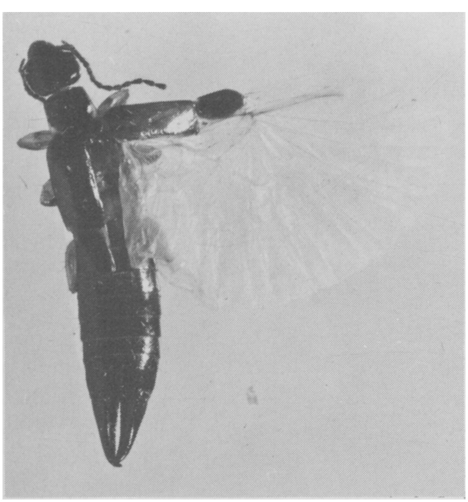


Fig. 3. Wing in unfolded position, adult female.

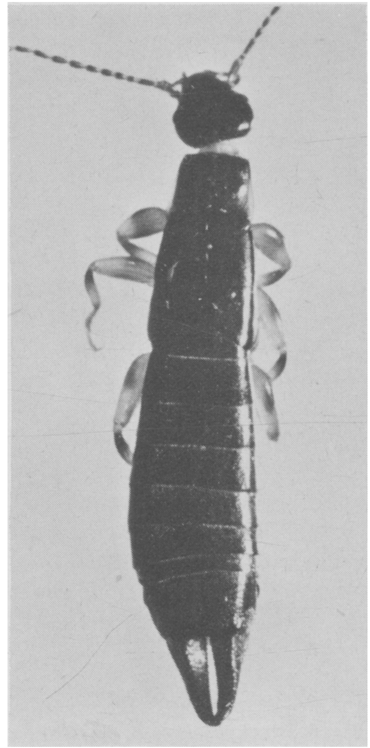


Fig. 4. Wingless form of *E. cincticollis*, adult female.

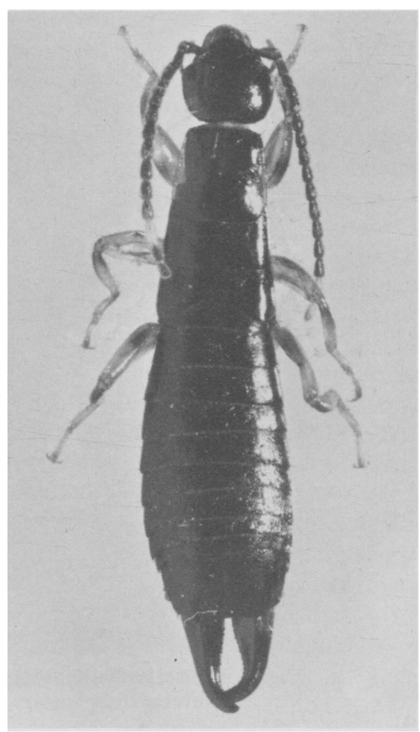


Fig. 5. Wingless form of *E. cincticollis*, adult male.

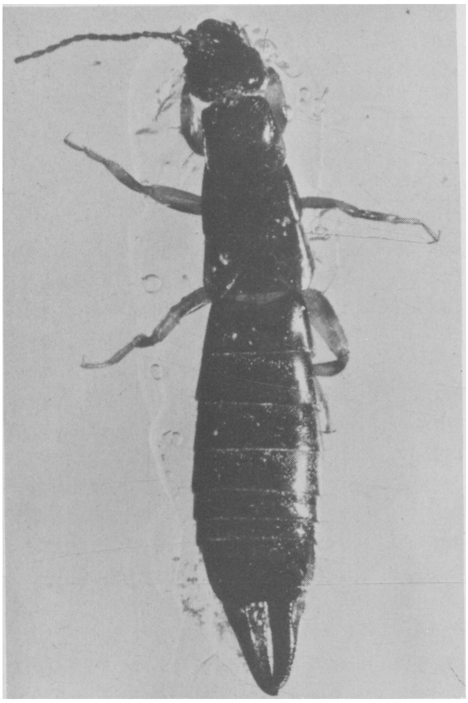


Fig. 6. Brachypterous *E cincticollis,* adult female.

Fig. 7. Brachypterous *E. cincticollis,* adult male, with small tegmina.

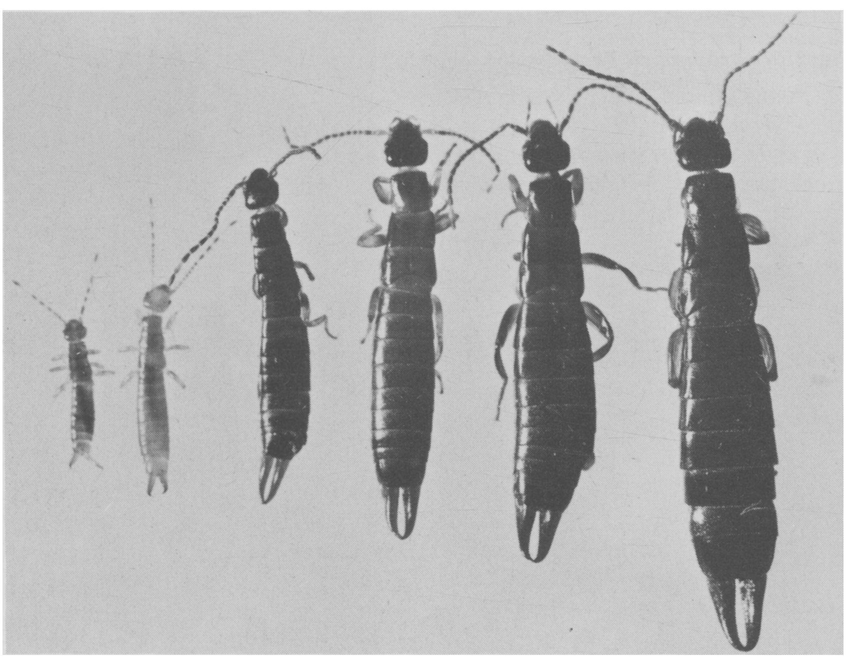


Fig. 8. *E. cincticollis,* showing (from left to right) first, second, three intermediate instars, and an adult wingless female.

Form elongate: nearly five times longer than broad. Average length of specimens 14 mm; width 3 mm. Color of body black with reddish tinge; antennae dark brown except for segments 15 and 16 which are usually white; tegmina and folded metathoracic wings tan or dark brown; legs yellow or amber, usually with faint smoky markings on the femora and tibiae. Forceps of males often asymmetrical with right process bent or curved more than left; in some males the forceps are nearly straight with both processes slightly curved inward, similar to the females. Subgenital plate (8th visible sternite) of males evenly emarginate at apex.

Adult males have 10 abdominal segments whereas females have eight. Adult females have more or less straight forceps as do the nymphs, but the nymphs have 10 abdominal segments.

Several characters separate the African earwig from the closely related *annulipes.* Winged specimens are always *cincticollis.* Brachypterous specimens also must be *cincticollis,* although they may be confused with wingless *annulipes.* As Ting (1951) states, the most positive separation of the two species is made with the male genitalia. The apical median margins of the parameres in *cincticollis* are concave, whereas in *annulipes* they are straight or nearly so. Also the subgenital plate in *cincticollis* males is slightly emarginate along its posterior margin whereas in *annulipes* males it is truncate or slightly convex. The females are more difficult to separate. However, the antennae of mature *cincticollis* are usually 17–20 segmented, whereas those in *annulipes* are 15–16 segmented (Bharadwaj, 1966; Hincks, 1947; Klostermeyer, 1942), but can be from 14–17 segmented (Langston, in prep.). If some segments of the antennae are white, the two species can usually be separated on this basis. Often all segments of the antennae of both species will be dark. However, *E. annulipes* usually has one or two contiguous white segments occurring between segments 11 and 13 (Bharadwaj, 1966) while *E. cincticollis* usually has segments 15 and 16 white. Dark rings can occur on the femora of both species.

Nymphs. The nymphs look much like the adults except they lack the sexual characteristics, are smaller, and appear less heavily sclerotized. The size range is such that it is possible to have some late instar nymphs that are larger than adults.

Nymphs can be distinguished readily from the female adults because they always have 10 abdominal segments whereas the adult females have eight. The adult males have 10 abdominal segments as do the nymphs, but the subgenital plate of the male is truncate posteriorly and slightly emarginate mesally. This contrasts with a rounded subgenital plate on the nymph. The forceps of the nymphs are shaped much like those of the adult female (figure 8). The forceps are nearly triangular in cross section, are gradually tapered distally, and are gently curved inwardly.

The various nymphal instars cannot always be separated easily by morphological criteria. The body length, size of parts and number of antennal segments often overlap between successive instars. The fact that the number of nymphal instars can vary indicates that there are not specific developmental boundaries to be attained in a given instar.

The variable size, number of antennal segments, and number of instars are stated in relation to temperature in a later section on nymphal instars. A mean body length and number of antennal segments for several temperatures is presented here as a part of the general description of the first five instars. Tables 5 to 7 provide additional information on determination of instars and body measurements.

The first instar is readily recognized. The length of the first instar nymph averages about 3.7 mm (measured from eyes to end of abdomen). The color of these nymphs is usually orangish-brown to fuscous. The last abdominal segment is often lighter than the preceding segments. Eyes are dark and a dark ring may occur around the femur. The distinguishing character of the first instar is the fact that it always has eight antennal segments with the seventh one being white.

The second instar nymphs can be usually distinguished by their having 12 or 13 antennal segments. The next to last segment is usually white. Occasionally, the two segments preceding the apical segment are white, and sometimes the apical segment is white. When the apical segment is white, the last segments may have been lost because of their fragile nature. The body length of the second instar nymphs is approximately 4.8 mm. The color is much the same as that of the first instar.

The third instar usually has 13–15 antennal segments. The next to the last segment or the two segments next to the last are often white but occasionally are dark. The body length of this instar averages 5.5 mm.

In the fourth instar, the number of antennal segments is usually 14–16. Usually one or two white segments precede the last segment. Again, some antennae have no white segments. The average body length of this instar is 6.7 mm.

In the fifth instar, the antennal number varies from 15–19 segments. The number of white antennal segments varies from one to two and occasionally three. Average body length is 8.1 mm.

In the sixth or later instars, the number of antennal segments and their markings remained more or less the same. The body length tended to increase in those individuals that had six or more nymphal instars. A minimum of four instars and maximum of eight was found at the temperatures used in this study.

Eggs. The eggs of *E. cincticollis* are approximately 880 × 1150 microns when first laid, and creamy white. They gradually enlarge, become translucent, and attain a size of approximately 1200 × 1557 microns. Size and development of eggs are treated more fully in a later section.

GEOGRAPHICAL DISTRIBUTION

The African earwig has been reported from the continents of Africa and North America. It is apparently native to Africa and was first described from The Cameroons, Africa. Subsequent literature has shown *E. cincticollis* to be widely distributed in western and equatorial Africa. Some localities reported have been Victoria, Gambia, the lower Congo, the upper Congo, and Liberia. Other reports have been from Uganda, the Kasai, and the central Lualaba (Kasongo). Important references on this distribution are given by Burr (1909b; 1915) and Rehn (1924; 1936).

The African earwig was first collected in the United States at Ripley, California, by J. W. McSwain in 1946 (Gurney, 1950; Langston, in prep.). Gurney wrote the initial paper concerning the first known presence of *E. cincticollis* in the United States and the Nearctic region. He reported adults from Blythe, Palo Verde, Ripley, and Fort Yuma, California. Langston stated that workers in Arizona first found *cincticollis* at Yuma in 1948. Moore and Werner (1966) reported that *cincticollis* had been found at Arlington, Hassayampa, Mesa, Florence, and Tucson, Arizona, by 1959. As far as can be determined, *cincticollis* is limited to these two states.

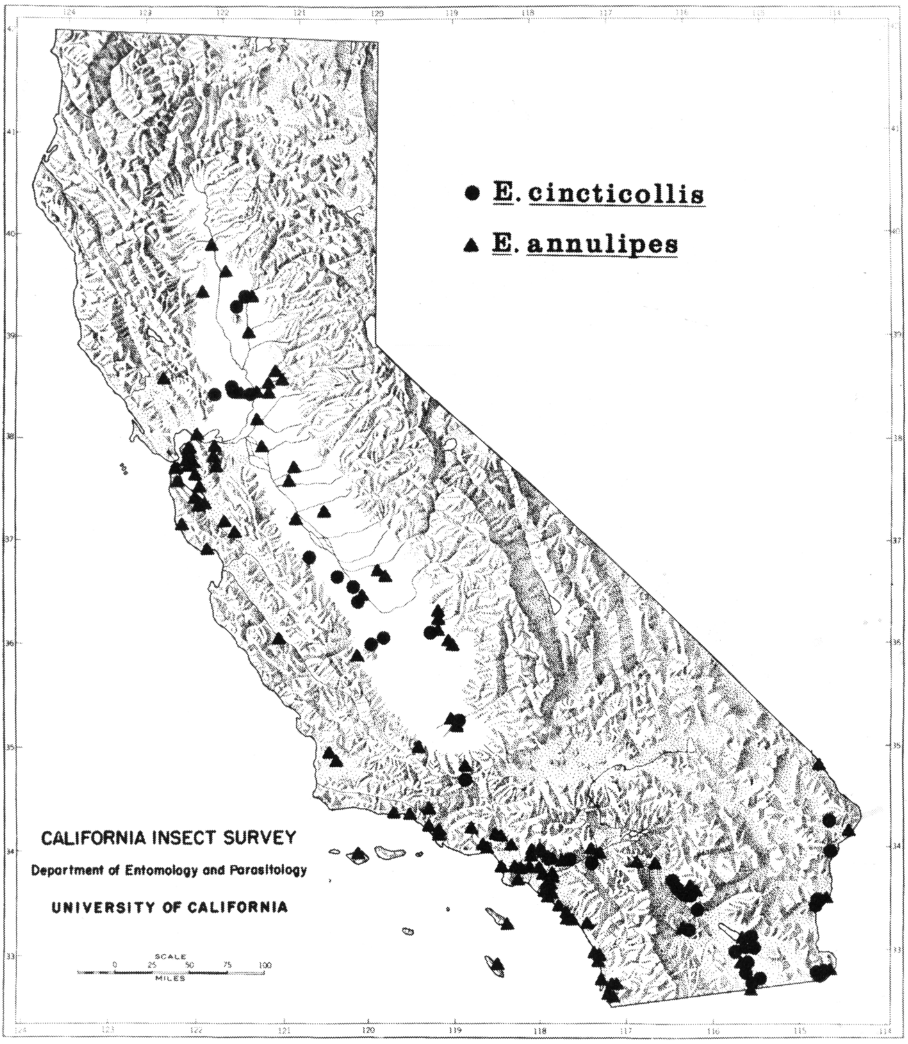


Fig. 9. Distribution of *E. cincticollis* and *E. annulipes* in California.

The distribution of *E. cincticollis* and *E. annulipes* in California is presented in figure 9. Most of the distributional data is taken from Langston (in prep.) but some new localities were included from collections made during this study. The plotted distribution shows *cincticollis* to be limited to the interior localities, whereas *annulipes* occurs both on the coast and inland.

Gurney (1950) suggested that *E. cincticollis* probably entered California via airplane. At that time Gurney was a member of the USDA Bureau of Entomology and Plant Quarantine. He stated that about two dozen species of earwigs were intercepted with some regularity in plant material, and that many aircraft flights between Blythe, California, and West Africa were made because of the plane ferrying during World War II. The only other source of possible introduction might have been through an association with date palms or camels introduced many years previously.

LIFE HISTORY AND HABITS

Materials and rearing methods

The life history as well as some aspects of behavior of *E. cincticollis* were observed by rearing the species in the laboratory. Specimens used in these laboratory studies were collected from January to August of 1967, at Davis and Winters, Yolo County, and near Los Banos and Mendota in Fresno County. Most of the earwigs from Davis were collected in uncultivated areas and at the edges of fields on the campus of the University of California. Most earwigs were found about two inches below loosely packed soil that was overgrown with weeds.

The specimens of *E. annulipes* used in this study were collected at the east end of the Dumbarton Bridge and at Golden Gate Field in Alameda County. They were found under rocks and in piles of dirt fill.

Members of *E. cincticollis* from the first collections were kept in large plastic refrigerator boxes (13 × 10 × 4 inches), at 50 to 75 earwigs per box. A layer of soil about ¼ inch deep from the collection site was placed in these containers and several pieces of cellulose sponge (Dupont)—about ½ × 1 inch—were added and kept moist. This arrangement proved unsuitable and was abandoned because not enough protective shelter was available and many earwigs killed one another.

Subsequently collected earwigs were kept individually or in pairs in glass Petri dishes (100 × 20 mm). A layer of soil (approximately ⅛ to ¼ of an inch deep) was placed in these Petri dishes, and a piece of sponge (approximately ¼ inch square) was usually added and moistened as needed to maintain humidity. The earwigs sometimes hid their egg clutches in the cavities of the sponges so the latter were eliminated from oviposition studies, and moisture was maintained by occasionally adding a few drops of water to the soil.

To determine the effects of temperature on their development, earwigs were kept under three temperature ranges: 72°–80°F in a laboratory; 80°–85°F in an insectary, (later narrowed to 82°–83°F in a constant-temperature chamber); and 90°–92°F in a constant-temperature chamber.

The light cycle maintained in this work was 16 hours of light at the two higher temperatures. The lowest temperature was also maintained with a minimum of 16 hours of light, but occasionally more hours of light occurred at this temperature when the laboratory was in use at night.

The eggs used for studies of size increase were incubated in Petri dishes (55 × 13 mm, figure 10) which had pieces of Whatman filter paper on their bottoms. The filter paper was kept saturated with sodium hypochlorite for mold inhibition (Chlorox® diluted with distilled water to about 1:200). Eggs were placed on numbered pieces of paper and isolated in pieces of 3 mm plastic tubing. The Petri dish containing eggs was then set on a piece of galvanized window screen within a larger Petri dish (100 × 20 mm). The larger Petri dish had a piece of water saturated filter paper on its bottom.

The embryology of the egg was studied in a gross fashion by making periodic weighings to determine if weight changes occurred in conjunction with an observed size increase. These weight changes in the egg were also studied in relation to a range of relative humidities. Saturated salt solutions in a closed system were used to maintain the desired humidities. The following salts were selected from references by O'Brien (1948) and Rockland (1960) to obtain the corresponding relative humidities at 72°–80°F: $MgCl_2 \cdot 6H_2O$—

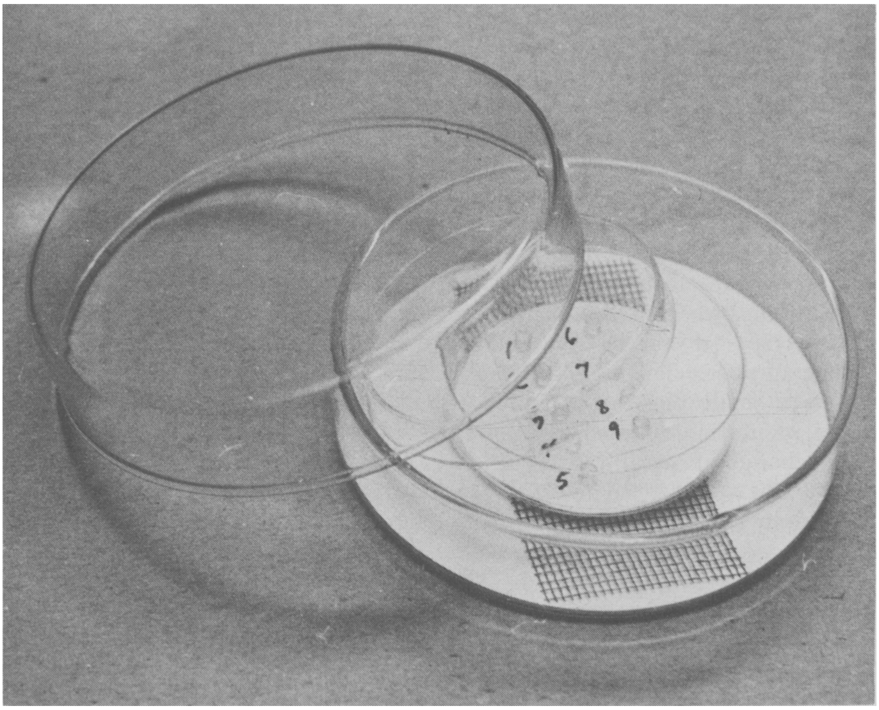


Fig. 10. Incubation chamber used to study size increase of eggs.

33 per cent; $CaNO_3$—50 to 56 per cent; $CaCl_2$—62 to 67 per cent; $K_2C_4H_6O_6 \cdot \frac{1}{2} H_2O$—75 per cent; KBr—82 to 84 per cent; KCl—86 per cent; $Na_2C_4H_4O_6 \cdot \frac{1}{2} H_2O$—92 per cent; K_2SO_4—97 per cent; and H_2O—100 per cent.

The salt and distilled water were added to a 275 ml jar 7 cm in diameter to form a saturated salt solution 1 cm deep. A glass dish was placed on the bottom of the jar to support the containers with the test organisms above the solution.

Eggs were taken randomly from different females held at 72°–80°F. The eggs were collected twice daily so that they were not more than 24 hours and usually 0–12 hours old. They were placed in paper holders in the bottom half of a plastic Petri dish (55 × 15 mm) placed in the humidity chamber. Whatman filter paper covered the bottom of the Petri dish.

On the basis of preliminary trials it was concluded that paper egg holders dipped in sodium hypochlorite had to be used in subsequent tests to retard mold formation. This necessitated transfering the eggs from the paper holder in the humidity chamber to a paper holder at the relative humidity of the weighing room to omit errors in weight due to condensation or evaporation of water on or from the paper holders held at different humidities. The eggs were then returned to the original holder and placed in the humidity chamber. The weight of the holder was determined after each weighing so that the total weight of the eggs could be calculated. All weights were recorded to the nearest microgram on a Mettler M5 microbalance.

The same humidity chambers and saturated salts were used at 72°–80°F to study the effect of humidity on first instar nymphs. Each chamber contained five numbered vials (48 × 13 mm). First instar nymphs were individually placed in the vials by the 12th hour after hatching. In Test I the nymphs were examined daily for 13 days, but Test II was continued until all nymphs died. Nymphs were not provided with food or water during these tests because these materials could change the predetermined relative humidity.

To study the number of moults of the nymphal stage, we kept the earwigs in glass vials (95 × 24 mm, or 67 × 20 mm) with cork stoppers. The vials contained food and a small piece of sponge for moisture regulation. The corks allowed a slow exchange of air and gradual loss of moisture. If condensed moisture accumulated in the vial (rare), the cork was exchanged with a cotton plug until the excess moisture diminished. The newly hatched nymphs were checked daily until they moulted to adults.

Several methods were tried to determine when a nymph had moulted. There usually was little evidence to indicate a new instar because the nymphs darkened a few hours after moulting and usually ate their entire exuviae. Marking with paint (Testor's butyrate dope) was not successful because it did not stick to the nymphs. Finally, a method used by Bharadwaj (1966) on *E. annulipes* was selected. We removed the left forceps of the nymph on the day of or following each moult after the nymph darkened. The best way to remove the forceps was to grip it with a pair of tweezers and allow the nymph to pull away. Teasing the tissue with a needle at the base of the forceps hastened its removal. The forceps was regenerated during each moult.

Body measurements and observations on the number and characteristics of antennal segments and the number of abdominal segments were made immediately after the left forceps was removed. The nymph was lightly anesthetized with CO_2, and it was then observed with a dissecting microscope and measured with an ocular micrometer.

Nymphs reared to determine the effect of temperature on alary polymorphism were taken from the egg clutches of field-collected females. The nymphs were kept in 275 ml jars that were one-half filled with moist soil until becoming adults. Only nymphs produced by one female were kept in the same jar.

Small pieces of fresh carrot were used as the primary food source in these experiments. Other foods such as potato and fresh string beans were tried occasionally. When confined with pea aphids, the earwigs ate those also. The first and second instar nymphs survived better on carrot than on potato or sugar beet. Carrot was readily accepted and convenient to use but occasionally it became moldy.

Habits

When field-collected earwigs were placed in Petri dishes they immediately tried to escape. Following such attempts they carefully investigated the contents of the dish and, in a day or two, they usually found a hiding place or an area of the dish in which they stayed. Earwigs held at a temperature of 90°–92°F seemed to be more excitable when disturbed by the daily observation than were earwigs kept at the lower temperatures.

Earwigs transported from the field would get small particles of dust and dirt adhering to their bodies. The first thing they usually did when the jostling stopped was to begin grooming, an activity which took much of their time. The hind tarsi were used to clean the posterior parts of their bodies, and the fore tarsi, the head region. The earwigs cleaned their antennae diligently, and this was the most frequently performed grooming task. They moved an antenna toward their bodies with the aid of their forelegs, and then starting basally, drew each segment through their mouthparts. The earwigs were normally almost shiny. However, old, inactive earwigs became dull and dirty. Winged adults sometimes got dirt or mold on the part of the folded wing that protruded from beneath the elytra. Apparently this was a difficult spot to clean. A few earwigs were seen to twist sideways to use their mouthparts for cleaning the region around their forceps.

The forceps of *E. cincticollis* are used for both offense and defense. An earwig often remained more or less in a definite zone in its Petri dish and drove off other trespassing earwigs. If attacked or disturbed, an earwig immediately bent its abdomen forward over its thorax so that it was able to strike swiftly with its forcepts or to grasp an adversary. Neiswander (1944) reported that the prey of *E. annulipes* was sometimes held in the forceps and then seized with the mandibles so that the prey was instantly torn apart. A specimen of *E. cincticollis* was observed to hold a defeated earwig in its forceps and twist around to consume it. In general the largest females usually were the victors in any intraspecific confrontation while the males and smaller females usually lost. Both sexes were cannibalistic.

Mating

E. cincticollis mated at various times during the day. If a female had been alone for an interval of several days and then a male was placed in her cage, mating usually occurred immediately. Mating rarely was seen when a male and female were kept together continuously. The initial meeting of the sexes involved considerable antennal contact to the head and body. The act began with the male orienting himself so that the two individuals faced in opposite directions. He then either rotated his abdomen, or turned over (if a support was available) so that his abdomen was upside-down in relation to the female's abdomen. The male then backed toward the female, and copulation occurred when the subgenital plates of the pair came into contact (figure 11). The males frequently made jerking movements from side to side and rotated their antennae during copulation. Often the female would start to walk and drag the male along. Copulation lasted from several seconds to several minutes. The male often was killed by the female within a day or two after copulation. Multiple matings occurred within a brief period or after several months. Sometimes a female produced several viable clutches of eggs after mating once.

Attempts to hybridize species

An attempt was made to cross *E. cincticollis* and *E. annulipes*. This was done by placing a single male of *annulipes* with a virgin female of *cincticollis* in a standard Petri dish. Five such pairs were observed daily for one week and periodically thereafter for approximately four weeks.

No copulation was observed, and no eggs completed development. One *cincticollis* female laid eggs, but these were eaten. Virgin females of *cincticollis* were usually highly attractive to *cincticollis* males but the males of *annulipes* paid little attention to the females in these tests. While these limited observations do not rule out the possibility of interspecific hybridization, the apparent lack of copulation and egg development leads one to assume that good biological mechanisms keep these closely related sympatric species apart.

Egg laying and maternal care

Earwigs were collected from the field in the first and fourth weeks in January and began laying eggs in three weeks. Females collected in April took less time to start laying eggs. Just before egg deposition, the female became restless and would vigorously attack any other earwigs in her vicinity, even her own immature offspring from a previ-

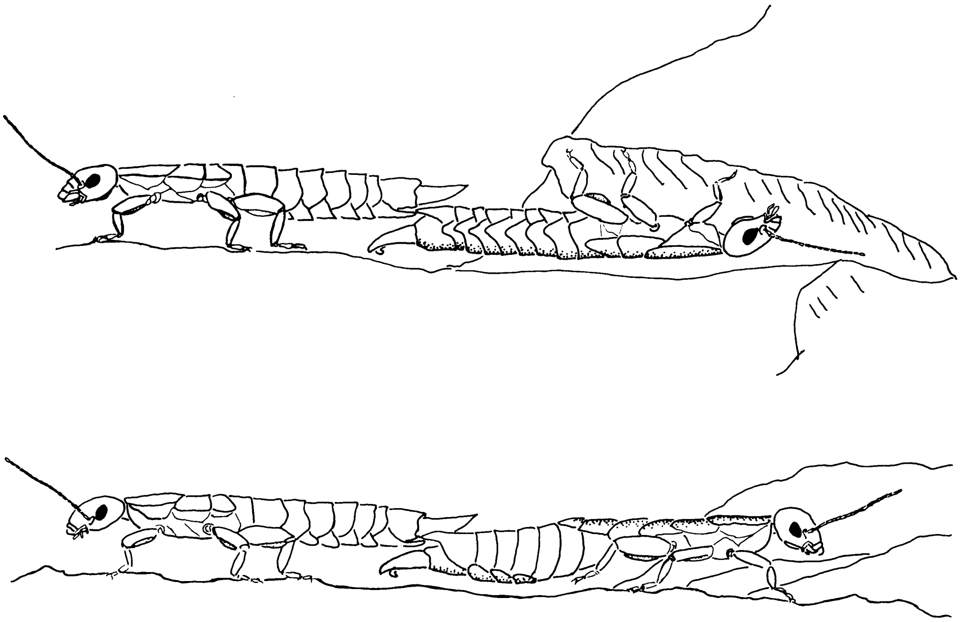


Fig. 11. Two mating positions commonly assumed by *E. cincticollis*. Male on right.

ous clutch. The aggressive behavior continued during the time the eggs were brooded. A similar brooding behavior of the female earwig has also been reported for *E. annulipes* (Bharadwaj, 1966; Neiswander, 1944; Klostermeyer, 1942), *Anisolabis maritima* (Bennett, 1904), and *Forficula auricularia* (Crumb *et al.,* 1941).

Clutches of eggs of *E. cincticollis* were usually laid during a period of three days, but some clutches were laid in a single day, and one clutch was laid over a nine-day period. The largest clutch recorded in the laboratory was 44 eggs at 90°–92°F. Successive clutches gradually declined in numbers of eggs. The most eggs laid by one female totaled 175 in eight clutches. These eggs were laid between February 3 and August 2. A record of the egg deposition by several females of *cinticollis* at different temperatures is given in table 1. The sizes of clutches found in the field were generally considerably larger than those produced in the laboratory and may reflect less than optimum conditions in the laboratory.

Records of egg deposition by several specimens of *E. annulipes* at 72°–80°F also were kept for comparison. The average number of eggs of the first clutch for seven females of *annulipes* was 36.7. This is comparable with the numbers reported by Klostermeyer (1942) and Neiswander (1944), but this average is larger than the number reported by Bharadwaj (1966). The average size of the first clutch of *annulipes* was larger than the 23.4 eggs recorded for *cincticollis* at 72°–80°F, possibly because of an inherent difference between the two species, or because *annulipes* were collected from the field when they were almost ready to lay whereas *cincticollis* matured their eggs in the laboratory. Adults of *annulipes* only produced one or two clutches in the laboratory while adults of *cincticollis* produced one to eight.

The eggs that were brooded by the females were most often under cover

TABLE 1
RECORD OF EGG CLUTCHES PRODUCED BY *E. CINCTICOLLIS* IN THE LABORATORY AT THREE TEMPERATURE LEVELS*

Number of ♀♀ ovipositing	Temperature Range	Successive clutches	Days to produce clutch		Number of eggs/♀		
			Range	Ave.	Range	Ave.	S.D.
	degree F						
20	72–80	1st	1–6	3.1	6–38	23.4	9.03
19		2nd	1–10	3.2	1–38	20.2	9.96
17		3rd	1–5	3.0	9–30	20.6	5.79
14		4th	1–5	2.9	7–30	16.4	7.38
9		5th	1–5	2.9	6–30	12.6	7.49
5		6th	1–4	2.2	5–27	11.0	10.42
3		7th	2–4	3.0	11–22	16.0	5.57
2		8th	1–2	1.5	1–16	8.5	10.61
5	80–85	1st	2–3	2.6	17–26	21.2	4.27
5		2nd	1–3	1.8	6–15	10.6	3.29
4		3rd	1–3	2.2	6–13	8.8	3.40
3		4th	1–2	1.7	3–20	11.0	8.54
1		5th	1	1	9	9	1
8	90–92	1st	2–4	2.6	10–44	22.8	10.71
8		2nd	1–6	3.1	1–40	20.0	13.28
7		3rd	1–3	1.9	2–43	17.6	15.20
4		4th	2–3	2.5	9–21	15.0	4.90
1		5th	2	2	7	7	1

* Eggs were laid between January 26 and August 9 by separate groups of females at each temperature.

although they were occasionally found in the open. The female usually remained with her eggs within a dirt excavation under a piece of carrot or beneath a piece of sponge. During the time the eggs were brooded, the female would often manipulate the eggs with her mouth and thus keep them free of dirt and mold. Normally, the eggs would not develop unless a female cared for them, but they could develop without the female if provided with humidity regulation and fungus control. The females often moved their eggs if the clutch was disturbed. For counting, the eggs were scattered slightly but the female gathered the eggs again within a short time.

Brooding females readily accepted eggs from other clutches, regardless of the age of the eggs. The females also collected miscellaneous, small objects of light color and guarded them with their eggs. This behavior was also reported for *E. annulipes* and *Forficula auricularia* by Bharadwaj (1966). Weyrauch (1929, cited by Bharadwaj, 1966) was able to dupe females of *F. auricularia* into accepting balls of wax and tiny stones. Bharadwaj (1966) was able to get *E. annulipes* to accept balls of wax three times the usual sized egg.

The brooding female of *cincticollis* normally did little except guard her eggs, but occasionally she would eat. Several variations in behavior were noted during the brood period. One female mated; another placed a mangled nymph on top of her eggs. Bharadwaj (1966) indicated that some females of *annulipes* provisioned their egg chambers with food. No similar action was observed for *cincticollis* except the incident of the forementioned nymph which was probably a manifestation of guarding. Occasionally, the females established brood chambers below pieces of carrot. This might be considered as provisioning, but it may also be a reaction to moisture.

The first few days after oviposition, the females were intolerant to any disturbance of their eggs: they would eat their eggs if the eggs or the female were disturbed excessively. Thereafter, the eggs as well as the earwigs, could be

TABLE 2
DURATION OF EMBRYONIC DEVELOPMENT OF EGGS OF *E. CINCTICOLLIS* AT THREE TEMPERATURES

Temperature	Number ♀ laying	Number of days from oviposition to 1st hatching in clutches	
		Range	Mean
72°-80° F			
Clutch 1	21	12–15	13.1
2	14	12–15	13.1
3	6	11–14	12.7
			13.0 ± 0.961 S.D.
80°-85° F			
Clutch 1	5	8–9	8.8
2	4	8–10	8.8
3	3	8–10	9.0
4	1	8	8.0
			8.8 ± 0.725 S.D.
90°-92° F			
Clutch 1	8	7–8	7.6
2	5	7–8	7.8
3	4	7–8	7.8
			7.7 ± 0.470 S.D.

manipulated with little risk of the female eating them. If an egg was accidentally broken while being counted, the female would readily eat it. The female would often eat more eggs than just the injured one if the eggs were only a few days old.

The incubation period varied with temperature. At the lowest temperature studied (72°–80°F) the average time for the eggs to hatch was 13.0 days (range: 11 to 14); at 80°–85°F the average time was 8.8 days (range: 8 to 10); and at 90°–92°F the average time was 7.7 days (range: 7 to 8). A complete summary of egg development appears in table 2.

Embryology and hatching

The gross embryology of eggs incubated at 72°–80°F was studied by examining whole eggs and dissections. The embryos were viewed by placing whole eggs in saline (Hayes, 1953). The salt solution caused the chorions to appear transparent. Dissections of other eggs were made at 6, 8, 9, 10 and 11 days after oviposition. Observations based on both techniques were as follows: sixth day—predominantly yolk, embryo occupied ¾ of the egg periphery, some segmentation evident, rudimentary appendages apparent; eighth day—embryo occupied most of egg, some central yolk present, segmentation and appendages more obvious; ninth day—embryo made pulsating movements; tenth day—heart rate approximately 150 beats per minute, antennae, head and legs distinguishable; eleventh day—nymphal outline including forceps obvious, eyes reddish. Few major changes were observed thereafter until the eggs hatched at 14 days.

In the process of hatching it appeared that the chorion split in the region of the anterior part of the pronotum and the vertex of the head. The nymph emerged from the transparent chorion immediately following the split without using its appendages, much like a vermiform larva. The wet nymph maintained a curved position for a few minutes after emerging; it then gradually straightened out. The mouthparts and forceps were partially darkened at the time of hatching; complete darkening of the body took several hours.

TABLE 3
INCREASE IN SIZE OF EGGS OF *E. CINCTICOLLIS* FROM OVIPOSITION TO HATCHING*

Days from first measurement	Number of eggs measured	Length			Width		
		Min.	Max.	Avg.	Min.	Max.	Avg.
		microns					
TEST I							
0	9	1140	1190	1150	877	914	893
2	9	1140	1210	1160	877	914	895
4	9	1140	1210	1160	877	933	897
6	9	1140	1270	1190	895	1010	935
8	9	1290	1580	1470	1030	1270	1190
10	8	1400	1600	1510	1140	1310	1230
12	8	1400	1620	1520	1160	1310	1270
14	7	1400	1580	1490	1160	1250	1210
TEST II							
0.0	10	1120	1160	1140	858	877	865
3.1	10	1120	1170	1140	858	895	869
5.3	9	1140	1210	1170	858	895	877
6.1	9	1210	1360	1300	970	1060	1010
8.1	8	1530	1580	1550	1140	1210	1140
9.3	7	1530	1580	1550	1160	1210	1180
10.0	7	1530	1580	1550	1160	1210	1190
12.2	6	1550	1580	1560	1160	1230	1180
14.2	Hatched						

* Eggs in Test I 0–16 hours old at first measurement; eggs in Tests II 0–12 hours old.

Size increase of eggs

Studies of the size increase of eggs were undertaken in conjunction with tests on the effect of humidity. The manner and the time that size increase took place was of interest here. Also, limited work was done to compare eggs of *E. cincticollis* with *E. annulipes* to see if there were any major differences during development.

Eggs were taken as they were laid by various females and incubated at 72°–80°F with 100 per cent RH in chambers as shown in figure 10. The females were checked one or more times a day and the eggs used were from 0–24 hours old when the tests began. Three groups of eggs (9–10 per group) from several females of *cincticollis* were observed as was one group (7 eggs) from several *annulipes* females.

Lengths and widths were measured when the eggs were put in the Petri dishes and approximately every two days thereafter until they hatched. The eggs were more or less symmetrically oval to slightly elongate when first laid, but later they became reinform in shape. The width was measured as the distance perpendicular to the longest axis. The third dimension or depth of the egg was subequal to the width initially but averaged about 100 microns less than the width just prior to eclosion.

The results of the measurements of two tests with *E. cincticollis* are given in table 3. The average linear growth of *E. cincticollis* and *E. annulipes* eggs in a third test are graphed in figure 12. The average length of eggs at the beginning of the third test was 1160 microns and 1040 microns for *cincticollis* and *annulipes* respectively. The average lengths at the end of the tests were 1600 microns for *cincticollis* and 1440 microns for *annulipes*. The average widths at the beginning were 881 microns for *cincticollis* and 804 microns for *annulipes*. At the end, the widths were

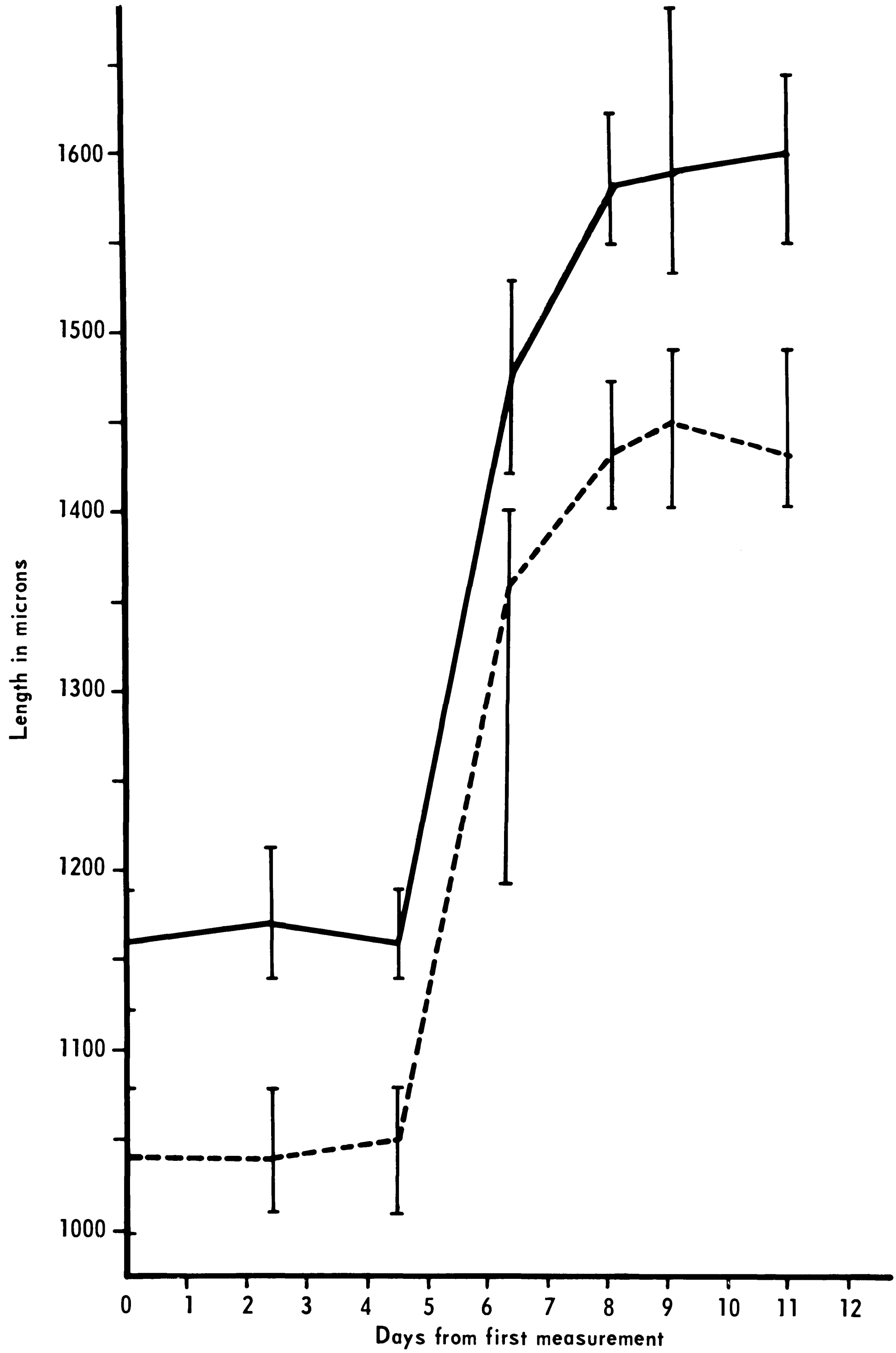


Fig. 12. Linear dimensions of eggs during their development. The solid line represents the average length of seven *cincticollis* eggs (five hatched) ; the broken line represents the average length of nine *annulipes* eggs (eight hatched). Vertical lines represent size range.

TABLE 4
CHANGE IN WEIGHT OF *E. CINCTICOLLIS* EGGS AT VARIOUS RELATIVE HUMIDITIES

Number of eggs weighed	Relative humidity	Average egg weight at							
		0 days*	2 days	4 days	6 days	8 days	10 days	12 days	14 days
	per cent	*mg*							
6	100	.572	.579	.573	.802	1.294	1.313	1.317	all hatched
7	92	.463	.299	.275	.281	.278	.277	.276	.277
7	86	.551	.483	.410	.362	.361	.361	.361	.365
14	100	.469	....	.491†13	.536†12	1.036†10	1.095	1.118	all hatched except one
		0 days*	3.4 days	5.5 days	7.3 days	9.0 days	9.9 days	11.0 days	13.0 days
6	100	.472	.474	.531†5	1.075	1.095	1.102	1.116	all hatched
7	97	.472	.479	.462	.446	.450	.442	.450	.454
7	92	.472	.372	.306	.311	.309	.310	.309	.307

* Eggs 0–12 hours old at zero days.
† The dagger followed by a number indicates the remaining eggs after a loss because of injury or mold.

1210 and 1100 microns respectively. The results of the tests of both species indicate that there was a great increase in length and width between the fifth and eighth days with considerably less change before or after that period. The major difference between *cincticollis* and *annulipes* eggs was their smaller size in the latter species.

Weight increase of eggs in relation to humidity

Excessive dryness was detrimental to egg development. The physical development of eggs was studied at various humidities in gross fashion by making periodic weighings to determine if weight changes are concomitant with size increase.

A preliminary test was conducted with eggs held over various saturated salts which produced relative humidities ranging from 33 to 100 per cent. Only eggs incubated at 100 per cent relative humidity completed development. Consequently, eggs used in the final trials were tested only in the narrower relative humidity range of 86 to 100 per cent. The results of the latter tests are presented in table 4. At 97 per cent relative humidity there was no weight gain and the eggs tended to lose weight slowly. At 92 per cent relative humidity and below, weight loss was more rapid and the eggs became dry and hard. The results also show a substantial increase in egg weight during embryogensis of eggs that hatched. The average weight per egg of the three groups (26 eggs) of eggs incubated at 100 per cent relative humidity was 0.504 mg at 0–24 hours. This increased to an average of 1.174 mg (based on 21 eggs) 12 days later. The eggs hatched on the thirteenth or fourteenth day after incubation started. Most of the weight gain took place over a short period. One group of six eggs gained 66 per cent of the total weight increase between the sixth to eighth day after incubation started; another group of 12 eggs gained 77 per cent of the total increase between the sixth and eighth days; another group of five eggs had 84 per cent of the total weight gain between 5.5 and 7.3 days after incubation started. Figure 13 shows the increase in egg weight during incubation and, for comparison, also the increase in length of eggs. The growth curve showing increase in length of the eggs and the weight increase curve are sigmoid

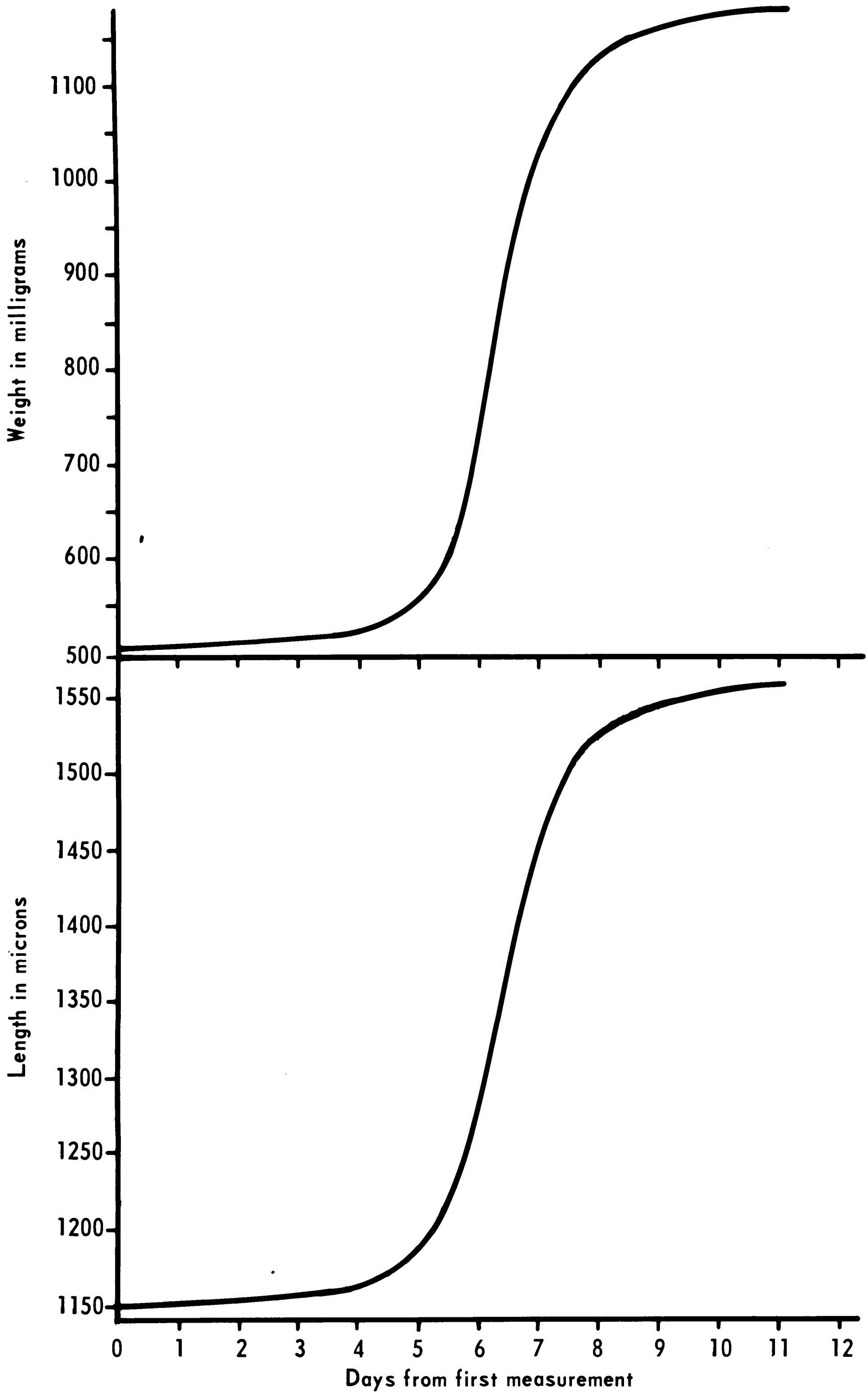


Fig. 13. The increase in length of *E. cincticollis* eggs (lower graph) compared to their weight change (upper graph) over their developmental period. Values are the interpolated averages from tables 3 and 4 (based on 26 eggs at 100 per cent R.H.).

TABLE 5
NUMBER OF NYMPHAL INSTARS COMPLETED AT THREE TEMPERATURE REGIMES BEFORE ADULTHOOD

Temperature range	Number becoming adults at instars 4 to 8				
	4	5	6	7	8
degree F					
72–80	1	16	2		
80–85		6	3		
90–92			3	3	1*

* Died before becoming adult.

curves which appear essentially similar.

These results suggest the importance of the female's brooding of her eggs under natural conditions. Both in the field and in the laboratory, the female will move her eggs on occasion. This might be due to the necessity of maintaining the eggs at 100 per cent relative humidity. Also it has been noted in this study that the female will pick up the eggs and manipulate them with her mouth occasionally. This has been mentioned as being important in keeping mold from growing (Klostermeyer, 1942) because unattended eggs usually mold quickly. However, in some cases this might also be important in maintaining the high moisture level necessary for development.

This study did not determine if 100 per cent relative humidity is needed for the entire period of embryogenesis or only at some critical point. One might expect that a high relative humidity would be needed at least during the period of rapid weight gain.

Nymphal instars

The maternal care of newly hatched nymphs is minor. Although the female is very protective toward her eggs, she shows no obvious behavioral pattern toward her freshly hatched brood. On occasions when the clutch hatches over several days, females continue to guard the unhatched eggs and pay little attention to the emerged nymphs. The nymphs remain bunched together under the female for several days if she is not disturbed. If the female moves a short distance, the nymphs follow. The female will seek shelter rather than become aggressive if disturbed after the eggs hatch. The nymphs are ignored and they scatter to grow on their own.

The number of nymphal instars in the life cycle varied depending on the temperature at which they were reared (table 5). Five nymphal instars were most common at the lower temperature range of 72°–80°F. Six or seven instars were most common at 90°–92°F, but one individual achieved eight instars. The effects of temperature on the duration of various nymphal instars and total time of development are summarized in table 6. The mean time from hatching to adult at the lowest temperature range (72°–80°F) was 115.5 days, with a variation of 81 to 187 days. Two groups of offspring from different females were used in determining the mean developmental time at the lowest temperature range. The mean of these two groups was 103.7 days and 122.4 days. This difference in development was probably due to heritable variations. The average times required to develop at the 80°–85°F temperature and at the 90°–92°F temperature were relatively close—69.7 days and 74.3 days, repectively. Although there were generally more instars at the 90°–92°F temperature, the nymphs exposed to that temperature became adults much faster than at the lowest temperature.

TABLE 6
DEVELOPMENT OF *E. CINCTICOLLIS* NYMPHS AT THREE TEMPERATURE REGIMES

	Days spent in various instars							Number of days from hatching to adult
	1st	2nd	3rd	4th	5th	6th	7th	
	72°-80° F (21 individuals started—18 became adults)							
Minimum	13	10	14	19	26	42		81
Maximum	49	27	25	44	53	42		187
Average	19.9	15.8	17.9	27.8	34.1	42		115.5
								S.D. 24.503
	80°-85° F (10 individuals started—9 became adults)							
Minimum	9	8	10	11	12	15		56
Maximum	11	14	21	17	21	19		81
Average	9.9	10.4	13.3	13.5	17.1	16.7		69.7
								S.D. 7.648
	90°-92° F (10 individuals started—6 became adults)							
Minimum	8	5	7	8	9	6	12	59
Maximum	18	13	17	16	24	17	23	90
Average	11.7	8.7	9.9	11.1	13.5	13.0	17.5	74.3
								S.D. 13.662

However, mortality was greater at 90°–92°F and development time to adulthood slightly longer than at 80°–85°F which indicates that the higher range was not an optimum temperature.

Laboratory conditions and food may not have been ideal for development. Those conditions may, inpart, account for the wide variability in duration of instars within a single temperature range. Table 7 shows that the lowest temperature generally resulted in smaller adults. The higher temperatures led to adults that compare closely to the size of adults collected in the field. A sample of 15 adults collected in August, 1967, in Fresno County, averaged 10.12 mm in length. This was close to the average length of laboratory-reared specimens at the higher temperatures. Of 15 field-collected individuals, three were 12 mm or longer; the largest female was 12.94 mm long. These sizes were somewhat larger than the laboratory maximum of 11.8 mm.

Crumb *et al.* (1941) found the duration of nymphal growth of *F. auricularia* was considerably shorter in the field than in the laboratory. Neiswander (1944) indicated that different foods resulted in different growth rates for *E. annulipes*. He also mentioned that a diet of carrot led to shorter developmental periods during the early instars than potato, but potato resulted in shorter growth periods in the later instars. Consequently, developmental time and overall growth could be expected to vary in the field as well as the laboratory, depending on combinations of factors such as food source and temperature.

The size of the various body parts (table 7) is of some value for determining the instar. The average length and width of the pronotum increase as does the body length. The ratio of the mean pronotal width to length steadily decreases. However, there is overlap between instars in these size relationships. The exact determination of nymphal instar is difficult, but by checking the mean size figures and observing the total number of antennal segments

TABLE 7

DIMENSIONS OF BODY PARTS FOR INSTARS OF *E. CINCTICOLLIS* REARED AT THREE TEMPERATURE REGIMES

Nymphal instar	Temp.	Sample size	Body length*			Pronotum length			Pronotum width			Pronotal ratio†
			Min.	Max.	Ave.	Min.	Max.	Ave.	Min.	Max.	Ave.	
	degree F						*mm*					
	72–80	22	3.03	4.38	3.74	.448	.522	.488	.560	.634	.599	1.23
1	80–85	15	3.08	3.87	3.62	.504	.541	.530	.615	.634	.630	1.19
	90–92	13	3.59	4.05	3.80	.485	.541	.519	.560	.634	.613	1.18
	72–80	22	4.15	5.03	4.54	.578	.709	.650	.671	.783	.732	1.13
2	80–85	10	4.43	5.45	5.04	.653	.709	.673	.746	.783	.761	1.13
	90–92	10	4.47	5.59	4.81	.578	.653	.625	.634	.727	.696	1.11
	72–80	21	4.93	6.49	5.49	.727	.970	.835	.765	.970	.902	1.08
3	80–85	9	5.22	6.42	5.87	.765	.877	.824	.839	.933	.888	1.08
	90–92	10	4.85	5.97	5.27	.671	.839	.738	.709	.839	.781	1.06
	72–80	21	6.04	7.99	6.88	.858	1.18	1.04	.951	1.12	1.11	1.07
4	80–85	9	6.27	7.69	7.06	.914	1.12	1.01	.988	1.14	1.06	1.05
	90–92	9	5.75	7.46	6.28	.783	.933	.866	.802	.951	.885	1.02
	72–80	19	7.18	9.88	8.26	1.12	1.42	1.27	1.12	1.49	1.31	1.03
5	80–85	9	7.41	9.41	8.59	1.08	1.25	1.21	1.16	1.27	1.23	1.02
	90–92	9	6.72	7.91	7.36	.914	1.16	1.02	.877	1.12	1.02	1.00
	72–80‡	2	9.06	9.41	9.24	1.34	1.36	1.35	1.32	1.46	1.39	1.03
6	80–85‡	3	9.41	10.60	9.92	1.32	1.42	1.38	1.36	1.42	1.39	1.01
	90–92	8	7.65	9.77	8.71	1.03	1.36	1.17	1.01	1.29	1.16	.99
7	90–92	6	8.35	10.70	9.51	1.12	1.46	1.28	1.12	1.42	1.26	.98
8	90–92	1	—	—	9.41	—	—	1.29	—	—	1.25	.97
Adult	72–80	19	8.59	10.80	9.76	1.27	1.59	1.46	1.17	1.59	1.44	.99
	80–85	9	9.76	11.80	10.50	1.31	1.60	1.46	1.32	1.59	1.43	.98
	90–92	5	9.65	11.30	10.60	1.29	1.55	1.45	1.14	1.46	1.36	.94

* Measured from eyes to end of abdomen, forceps not included.
† Averages of Pronotal width/pronotal length.
‡ No further instars past the sixth.

Table 8

NUMBER OF ANTENNAL SEGMENTS OF *E. CINCTICOLLIS* REARED AT THREE TEMPERATURES

	Temperature range	Sample size*	Percentage of antennae with indicated number of segments												
			8	9	10	11	12	13	14	15	16	17	18	19	20
	degree F		*per cent*												
NYMPHAL INSTAR															
1	72–80	56	100												
	80–85	29	100												
	90–92	25	100												
2	72–80	40		2	7	10	68	13							
	80–85	20			5	5	70	20							
	90–92	19	16	5		16	63								
3	72–80	38					3	21	21	55					
	80–85	20						5	5	90					
	90–92	18			11	11		22	56						
4	72–80	41							5	22	56	17			
	80–85	18								5	95				
	90–92	18						17	28	50	5				
5	72–80	38									3	47	42	8	
	80–85	18										33	67		
	90–92	18								28	67	5			
6	72–80	4											100		
	80–85	6											50	50	
	90–92	16									27	53	20		
7	90–92	12									8	50	42		
8	90–92	2									50	50			
ADULT															
	72–80	37									8	22	54	13	3
	80–85	18										28	56	16	
	90–92	8								12		76	12		

* Sample includes both right and left antennae, but antennae obviously broken were not included.

TABLE 9
LONGEVITY OF FIRST INSTAR NYMPHS OF THE AFRICAN EARWIG AT VARIOUS RELATIVE HUMIDITIES*

Longevity†	Relative humidity (per cent)								
	100	97	92	86	84–82	75	67–62	56–50	33
	days								
TEST I									
Minimum	6	6	6	5	7	4	4	2	2
Maximum	13	13	12	12	12	7	5	4	3
Average	11.0‡	11.2‡	8.75	8.5‡	8.75‡	5.4	4.4	3.6	2.4
TEST II									
Minimum	10	10	9	7	7	3	3	2	1
Maximum	12	14	13	10	9	7	5	4	3
Average	10.8	12.6	11.2	8.2	7.8	5.6	4.2	3.2	2.2

* Five nymphs with no food or water were kept at 72°-80° F at each relative humidity.
† In Test I, the nymphs were examined for 13 days; in Test II, the nymphs were checked until all were dead.
‡ Based on four nymphs only.

(table 8), it is possible to make a close estimate. Bharadwaj (1966) found a similar case of overlap of characters as well as variation in number of instars of *E. annulipes*. He advocated that a combination of characters be employed. Table 8 shows that the highest temperature resulted in fewer antennal segments of nymphs after the first instar and fewer segments in adults. The modal number was generally one segment less at 90°–92°F.

Effect of humidity on first instar nymphs

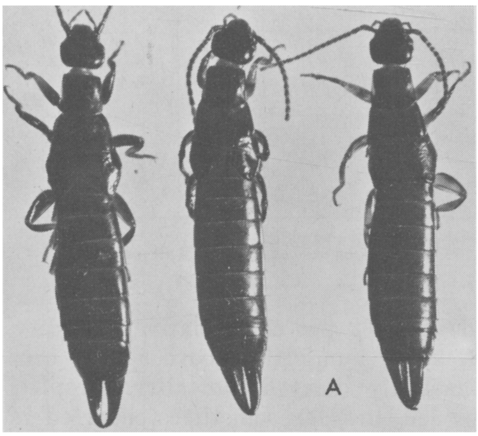
A graded set of relative humidities was obtained at 72° to 80°F by using the techniques applied to the study of eggs. No food or water were provided so that the desired humidity could be maintained. This limited maximum survival to approximately two weeks.

The results of two tests appear in table 9. In both tests the greatest mean longevity of the first instars occurred at 97 per cent relative humidity. Longevity at the different relative humidities varied in the first and second tests. The maximum longevity for any nymph was 14–15 days at 97 per cent relative humidity; the minimum longevity for any nymph was between one and two days at 33 per cent relative humidity. Relative humidities above 90 per cent markedly delayed mortality. Droplets of condensation sometimes occurred in vials at 100 per cent relative humidity and this occasionally entrapped the small nymphs.

Wing-pad development

Some individuals of *cinticollis* are winged or brachypterous as adults. These forms have wing-pads in the later part of the nymphal stage (figure 14). The nymphs measured during each instar (table 7) did not develop wing-pads. Twelve nymphs with wing-pads were collected in the field from a mixed age group. These were measured and compared with those of tables 7 and 8 to estimate at which instar the wing-pads became visible. There was considerable range between the measurements of individuals but none of these 12 nymphs had dimensions that would categorize them below fifth instars. Apparently, the wing-pads do not become evident until the last or next to last nymphal instar, depending on the number of moults occurring in the field.

Crumb *et al.* (1941) found that wing-pad formation was not evident in *Forficula auricularia,* which has four nymphal instars, until the last nymphal instar. Bhatnagar (1967) found that the metanotum becomes more deeply emarginate posteriorly at each successive nymphal instar in both *Labidura riparia* and *Euborellia annulipes*. However, not until the fifth instar (last) of *L. riparia* was a typical wing-pad evident.



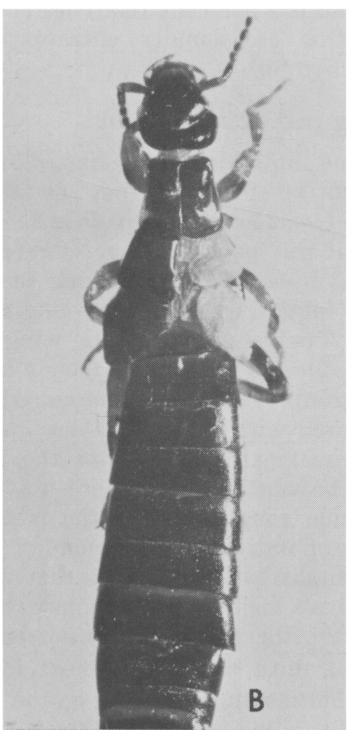


Fig. 14. *E. cincticollis*, A. Nymphs with wing pads; B. nymph with part of meso- and metanotum removed to show developing elytron and wing.

First oviposition

Eight newly moulted adult females were placed at 72°–80°F in Petri dishes, each with a mature male, and checked daily for eggs. The average number of days to the first oviposition was 29.3 days, with the range from 19 to 47 (S.D.—10.2); one did not deposit eggs after 54 days. The average size of clutch was 11.9 eggs and ranged from 5 to 24. The time required for egg maturation and deposition may be less under field conditions. Bharadwaj (1966) reported *E. annulipes* to deposit eggs within one day after becoming an adult. Virgin females kept in isolation and not allowed to mate, occasionally laid a few eggs. These eggs never developed and the females eventually ate them.

Total development time and adult longevity

Average developmental period from egg to adult varied considerably within the temperature range studied. The average times for the respective temperatures were 128.5 ± 25.5 days at 72°–80°F; 78.5 ± 8.4 days at 80°–85°F; and 82.0 ± 14.1 days at 90°–92°F. The average time from egg to egg at 72°–80°F was 157.8 days.

Females usually survived for a considerable period after laying their first clutch of eggs. Individual adults that were field-collected during the first week of January, 1967, and kept at 72°–80°F lived until August 12 and September 1 (218 and 240 days, respectively). An adult placed at 80°–85°F on March 6, 1967, lived until September 10, 1967 (188 days). An adult collected on January 6, 1967, and placed at 90°–92°F on February 11, lived until June 28 (173 days). These field-collected specimens were probably overwintering adults because late fall and winter soil temperatures are not likely to be conducive to continuous development. If these adults were from eggs that had hatched the previous spring, then they would have lived one year or more.

EFFECT OF TEMPERATURE ON PHENOTYPE

Ting (1951) asserted that there were wingless and brachypterous forms as well as the winged form of *cincticollis*. His comparisons were made on the basis of field-collected specimens of *cincticollis* and not on reared material.

An experiment was designed to determine if any one of the winged, brachypterous, or wingless forms could produce the other two types as well as its own form. The effect of temperature on the expression of these phenotypes was also investigated.

Offspring from phenotypically different earwigs were reared at 72°–80°, 80°–85°, and 90°–92°F under a light cycle that was at least 16 hours. Fertilized females were usually obtained from the field; hence, the male phenotype was unknown. In a few cases controlled matings were accomplished by using virgin females from the laboratory.

A readily apparent result (table 10) was that the winged and brachypterous phenotypes were produced only at the two highest temperatures. The wingless form occurred in greatest numbers at all temperatures. The results also show that a female may produce offspring with one, two, or three distinct phenotypes at the higher temperatures irrespective of her phenotype.

The polymorphic nature of this species is apparently influenced by temperature. The genetic control of the winged condition is an interesting speculation. Similar cases of polymorphism occur in other insects (Da Cunha, 1949; Dobzhansky, 1943). The data of table 10 tend to indicate that the character is not monogenic because all three types of females produced three types of offspring. Other than that, little can be said about the genetic mechanism. A statement by Dobzhansky (1963) might be applicable here:

> Populations of many species consist of two or more "phases" which differ in color, in shape of some body parts, or in other traits. Although the phases may appear very strikingly different to the human eye . . . , they interbreed freely both in nature and in experiments.

This variation in phenotype, increase of temperature in the summer, and dispersal by flight appear to be correlated. Dispersal at the end of a period of maximum reproduction by a species should reduce the pressure on the old habitat and possibly provide new food sources. Information was obtained in field studies that tends to support the notion that these factors are correlated. Several collections were made throughout the spring and summer of 1967. The types of individuals collected on different dates appear in table 11. The collection made in August showed that the number of adult winged and brachypterous forms was much higher than in May. Even more striking is the fact that more than 70 per cent of the nymphs collected in August had metanota which indicated they would become winged or brachypterous adults. Only 1 per cent of those collected in May were similarly developed. The presence of a higher incidence of nymphs with wing pads in August would correspond rather closely to the peak earwig flights which occurred from mid-August to mid-September (see flight studies).

Johnson (1966) discussed some of the factors concerned with dispersal and some of the dispersal forms found in insects. He stated that a prominent theory of adaptive dispersal is that adver-

TABLE 10
EFFECT OF TEMPERATURE ON PHENOTYPE OF *E. CINCTICOLLIS*

Temperature	Phenotype of parental female	Total number of earwigs with the indicated phenotype reared from a single female		
		Winged	Brachypterous	Wingless
72°–80° F	winged	0	0	5
	winged	0	0	6
	winged	0	0	4
	winged	0	0	3
	winged	0	0	6
	winged	0	0	8
	winged	0	0	7
	brachypterous	0	0	3
	brachypterous	0	0	19
	brachypterous*	0	0	17
	brachypterous	0	0	24
	brachypterous	0	0	13
	wingless	0	0	16
	wingless	0	0	5
	wingless	0	0	27
	wingless	0	0	7
	TOTALS	0	0	170 (81♂, 89♀)
80°–85° F	winged	7	2	17
	winged	2	0	11
	winged	0	2	12
	wingless	0	0	17
	wingless	0	0	10
	TOTALS	9 (4♂, 5♀)	4 (3♂, 1♀)	67 (35♂, 32♀)
90°–92° F	winged	2	0	6
	winged	0	0	22
	winged	2	0	14
	winged	0	0	13
	brachypterous	2	2	4
	brachypterous	0	0	4
	wingless	5	2	1
	TOTALS	11 (0♂, 11♀)	4 (3♂, 1♀)	64 (29♂, 35♀)

* Mated with winged male in the laboratory.

TABLE 11
FLUCTUATION IN WINGED CONDITION OF *E. CINCTICOLLIS* COLLECTED FROM THE SOIL AT TWO SITES DURING 1967

Collection site	Date	Numbers (and percentages) of each form caught in the field				
		Adults			Nymphs (late instars)	
		Winged	Brachypterous	Wingless	Wing pads	Wingless
Yolo County.........	May 10–30	7 (3.5)	9 (4.5)	186 (92.0)	2 (1.0)	195 (99.0)
Fresno County.......	Aug. 2	12 (13.0)	2 (2.2)	78 (84.8)	45 (76.3)	14 (23.7)

sity factors act ontogenetically and that migratory flight "is a symptom in an endocrine deficiency syndrome concomitant with early adult life and ovarial immaturity, ovarial diapause, and structural polymorphism." Brinkhurst (1959) studied polymorphism in some British Gerroidea and found that alary polymorphism was a factor of genotype and environment. He also found that one genotype could vary phenotypically depending on the environment. Southwood (1961) discussed the modes of action that hormones could have on wing polymorphism in Heteroptera. The polymorphism in *E. cincticollis* is probably a complex of factors that is affected by temperature, genetics, and hormonal balance.

ORGANISMS ASSOCIATED WITH *E. CINCTICOLLIS*

Two species of mites were commonly found in association with *E. cincticollis.* One mite was a *Tyrophagus* sp., apparently a soil mite, which was found in the laboratory culture. The other was *Histiostoma* sp. (figure 15) which was apparently a case of phoresy (Baker and Wharton, 1952). During the beginning of this study, several earwigs in the laboratory cultures became associated with mold and died. A diagnosis made at the Invertebrate Pathology Laboratory, University of California, Berkeley, recovered several saprophytic fungi (*Penicillium* sp., *Aspergillus glacous,* and *Rhizopus nigricans*) and bacteria (*Pseudomonas aeruginosa* and *Alcaligenes* sp.) from the earwigs, but a definite microbial etiology could not be found. The death of earwigs in the culture subsided and did not recur.

Although no specific predators were observed to feed on *E. cincticollis,* probably some predation by invertebrates, amphibians, reptiles, birds, and mammals does occur. Crumb *et al.* (1941) reported most of these animals to be predators of *Forficula auricularia.*

E. annulipes has been reported to be the intermediate host of a cysticercoid (Pierce, 1921, cited in Bharadwaj, 1966) and a secondary host to a rodent cestode (Hall, 1929, cited in Bharadwaj, 1966). *E. annulipes* has also been mentioned as an intermediate host of two poultry ascarids (cited by Bharadwaj, 1966). Because *E. cincticollis* and *E. annulipes* are closely related, *E. cincticollis* also may serve as an intermediate host of certain cysticercoids or ascarids.

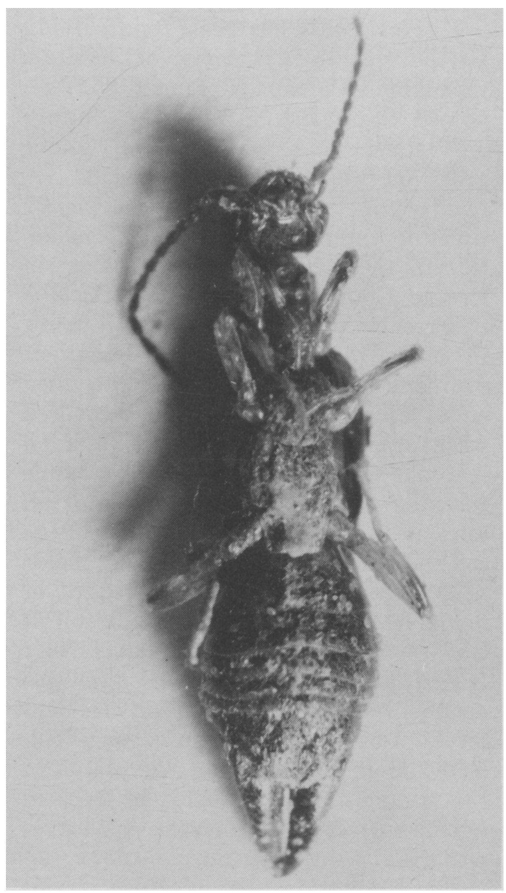


Fig. 15. Mites (*Histiostoma* sp.) on *E. cincticollis.*

FIELD STUDIES

Little is reported in literature concerning the field biology of *E. cincticollis*. Ting (1951) briefly mentioned the habits of this earwig, and Schlinger *et al.* (1959), in a paper on *Labidura riparia,* mentioned that *E. cincticollis* was found in association with *L. riparia* in alfalfa fields in Imperial County.

Studies of the field habits of *E. cincticollis* were made at Davis and in the west of Fresno County. *E. cincticollis* is sometimes a pest in Fresno County where it feeds on melon seedlings and fruits.

Habitats

E. cincticollis has been found living in the soil in a variety of habitats throughout California. Ting (1951) reported *cincticollis* in Imperial County on "moist (not wet) ground under grass or weeds or under boards . . . (and) puncture vine mats near leaky pipes or water coolers . . ." He also mentioned their presence on melons in Fresno County. We found *cincticollis* in Fresno County in alfalfa seed fields, in melon fields, along the banks of drainage canals, in the uncultivated edges of fields, and in grass covered waste areas. *E. cincticollis* was observed in Yolo County near the coast range foothills at Winters at the edge of an apricot orchard under stones and in the soil; at the edge of sugar beet fields near Woodland; and at the edges of fields, in waste areas, and in the soil at the base of almond trees at Davis. Near Biggs, Butte County, *cincticollis* was commonly found in the soil on rice field levees. Some winged adults were collected from the stalks of rice plants in the middle of flooded fields in August, but no earwig feeding on the rice leaves was noted.

The habitats where *cincticollis* was most abundant had several factors in common. They were usually open fields with some type of low-growing plants. Moisture and proper drainage were other requisites. The more common habitats had some type of raised ground where various moisture conditions could be found. The furrows of seed alfalfa fields were ideal. The earwigs could stay at different depths in the soil and at different levels in the banks or top of the furrow. Areas with dirt piles or levees or banks offered this same advantage.

Another requisite of a favorable habitat was that it should be relatively undisturbed. Annual crops that are frequently cultivated rarely contained African earwigs until the crop approached maturity which usually occurred during the flight period of *cincticollis*. Cultivation would evidently deter nest establishment or destroy one or all stages of development.

Davis, Yolo County

Two uncultivated and undisturbed areas about one quarter of a mile apart on the campus at the University of California, Davis, had abundant populations of *cincticollis*. These places were selected as study areas and observed during 1966 and 1967. During the winter months the ground was cold and wet and the earwigs were inactive. They were found from 1 to 12 inches below the soil surface. Sometimes there was a chamber in which one or occasionally more than one (rarely up to three or four) earwig was found. Usually they were solitary. Intermediate instars and adults were found throughout the winter months but no first instar nymphs were found until April (1967). The 1966–1967 seasonal precipitation totaled 27.64 inches (10.99 inches above average) and this rain and cool weather extended into April. The earwigs responded to increasing moisture of the soil by moving closer to the surface. On

March 7, 1967, about 40 earwigs were collected, all were active and within about the top one inch of the soil surface. Considerable soil was excavated in search of egg clutches through March and April, but it was not until April 25 that eggs were found in the field. It is believed that egg laying may start earlier in years which do not have excessive cold, wet weather as in 1967. Two egg clutches found on April 25 were located in a grassy area in which the soil was very wet but not muddy. One clutch had 14 eggs and the other had 17 eggs.

The development of eggs was difficult to follow in the field. If the eggs were not disturbed or injured when uncovered, exposure to the air caused the soil to dry and the females usually moved them. Egg clutches were found easily early in May. On May 8 approximately 50 earwigs were collected. Most of the mature females had their abdomens distended in gravid condition. One such female brought into the laboratory laid 17 eggs overnight. On May 23, first instar nymphs were located in the soil. One clutch had 24 eggs and a single newly hatched nymph. From May 23 to 25 many egg clutches were about to hatch. The number of eggs in 14 such clutches ranged from 20 to 60, with an average of 36.2. These egg clutches were found about 2 to 10 inches below the soil surface. By June 12 many first and second instar nymphs could be found but egg clutches were not readily located.

Towards the end of June the study areas were becoming dry. On June 20 only two egg clutches were found. On July 4 only immatures and adults were observed. There was a noticeable decrease in the ease with which earwigs could be located and one had to dig deeper to find them. By the end of July, fewer earwigs were found and only in such protected and moist areas as under large pieces of plywood, or below 5–6 inches of soil. The annual grasses were dry; wild lettuce and yellow star thistle were about the only species of the conglomerate plant flora still alive.

The temperature on the surface of the soil reached 104°F on July 30. It ranged from 79°–86°F between 3–4 inches below the soil surface; at 10 inches below the soil surface the temperature was 79°F. The soil was moist at the 10 inch depth.

Fresno County

Field studies were concentrated in the vicinity of two agricultural crops, seed alfalfa and melons. In January, 1967, an abundant population of the African earwig was found in recent dredgings along the banks of a drainage ditch beside a seed alfalfa field. Earwigs could also be found in a grassy waste area beyond the end of this field. The seed alfalfa field at this time had been recently disked in several directions so that only the crowns of the plants were visible. The field was free of cover, and no earwigs were found in it.

The same alfalfa seed field was checked again at the end of June and several changes had taken place. The piles of dirt along the drain ditch had been smoothed over and the waste area beyond the end of the field was very dry. A few earwigs were found in these situations, but fewer than during the winter. The field now supported a luxuriant growth and all stages of earwigs were found abundantly along the tops of the irrigation furrows. The soil along the tops of these furrows was moist but not wet. The temperature (over 100°F) and humidity above the alfalfa foliage were high but the soil in the furrows was much cooler.

The alfalfa seed field still supported many earwigs during July. On August 2 approximately 400 adults and late instar nymphs were collected. Four egg clutches and various nymphal instars were noticed. On August 9th, late instars and adult earwigs were collected from the top of furrows, under the heavy canopy of alfalfa. Five hundred and thirty-five earwigs were collected at an average rate of 6.8 earwigs per foot of row. This alfalfa seed field supported the largest population found in the area.

No earwigs were found in a field of Persian and Casaba melons in June, when the vines spread about two feet. Specimens of *E. cincticollis* were discovered here in July, when the melons were about two weeks from maturity. Surveys of cantaloupe fields (1967) did not reveal African earwigs until the melons started to mature. However, there is a good indication that the earwigs moved or could move into the field much earlier as all nymphal instars were found in one field of mature melons. One female with a clutch of 46 eggs was observed in a melon field as late as August 29.

The earwigs in melon fields are most easily found under melons that are in contact with the ground. They also may crawl into cracks in soil around the plants. The numbers of earwigs in melon fields varied greatly. An appraisal of feeding injury was made in one field of mature melons that appeared to have a high population of earwigs. Out of 100 melons examined, 66 had some feeding scars (figure 16) attributable to earwigs.

Habits in the field

The rather late appearance of earwigs in row crops indicates a possible migration to the crops by flight or by walking when the period of intensive cultivation ends. The shade, moisture and protection provided by the canopy of a maturing crop also provide a favorable habitat and food source. The extent of vertical movement of earwigs in soil is not fully known. Downward movement may allow some earwigs to escape injury from cultivation or adverse climatic conditions.

The food available in the field probably consists of a variety of substances similar to those eaten by other species of earwigs. There were many insects in the alfalfa field that could have served as food. No feeding was noticed on live portions of the alfalfa plants. Schlinger *et al.* (1959) reported that *Labidura riparia* ate alfalfa seeds when deprived of live food. As previously mentioned, *cincticollis* fed on aphids and other arthropods as well as several plant foods in the laboratory and it probably feeds on several plant and arthropod hosts in the field.

E. cincticollis is normally secretive, being rarely seen during the day, even in areas where it is abundant. They are almost entirely a soil dweller although they do have evening flights.

Flight studies

Two authors (Gurney, 1950; Ting, 1951) have reported on the flight of *E. cincticollis,* mostly in connection with light trap collections. The earliest mentioned flight of the season was July 18 at Blythe, California (Ting, 1951). The latest known date of flight prior to the present study was August 3, at Safford, Arizona, recorded from specimens in the U. C. Davis collection.

Investigations on the flight periods of the African earwig were made at Davis in 1966 and 1967. A light trap (Ellisco, 110103-2) which contained a 15 inch ultraviolet tube (15 watt) was used with cyanide for all collections. The trap was operated on warm nights in the spring of 1966 until the early part of June but no earwigs were collected. In 1967, a continuous record of the number of captured earwigs was kept from July 14 to October 12. On both years the trapping sites were within one-half mile of each other on the campus, adjacent to a variety of cultivated and fallow fields.

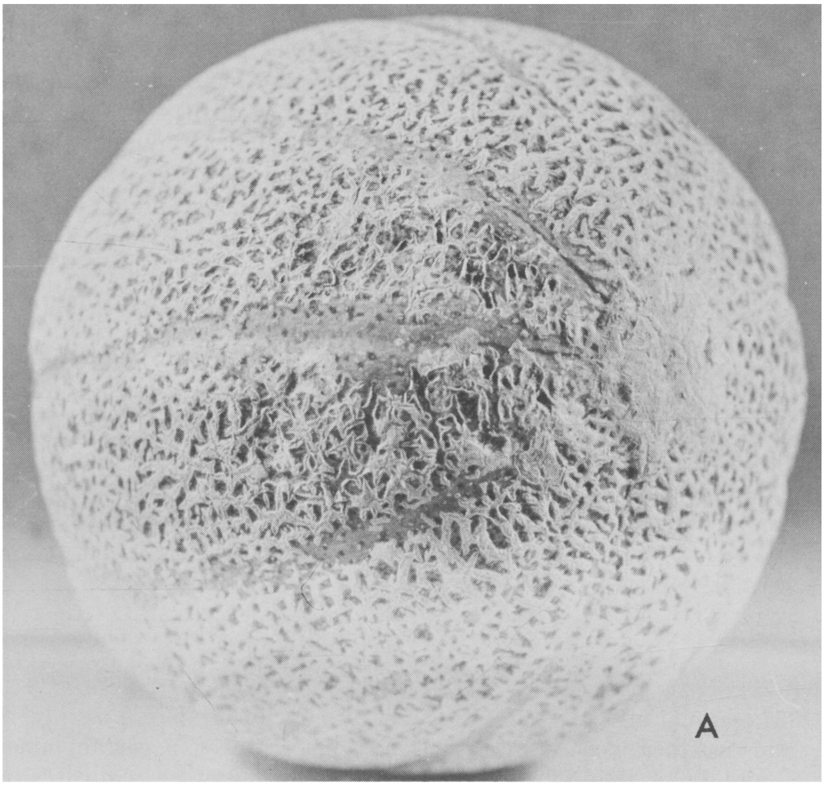
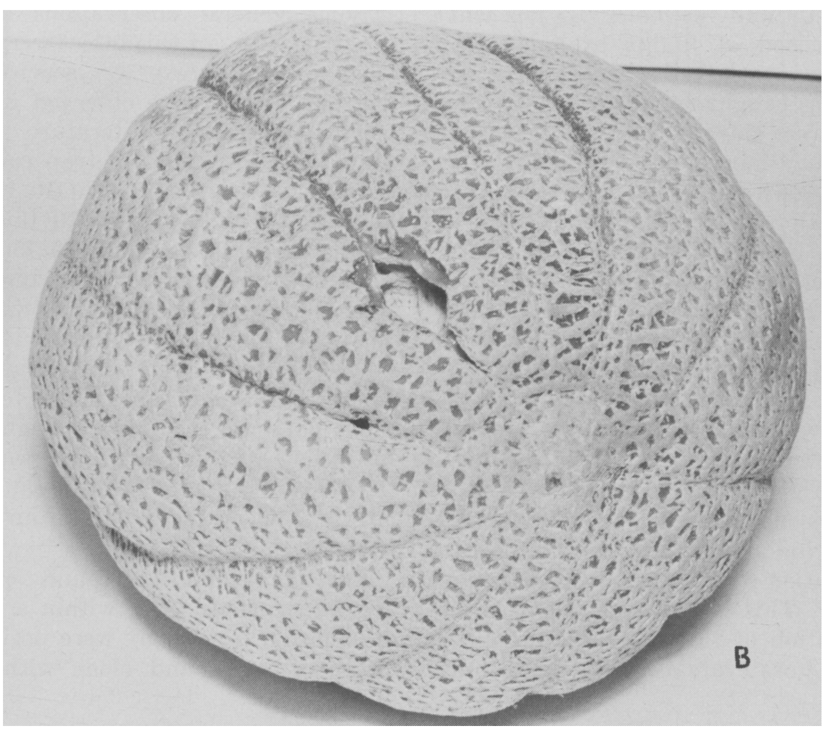


Fig. 16. A. Feeding scars on a mature, marketable cantaloupe;



B. feeding injury on an overripe cantaloupe.

Weather data were obtained from the U. C. Davis weather station which was 1/4 mile from the collection sites. These weather data were then analyzed in several ways in an attempt to find some relationship between physical factors and earwig flight. The temperature and relative humidity at 7 p.m. and the average wind velocity at 7–8 p.m. were plotted with the total numbers of earwigs collected. This time of day was used because it was just before initiation of flight. Also, an index value (x) was obtained through an arbitrary weighting of several factors apparently correlated with earwig flights. The index value was calculated for each day with the following formula devised for this study:

$$x = \text{temperature } (^\circ\text{F}) \times \frac{1}{\dfrac{\text{per cent relative humidity}}{100}} \times \frac{10}{\text{wind velocity (mph)}}$$

The 1967 seasonal flight record, index values, and weather data appear in figures 17 and 18. A total of 1087 earwigs were collected, 622 females (57 per cent) and 465 males (43 per cent). The period of flights extended from mid-July to late September. One earwig was caught on the first day collections were started, July 14. A few earwigs may have flown before this date, but large numbers of earwigs did not fly until August 12. Peak flights occurred in August and September. The last flight recorded was on September 26, and collections were terminated on October 12. During this 92 day period, 31 collections had more females than males, 10 had more males than females, and five had equal numbers. No captures were made on 36 days and seven days were omitted (dark bars) due to mechanical failure.

The index generally shows a positive correlation with the number of earwigs caught. This is, however, a theoretical association of these factors. The physical factors evaluated relative to numbers of earwigs collected should not be considered to be the only, or the most important, factors governing earwig flights. Most of the earwigs were caught on warm summer nights with relatively low wind velocity and low relative humidities. Although flights will not occur unless the physical factors are within favorable bounds, the triggering mechanism(s) that initiates these flights is unknown. No major flights occurred before August 12, even though conditions of temperature, relative humidity, and wind velocity were similar to later periods when major flights did occur. There could have been several reasons for this. One possibility is that there were not many mature, winged adults until that date. Possibly, also the earwigs required a certain amount of heat, light, or other requisites prior to flight.

Some general observations on the flight activities of this insect were made when the light trap was serviced. No daytime flights were observed or have been reported in the literature. On the night of August 13 the trap captured 98 earwigs from sunset to 10:15 p.m. and only 10 earwigs after 10:15 p.m.

On August 14, at dusk (8:15 p.m.), the first earwig was noticed flying about four feet above the ground to the trap. The wind was light at 40 feet elevation but the air was calm near the ground. For a distance of about 150 feet the flight path was level and straight. The insect flew with its abdomen lower than the thorax and head. The flight ended abruptly when the earwig hit an object near the light trap.

Earwigs could be found on the ground near the trap, within a radius of about 20 feet. Many were positioned on small rocks and clods with their

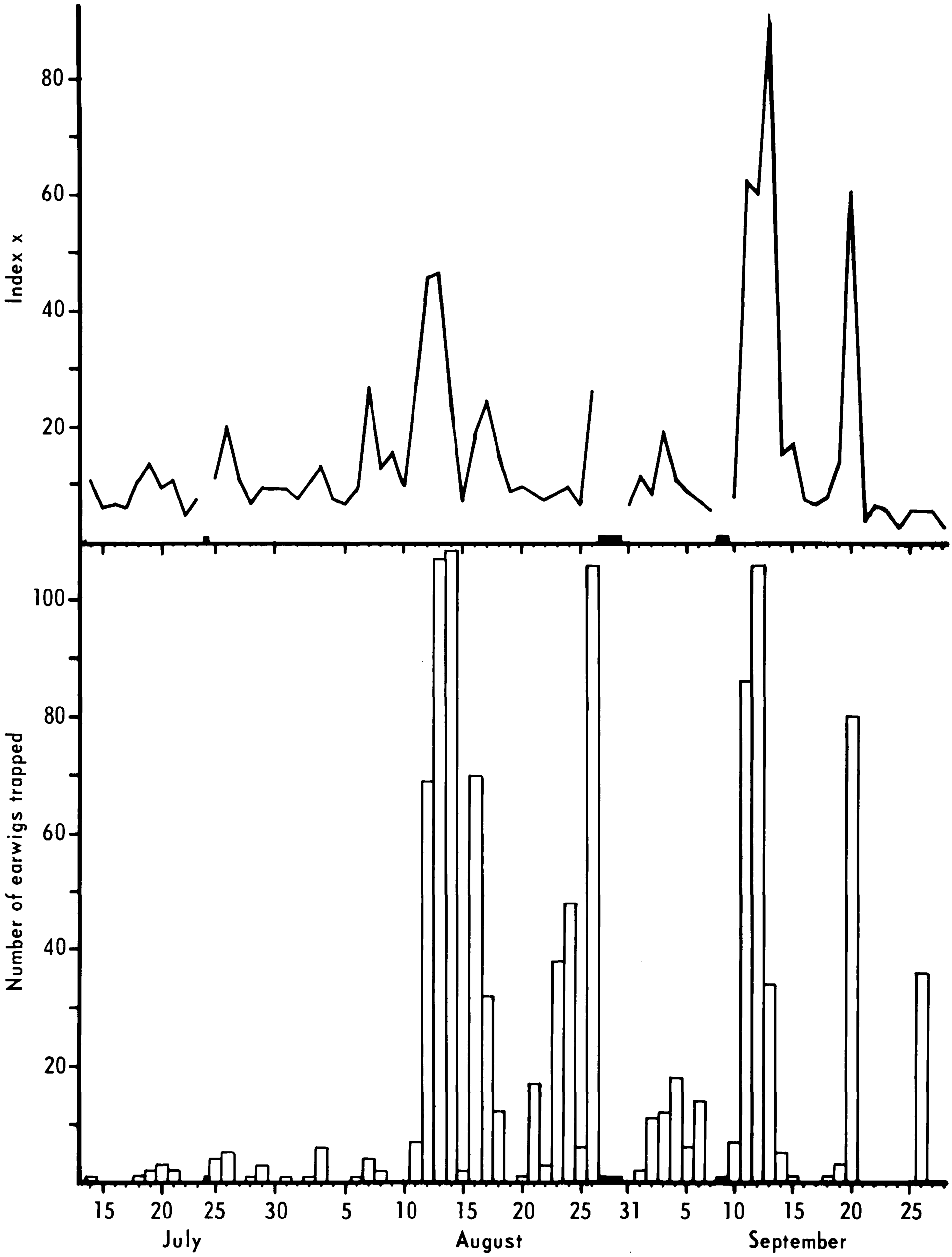


Fig. 17. Number of *E. cincticollis* collected daily with an ultraviolet light at Davis during 1967, in relation to an index (x) of weather factors.

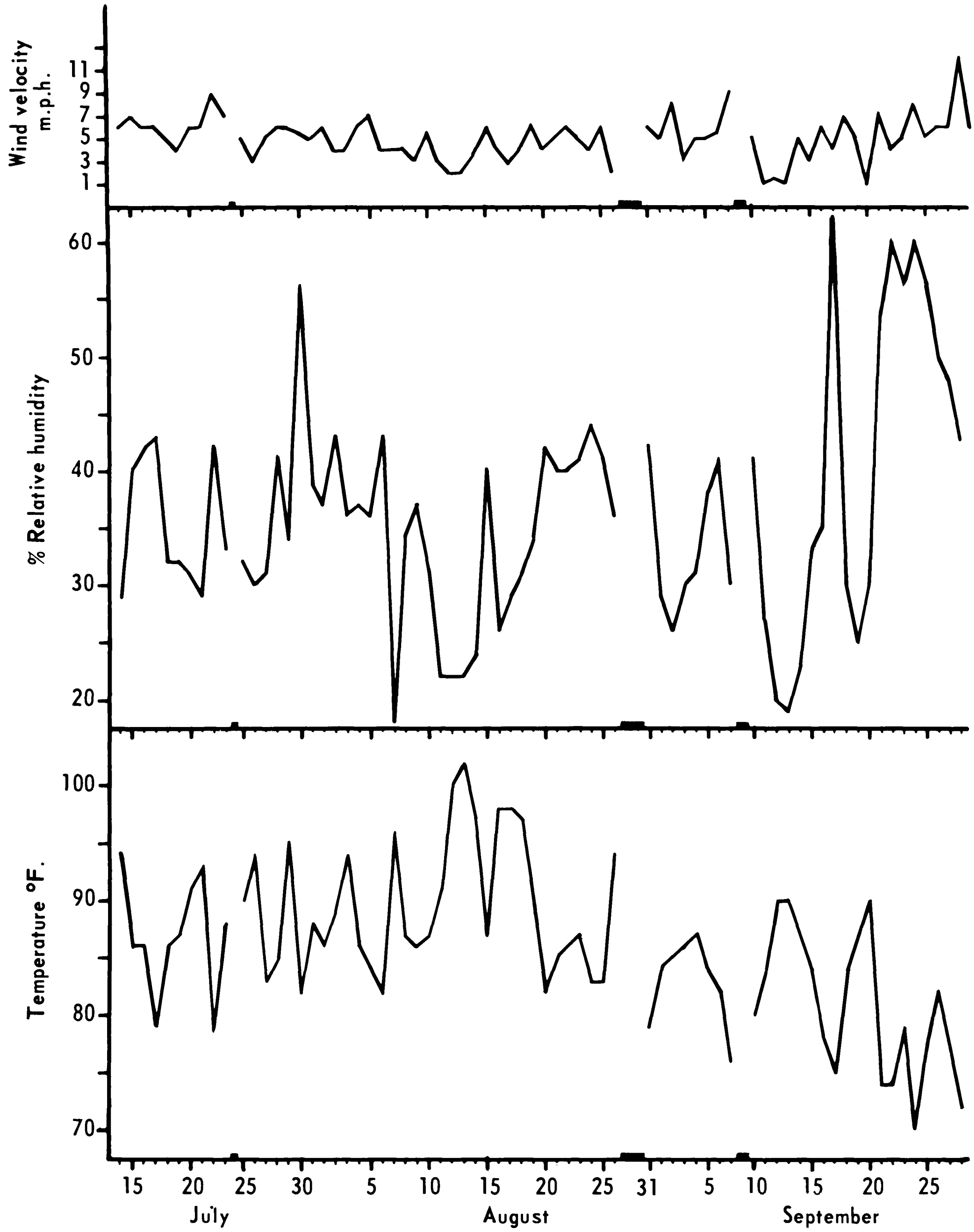


Fig. 18. Weather factors during flight period of *E. cincticollis*. Temperature and relative humidity are 7 P.M. readings. Wind velocity is the 7–8 P.M. average reading. Data from the University of California, Davis, weather station.

wings partially unfolded. None of those on the ground were seen to fly again. The initiation of flight from the top of a four and one-half foot fence post was observed. The earwig climbed to the top of this post and walked around for a few seconds. Then it raised its elytra and quickly flexed its wings and then refolded them. It again extended its wings and flew to the trap which was about two feet from the top of the post. This earwig was not observed to use its legs to aid in unfolding its wings as has been reported for *Labia minor* (Fulton, 1924). At no time were wingless or brachypterous earwigs seen around the light.

SUMMARY

Taxonomy and description. The African earwig was orginally described as *Brachylabis cincticollis* by Gerstaecker (1883) from specimens with abbreviated-tegmina from Africa. The erection of genera and species of earwigs on variable characters led to errors in the taxonomic designations of early workers. Burr (1915) ultimately separated genera of the group on the basis of genitalic differences, and *cincticollis* was placed in *Euborellia.*

Three forms of *cincticollis*—winged, wingless, and brachypterous—commonly occur in California. A few specimens with abbreviated tegmina (wingless) were encountered in California during this study, but they differed from the form of the original description which was also abbreviated-tegmined (wingless).

Geographic distribution. The African earwig has been reported from a number of locations in Africa where it is endemic. It has also been found in the Nearctic region from California and Arizona.

Life history and habits. *E. cincticollis* was collected from several fields in Yolo and Fresno counties and reared in the laboratory. Field-collected females produced and brooded several clutches of eggs in the laboratory. The clutches were deposited at two to four week intervals. The number of eggs in the first clutch averaged 23.4 with a range of 6–38 at 72°–80°F, 21.2 with a range of 17–26 at 80°–85°F, and 22.8 with a range of 10–44 at 90°–92°F. The total number of eggs produced at these respective temperature ranges averaged 83.7 with a range of 15–175, 47.2 with a range of 23–70, and 66.5 with a range of 40–112.

The average time from attaining adulthood until first ovipisition was 29.3 days (72°–80°F). The average periods of time from egg to adult at various temperatures were as follows: 128.5 days with a range of 94–200 days at 72°–80°F, 78.5 days with a range of 65–90 days at 80°–85°F, and 82.0 days with a range of 67–98 days at 90°–92°F. Field-collected adults survived as long as 240 days in the laboratory and they probably live up to a year or more in the field.

Increase in weight and linear growth (length, width) of eggs during their embryogenesis were determined. Average weight during this period increased from 0.504 mg to 1.174 mg; average length increased from 1150 to 1550 microns. The dimension and weight increases occurred almost entirely between the sixth and eighth days of the 13–14 day developmental period at 72°–80°F.

The effects of humidity on eggs and first instar nymphs were studied by exposing these stages to a graded series of relative humidities from 33 to 100 per cent. Eggs completed embryogenesis only at 100 per cent relative humidity. First instar nymphs survived longest at 97 per cent relative humidity.

The number and duration of nymphal

instars varied with the rearing temperature. Five nymphal instars (rarely four or six) occurred at 72°–80°F, and the average duration of each instar was (starting with the first) 19.9, 15.8, 17.9, 27.8, and 34.1 for an average nymphal developmental period of 115.5 days. Five nymphal instars were most common at 80°–85°F but six also occurred; the average number of days spent in each successive instar was 9.9, 10.4, 13.3, 13.5, 17.1, and 16.7 with an average developmental period of 69.7 days. At 90°–92°F six or seven nymphal instars occurred, and the average number of days spent in each instar was 11.7, 8.7, 9.9, 11.1, 13.5, 13.0, and 17.5 with an average developmental period of 74.3 days.

Effect of temperature on phenotype. The phenotypes of individuals apparently can be affected by temperature. Only wingless individuals—no winged or brachypterous forms—occurred at 72°–80°F while at 80°–85°F and 90°–92°F all three forms were produced. The percentages of each form at 80°–85°F and 90°–92°F respectively were 5.0 and 5.1 brachypterous, 11.2 and 13.9 winged, and 83.8 and 81.0 wingless. Also, there is some evidence for a seasonal fluctuation in the numbers of the different phenotypes.

Organisms associated with E. cincticollis. Two mites, *Tyrophagous* sp. and *Histiostoma* sp., were associated with *E. cincticollis* but apparently were not parasitic. No predation on the earwigs was observed except by other *cincticollis*.

Field studies. *E. cincticollis* was observed in both Yolo and Fresno counties, in several field habitats. Normally this species remains almost entirely hidden, either in the soil at a depth of about 1–12 inches or under vegetative growth. In 1967, eggs could not be found in Davis until April 25. Egg deposition was largely completed by early June in the Davis habitats but extended into July and August in an irrigated alfalfa field in Fresno County. The difference in the period of egg deposition was probably due to the drying conditions in the Davis habitat rather than to any other regional difference. Various instars can be found throughout the year; both nymphs and adults overwinter. The earwigs are found in relatively undisturbed areas (at the edges of fields, along ditch banks, or in fields infrequently cultivated) that are moist but not continuously wet. One to two generations a year are estimated to be produced in the field.

An ultraviolet light trap was operated from July 14 to October 12, 1967. The trap revealed that *cincticollis* flights occurred during the period between July 14 to September 26. Temperature, relative humidity, and wind velocity were studied in relation to flights. A combination of these factors gave an index that correlated fairly well to the numbers in the flights. Major flights did not start, however, until August 12 despite apparently favorable weather conditions prior to that date. Flights mainly occurred in the early evening, from sunset to about 10 p.m.

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