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ACHETA DOMESTICUS.

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**THE EFFECTS OF SOCIAL EXPERIENCE ON THE MATING BEHAVIOR
OF THE HOUSE CRICKET, ACHETA DOMESTICUS**

by

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of the requirements for the degree of Doctor of Philosophy, The City University
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Abstract

An experiment was done on the effects of social (tactile and visual) experience on the mating behavior of the male house cricket, Acheta domesticus. A factorial design with two variables was used. The variables were: 1) age at the time of observation and 2) type of social experience. The ages at the time of observation were 2-3 days adult (younger) and 8-15 days adult (older). The four experience categories were 1) deprived of social experience from the egg stage; 2) deprived of social experience from the last nymphal stadium; 3) deprived of social experience 2-24 hours after the final molt; and 4) group reared throughout life.

A description of the mating behavior was given.

The most obvious effects of experience concerned the occurrence of copulation. Older males in the two groups having adult social experience copulated in greater numbers than younger males with similar experience. Unexpectedly, it was found that younger males deprived in the egg or nymphal stages were as likely to copulate as their older counterparts. No differences were found among the older groups.

Of the behavior items recorded, the following could not be clearly related to the occurrence of copulation: 1) time spent near the female; 2) unsuccessful mounts by the females; 3) latency to first mount; 4) stridulation. While the younger group that was deprived during the last nymphal stadium was similar to older groups in likelihood to copulate, it differed significantly in the amount of stridulation before copulation.

All groups of younger males had longer latencies to the first copulation than did older groups. Apparently, responsiveness to sexual stimuli is lower in the younger males. It seems that social stimulation further decreases this already low responsiveness.

It was hypothesized that social deprivation affects the activity of the corpora allata which in turn affects the activity of the accessory glands.

The results of the study were compared to vertebrate studies showing positioning in regard to the sexual partner (positional orientation) to be most affected by social deprivation. Difficulties in positional orientation appeared to be common in one older and two younger deprived groups. These difficulties were expressed in failure to attach the spermatophore to the female adequately and in the number of unsuccessful mounts.

It was suggested that early maturation of individually reared animals provides a mechanism for rapidly increasing the population density.

The significance of the study and implications for research were discussed. The paper includes a review of the biology of the house cricket.

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L. INTRODUCTION

Adult mating behavior has been modified by social experience in a variety of animals (turkeys, Schein and Hale, 1959; cats, Schneirla and Rosenblatt, 1961; fish, Shaw, 1962; rats, Hard and Larsson, 1968). Arthropod courtship behavior has been found more difficult to modify (e.g., spiders, Drees, 1952; houseflies, Vogel, 1957). The work of both Drees and Vogel dealt with the stimuli that evoke aspects of the courtship sequence. However, quantitative comparisons of the behavior of the "Kaspar Hauser" (socially deprived) individuals to that of more typically reared individuals of the species were not made. It is therefore not possible to conclude that social deprivation is completely without effect in these animals.

An insect mating behavior pattern may have the capacity to be modified. One approach is to select a behavior pattern that has several distinct components. In this way, the effects of social experience may be more readily identified. As mating behavior is a type of social behavior, variations in social experience may be more likely to affect its expression than would other kinds of stimulation.

The house cricket, Acheta domesticus (Orthoptera: Gryllidae), has several characteristics that make it a suitable subject for the investigation of the effects of social experience on insect mating behavior. These characteristics are:

- 1) its mating pattern can be subdivided into three subunits of behavior, each of which has at least one component that is not present in the other two; 2) it makes sounds during mating behavior, and these sounds are seldom, if ever, made in other situations; 3) it may live either as a solitary animal or in an aggregation;

4) eggs are laid singly but close together so that there is a possibility for social experience right after hatching even in those individuals that live alone at later stages; 5) the animal and its behavior are suited for study in the laboratory.

In the present study, male house crickets were deprived of social experience at different stages during the life history. Several aspects of the mating pattern were subsequently studied, and comparisons made, to determine the effect of social deprivation on each aspect.

II. BIOLOGY OF THE HOUSE CRICKET

A. ECOLOGY

The house cricket, Acheta domesticus (= Gryllus domesticus = Gryllulus domesticus; Gurney, 1951) is a cosmopolitan, non-diapausing Orthopteran (Bastin, 1913; Chauvin, 1958; Belyaeva, 1966; Alexander, 1968a) commonly found near dwellings of man. All stages of growth may be found throughout the year (Bastin, 1913; Caesar and Dustan, 1938). Practically any type of food will be eaten if a free water source is available (Kemper, 1937; Ghouri and McFarlane, 1958; Nowosielski, 1961; Patton, 1963). It is seldom of economic importance, although at times it becomes a serious pest of irrigated crops (Ahmad and Ghouri, 1953).

B. MORPHOLOGY

The body form of the adult house cricket is that of a typical insect. The two tapering antennae are slender and longer than the entire body. Two well developed cerci project posteriorly from the last abdominal segment (Macgillivray, 1923). The two pairs of wings are distinctly different; the hardened forewings (tegmina) do not quite project to the end of the abdomen and are bent down rather sharply at the sides of the body. In males, the tegmina bear a sound-producing structure. The membranous hind wings are usually folded, projecting beyond the tegmina to form a pair of slender filaments 3 or 4 mm longer than the abdomen (Wood, 1872; Borror and DeLong, 1964).

The legs are unequal in size; the hind legs being much thicker and longer

than the more anterior pairs. The proximal ends of the tibiae of the anterior legs bear auditory organs (Kroning, 1930).

The female is easily distinguishable from the male by the presence of an elongated ovipositor. The ovipositor is used to penetrate a soft, moist substrate into which the eggs are deposited (Snodgrass, 1931).

C. METAMORPHOSIS

Metamorphosis is hemimetabolous. The immature forms, called nymphs (or hoppers), are externally similar to the adults but can be identified readily since they lack developed wings. The wings do not expand to their full adult size nor take up the adult position until after the final molt. The principal external changes during growth are in size of body and in development of wings (Imms, 1957). The auditory organs make their first appearance in the last nymphal stage, but are fully developed only in adults (Carthy, 1958).

D. SOUND EMITTING STRUCTURES

The forewings of the house cricket have become specialized as sound emitters (Haskell, 1961; Dumortier, 1963a). The lower cubital vein of the tegmen starts from a thickened spot almost one-third the length of the tegmen from the base and extends crosswise through the wing. It is marked underneath with a series of unevenly spaced, sclerotized lamellae called the file (Wood, 1872; Pierce, 1948), or *pars stridens* (Dumortier, 1963a). A portion of the edge of the wing near the file is also thickened. This structure, the scraper, can be rubbed against the file to produce stridulatory sounds. Both tegmina

bear well-developed files and scrapers (Dumortier, 1963a, b).

Typically the right tegmen lies above the left one. If the positions of the two are reversed in a mature field cricket, they return to their normal positions on their first opening and closing (Huber, 1962). On the other hand, if reversal is accomplished prior to hardening of the cuticle, the wings may remain in the reversed position (Stark, 1958; Huber, 1962). The sounds emitted by wings in reversed positions are similar to those typical of the species (Huber, 1962).

E. SPECIALIZED RECEPTOR ORGANS

The antennae combine several functions but touch and chemoreception are probably their most important functions. Alexander (1961) states that the antennae are the most important sensory apparatus used in dealing with objects at close range.

The cerci are mechanoreceptors (Sihler, 1924; Wigglesworth, 1942). Evidence has been produced to show that they have a partly auditory function (Pumphrey and Rawdon-Smith, 1936). The response is probably derived from small movements of the hair sensilla since it is abolished if vaseline is applied to the ventral surface from which they arise.

Male and female crickets have tympanal (auditory) organs (Schwabe, 1906; Wever and Vernon, 1959; Autrum, 1963) in the proximal ends of the fore-tibiae. Associated with the tympanal organ are the subgenual organ (a vibration receptor) and the intermedial (tracheal) organ whose function is unknown (Eggers, 1928; Autrum, 1963). The tibiae of the second and third legs contain the latter two organs but do not contain the tympanal organ.

The tympanal organs are the primary receptors of airborne sound. Regen (1909) demonstrated the auditory function of these organs by showing that the response to sound was lost when the organs were extirpated.

F. ACTIVITY

Both Lutz (1932) and Nowosielski (1961) demonstrated circadian activity rhythms in house crickets. These animals are least active as measured by locomotion during the light period and most active following the onset of the dark period. Lutz (1932) reported that activity of both immature and mature males and females takes place chiefly between 7 PM and midnight with a definite peak at about 9 PM when on a natural day schedule. Nowosielski (1961), however, found that last instar nymphs generally did not show as much locomotor activity as did the adults. On a light/dark 12/12 cycle, adult crickets start locomotor activity at the onset of the dark period and this persists for several days in constant darkness or constant light. Some crickets in Nowosielski's experiment had a single period of locomotor activity following the onset of darkness, while others showed a secondary "afternoon" peak prior to the onset of darkness. Both adults and nymphs showed a daily feeding and drinking rhythm. Adult male crickets exhibit pre-copulatory display at highest levels during darkness and just before its onset when on a regular light/dark 12/12 cycle (Nowosielski and Patton, 1963).

Adults can be re-entrained to reversed lighting conditions even when either the ocelli or compound eyes are blacked out, but not if both are blacked out (Nowosielski, 1961).

The effect of light on house cricket activity does not preclude the possibility of other factors influencing cyclic activity. Ragge (1965) states that the usually nocturnal house cricket is sometimes quite active during the day in hot situations and even has been observed to fly under fairly warm conditions. The activity of other Orthoptera has also been shown to be influenced by temperature (e.g., field crickets, Cloudsley-Thompson, 1958; Alexander and Meral, 1967; locusts, Chapman, 1965). From a study of factors controlling the diurnal rhythm of activity of the cockroach Periplaneta americana, Harker (1956) concluded that in most cases light or darkness is the factor that entrains the rhythm while temperature may modify but not impress it.

G. COMMUNICATION CHANNELS AND MECHANISMS

On the basis of the major receptor structures of the cricket, there may be several channels of communication. Khalifa (1950) conjectured that chemicals play a role in enhancing courtship and copulation in A. domesticus. Such chemicals have not yet been demonstrated but a chemical attractant and a pheromone-like dispersant have been found to affect the local distribution of the house cricket (Sexton and Hess, 1968).

From the activities of field and house crickets, the visual, auditory and tactile senses appear to be important senses in their reactions to each other (Alexander, 1961). There is evidence that crickets respond to the visual stimuli presented by another cricket at close range. One individual often turns or flips an antenna toward a nearby cricket, even when the two are separated by a glass partition. This response only occurs if movement is involved.

The antennae are probably the most important organs involved in tactile "communication". In constant motion when the cricket is walking or running, they immediately begin to play over the antennae or body of another cricket when encountered. Antennal contact is usually followed by sound production (Alexander, 1961).

Auditory communication is universal in members of the family Gryllidae. Only the adult males are capable of producing the sounds in a process designated stridulation. These signals can be received by either males or females. The males stridulate only after the tegmina have hardened (Alexander, 1960). Friction of the left tegmen scraper against the right file (see Morphology) on sudden closing (Pierce, 1948; Rakspal, 1960, Walker, 1962; Dumortier, 1963a; Ewing and Hoyle, 1965) of the tegmina produces a series of audible vibrations. Each closure of the tegmina produces a tone called a pulse (Dumortier, 1963b, c). A short sequence of pulses is called a "chirp". A long series of rapidly emitted pulses is called a "trill". The word "song" is loosely applied to either a trill or a long series of pulses (Alexander, 1960).

Ewing and Hoyle (1965) reported that the house cricket has four different songs based on context and pulse repetition rate. Three of these songs are distinctly different in pulse repetition rate. They are 1. calling or normal song (1-4 pulses per chirp); 2. aggressive song (1-7 pulses per chirp); and 3. mating song (more than 7 pulses in a sequence with sounds produced both on opening and closing of the tegmina). These songs also differ in 1. position of the tegmina; 2. length of pulses; 3. intensity and 4. sound frequency (Huber, 1962). The fourth song is performed during the mating sequence but sounds

like the aggressive song (Ewing and Hoyle, 1965). Isolated males usually perform only the calling song, while the courtship song may be performed in the presence of either a male or a female. The "aggressive" song in an aggressive context is usually confined to encounters between males.

Alexander (1962a) cites the effects of the various kinds of stridulation. As they may apply to house crickets, these effects are: the calling song 1) attracts sexually responsive females (Regen, 1913; Walker, 1957; Alexander, 1960; Dumortier, 1963b); 2) elicits calling by other males (Alexander, 1961; Heiligenberg, 1966); 3) may inhibit calling at close range; and 4) is mildly aggressive among males (Alexander, 1961). The courtship song in Gryllus species promotes assumption of the copulatory position (Alexander, 1960, 1961). This also seems to be its function in A. domesticus. The aggressive song elicits aggressive behavior with reciprocal aggressive stridulation among males (Alexander, 1960, 1962a). In the mating context, the aggressive song attracts the female (Dumortier, 1963b; Ewing and Hoyle, 1965).

The frequency of the acoustic emissions of A. domesticus is in the range of 4,500 cycles per second (Busnel, 1953; Alexander, 1961). The calling song measured in the laboratory at a distance of 60 cm reaches an intensity of about 47 dB (Busnel, 1955). The aggressive song is more intense while the mating song is much less so (Ewing and Hoyle, 1965).

Cricket song and characteristic behavior are evoked by sensory impulses from the auditory organs, antennae and eyes. Both Alexander (1961), and Heiligenberg (1966), have shown that stridulation can be elicited by auditory stimuli alone. In field crickets the winners of aggressive encounters begin to

stridulate when the subordinate is no longer being touched by the antennae (Alexander, 1961).

H. REPRODUCTION

1. Sperm Production and Spermatophore Structure

Spermatozoa are produced in the follicles of the testes and are stored in the seminal vesicles until mating (Davey, 1965). Spermatogenesis in A. domesticus and several other species of crickets occurs mainly in the last three nymphal instars (Randell and Kevan, 1962; see also Davey, 1965). In the absence of Vitamin E in the last nymphal stadium spermatogenic activity is disrupted, the result being a drastic reduction in the number of sperm produced (Meikle and McFarlane, 1965). This vitamin affects the transformation of spermatids to spermatozoa.

The sperm are not conveyed to the female in a free fluid, but are enclosed in a membranous sac or "spermatophore" which is formed by the secretions of the adult male accessory glands (Wigglesworth, 1942; Khalifa, 1949, 1950). Formation of the spermatophore in A. domesticus is similar to that of Oecanthus which was described by Hohorst (see Wigglesworth, 1942). The atrium of the male system is first distended with the mass of sperm. Numerous accessory ducts then pour out their secretion, forming a covering like the shell of an egg (also see Chopard, 1961). The soft mass is driven by peristalsis into the cavity of the epiphallus (Chopard, 1961) or spermatophore mold (there is no intromittent organ). This first section of the spermatophore to be formed, the ampulla, is normally protected by two muscular flaps which almost cover it. The

spermatophore is nevertheless visible when present in the mold. Finally the terminal capillary tube and handle are formed by the secretion flowing into the genital groove and there rapidly hardening. Only the neck of the completed spermatophore is introduced into the spermathecal spout of the female; the spermatophore is anchored there by the lateral extensions of its handle which fit exactly on the base of the ovipositor from the ventral side.

Khalifa (1949) has described the structure and mode of action of the spermatophore. It consists largely of protein and contains no chitin. Its long capillary tube terminates in a pointed closure. The ampulla is at first white and of a very soft, viscous consistency but becomes glassy after about an hour. Sometime afterwards it becomes very hard and brittle. The wall of the ampulla has four layers: an outer thin layer, a transparent membrane, a proteinaceous pressure body and an inner layer.

When the closure at the tip of the capillary tube is removed, an evacuating fluid passes osmotically from the interior through the inner layer into the pressure body (see also Regen, 1924). The pressure exerted by the swelling of this body causes expulsion of the sperm. This process ordinarily occurs only when the spermatophore has been transferred to the female. The evacuating fluid dries up and is no longer functional if a spermatophore is kept in its mold for a long time. The spermatophore is emptied of sperm soon after it has been inserted into the spermatheca. Khalifa reports that this process is completed in less than one hour.

According to Khalifa (1949, 1950), a young male produces two or three spermatophores a day. Even castrated Gryllus males are capable of producing

and transferring empty spermatophores during copulation (Regen, 1910).

2. Egg Production and Oviposition

The shells of the cylindrical white eggs are the products of the follicular cells in the ovary (McFarlane, 1959; McFarlane, Ghouri and Kennard, 1959; McFarlane and Kennard, 1960; Davey, 1965). After copulation, the mature eggs are carried by peristalsis through the oviducts, pass the opening of the spermathecal duct where fertilization occurs, to the vagina (Wigglesworth, 1942; Davey, 1965). From the vagina the eggs pass singly down the elongated ovipositor. Ovipositional movements are under control of the last abdominal ganglion and are inhibited by centers in the esophageal ganglion (Roeder, 1963).

Copulation occurs one or more days prior to oviposition. However, females will not oviposit until they find a moist surface on which they can obtain footing and insert their ovipositors (Ghouri and McFarlane, 1958). The usual method of obtaining eggs for experimental purposes is to provide females with a dish of moist sand (Carothers, 1923; Browning, 1952; Stone, 1953; Ghouri and McFarlane, 1958). Eggs laid in moist surroundings absorb water through their cuticular membranes during the stage when the serosa surrounds the embryo and yolk (McFarlane, 1959; McFarlane, Ghouri and Kennard, 1959; McFarlane and Kennard, 1960).

Experimental study of the corpora allata indicates hormonal control of egg production. Removal of the corpora allata prevents egg production by terminating development of the sexual glands of A. domesticus females beginning at the stage of yolk deposition in oocytes. Females with implanted corpora allata

exhibit earlier and more intensive oviposition when compared with controls (Belaeva, 1966). This probably reflects earlier and increased maturation of eggs. In reviewing experiments on the role of the corpora allata, Hagadorn (1967) concluded that the corpora allata produce a gonadotropic hormone which acts on ova and follicle cells to promote formation of protein yolk and that the median neurosecretory cells of the brain, apart from their allatotrophic effect, may influence vitellogenesis by acting on protein metabolism.

Ghouri and McFarlane (1958) presented mean fecundity values for female house crickets. The mean preoviposition period is 10 days at 28° C and 5 days at 35° C. At both temperatures the oviposition period is about 35 days. Withholding vitamin E causes the preoviposition period to be lengthened and fewer eggs to be laid (Meikle and McFarlane, 1965). If the lipid contained in 2% wheat germ oil is withheld, eggs which will not hatch are produced (Ritchot and McFarlane, 1961). The female's reproductive life ends about 6 weeks after the final molt (Ghouri and McFarlane, 1958; see also McFarlane, 1967).

Temperature also affects the mean number of eggs produced by females; the number being greater at 35° C (1060 eggs) than at 28° C (728 eggs), (Ghouri and McFarlane, 1958). The total number of eggs can be quite variable. Kemper (1937) found the number to range from 40 to 170 while Stone (1953) obtained as many as 2600 offspring from one female during a 90-day adult stage. These differences most likely reflect variations in rearing conditions and methods of handling (including egg collection) (Ghouri and McFarlane, 1958).

I. DEVELOPMENT

The house cricket develops in 11 days at 35° C (Ghouri and McFarlane, 1958). At lower temperatures a longer time must elapse before hatching takes place. The number of stadia through which an individual passes is variable, ranging from as few as 7 (Schmidt and O'Brian, 1966) to as many as 16 (Rummel, 1963). Ghouri and McFarlane found 7-8 nymphal stadia at 28° and 8-9 at 35° C. Duration of the nymphal stage likewise varies, ranging from 30 days (Stone, 1953) to 165 days (Busvine, 1955). Each succeeding nymphal instar is slightly larger than the preceding one. The wing pads become visible in the penultimate instar (Ghouri and McFarlane, 1958). The variations in the number of stadia may be attributed to differences in rearing conditions.

Temperature exerts a dramatic influence on developmental time. The optimum temperature for rapid development lies between 32° and 35° C (Stone, 1953; Busvine, 1955; Ghouri and McFarlane, 1958). At higher temperatures the rate is slower and mortality is extremely great (Ghouri and McFarlane). At 28° mortality is essentially the same as at 35° but developmental time increases. The developmental rate is also affected by the type of food given. Nutritional deficiencies show up as high mortality of young nymphs, failure to grow, failure to develop and a high incidence of malformed wings (see Patton, 1963). Omission of either thiamine, pyridoxine, nicotinic acid, pantothenic acid, choline or biotin results in very poor growth and little or no survival to the adult stage (Ritchot and McFarlane, 1961). Lack of folic acid results in a significantly longer nymphal stage and in greater mortality towards the end of that period

(Ritchot and McFarlane). Commercial dog, fish, rabbit and unmedicated chick food all constitute satisfactory diets. The addition of medication or mold inhibitor retards growth (Patton, 1963). Lack of riboflavin or inositol also retards growth but a large percentage of nymphs fed on such a deficient diet do reach the adult stage (Ritchot and McFarlane, 1961).

Nymphs obtained from old females develop more rapidly when reared in groups than when reared singly, (Chauvin, 1958; McFarlane, 1962, 1966 b). At 29° C singly reared males have a mean larval stage duration of 71.8 days while group reared males have a mean of 65.7 days (McFarlane, 1966 b). The effect is temperature dependent, being less noticeable at 35° C. Methyl linolenate (a fatty acid ester chemically similar to described pheromones) absorbed on filter paper stimulates growth and development of singly reared larvae but not of group reared larvae (McFarlane, 1966a). Vitamin E added to the diet stimulates the growth of males and especially that of singly reared males (McFarlane, 1966a).

J. SOCIAL BEHAVIOR

The cricket has been found living singly as well as in aggregations (Galli-Valerio, 1930; Caesar and Dustan, 1938; Alexander, 1962b, 1968a). When the male lives alone, it is reported that he becomes aggressive (Heiligenberg, 1966; Alexander, 1961, 1968a). During circadian periods of increased activity, he engages in the calling song. This stridulation decreases or terminates after several hours of almost continuous song. If, while "calling", he is contacted by another animal that does not repel its advances, he shifts to the courtship song (Alexander, 1962a). Group-living males stridulate at any time during a

circadian period, but the stridulatory activity is increased during the early part of the dark period. Alexander (1968a) states that there is a decrease in calling stridulation by group living males.

Although calling stridulation sounds alone can induce males to stridulate (Heiligenberg, 1966), there is no alternation or synchronization as in some other cricket species (e.g., the snowy tree cricket, Walker, 1969; also see Dumortier, 1963b).

The mating act is preceded by a courtship phase during which the male orients his head away from the female and performs the courtship song. Copulation takes place after the female approaches the male from behind and mounts him. The spermatophore is then attached so that it projects externally from the female (Khalifa, 1949, 1950; Alexander, 1961, 1968a).

When the female dismounts, the male assumes a position near and with his head oriented toward the female. This position, called "watching" by Khalifa, (1950) does not prevent the spermatophore from being removed by the female, but apparently serves the function of maintaining the association for further copulation (Khalifa, 1950; Alexander, 1968a). The two animals remain in close proximity in the watching position until another round of mating behavior is initiated.

Although it is generally assumed that house crickets establish a territory and form dominant-subordinate relationships as the field crickets do (Alexander, 1961, 1968a), experimental proof of the existence of these two phenomena has not been reported in the literature.

III. METHODS AND PROCEDURES

A. METHODS

The present behavioral study was designed to test the effects of social experience on the adult mating behavior of house crickets. The social experience of only one sex, the male, was experimentally manipulated. The male sex was chosen because, under natural conditions, males initiate the encounters that result in copulation. Furthermore, the mating behavior of the male is more easily observed and identified than is that of the female.

The deprivation type experiment was used. Laboratory conditions were such that only the effects of visual and contact stimuli emanating from conspecifics could be controlled. Social experience with these two types of stimuli could be minimized by rearing individual animals (i. e. , separated from all others).

It was not experimentally feasible to separate animals at the beginning of each nymphal stage. As a result of preliminary investigations, the decision was made to select certain developmental stages for the experimental manipulation of social experience. These stages were: 1) egg stage; 2) last nymphal stadium; 3) adult. Individuals in this last stage were further assigned to one of two groups--one having very little social experience as adults and the other having no intentionally induced deprivation of social experience. Thus there were four main experimental groups.

Adults have been said to become mature about a week after the final molt (Alexander, 1961). In order to examine the effect of social experience on sexual maturation, further experimental categories were necessary. Each of the four

main experimental groups was further divided into two observational groups at final molt--one observed two days after reaching adulthood and the other observed one to two weeks after becoming adult.

The experiment was cross-sectional, and each subject was tested only once in a mating situation. A longitudinal study would have required many control groups in order to permit analysis of the effect of testing. As the role of experience in cricket mating behavior had not yet been studied, the decision was made to determine first whether or not social experience influences this behavior.

Therefore, some preliminary investigations were carried out to determine the experimental variations that could be most reliably and validly employed. The observations were done at 22° C. The commercially obtained subjects were kept in the laboratory at 34±1° C on a light/dark 12/12 hour natural day schedule. Variations in age and social experience produced differences in the expression of certain aspects of sexual behavior. Young adult males (2-3 days) were found to be unlikely to produce spermatophores as often as old adult males (8-15 days) and still less likely to transfer those spermatophores that were formed. However, young males deprived of social experience from late nymphal stages transferred or produced spermatophores in more cases than did those deprived as adults or kept in groups. Old males deprived in late nymphal stages or early adulthood differed from those kept in groups both in having longer latencies to spermatophore transfer and in the transfer of fewer preformed (i. e., present when the female was presented to the male) spermatophores. Latencies to successful mountings by females placed with old males were shorter if the males were group-reared than if the males had been socially deprived. Old males

deprived from late nymphal stages stridulated more during the observation period than did group-kept males.

B. EXPERIMENTAL DESIGN

A factorial design was used to investigate the effects on social behavior of two variables--age at the time of observation and type of social experience. The eight experimental groups are shown in the following diagram.

<u>Type of social experience</u>	<u>Age at the time of observation</u>	
	2-3 days adult	8-15 days adult
Deprived of social experience from the egg stage	N=15	N=15
Deprived of social experience from the last nymphal stadium	N=15	N=15
Deprived of social experience 2-24 hours after the final molt	N=15	N=15
Group reared throughout life	N=15	N=15

C. PROCEDURE

1. Subjects

a. Colony

The animals used were first generation progeny of stock obtained commercially from Fluker's Cricket Farm, Baton Rouge, Louisiana. On receipt,

the crickets were separated according to age and sex (if identifiable). All animals that were adult on arrival were discarded. The remaining nymphs were subsequently used as parental stock.

b. Eggs for experimental groups

A specific receptacle for oviposition was not provided. Because of the lack of a more suitable substrate, females oviposited in or under the moist filter paper of the water vials (see Feeding Regime). The eggs laid between the filter paper and the plastic disc could be collected easily by simply removing the vial and the filter paper. The eggs, adhering to either the disc or the filter paper, were picked up with a fine, moistened camel's hair brush. Although the use of filter paper rather than moist sand was found to be an extremely easy method of collecting and separating eggs, a distinct disadvantage of this method was that adults chewed away the filter paper and ate many of the eggs. Daily changing of the filter paper reduced the number of eggs lost in this manner. When eggs were needed for experimental rearing, collections were made daily.

2. Cages

The stock cages were plexi-glass containers 30 x 23.5 x 20 cm high and were covered with a wire mesh screen. Other cages were of two sizes. Large translucent containers 12 x 18 x 2.5 cm high were used for keeping large nymphs and adults. Small translucent containers 8 x 8 x 13.5 cm high were used for keeping small nymphs. To insure air circulation and to prevent the humidity from being too high the covers of these containers were perforated.

3. Environmental Control

A temperature of $34 \pm 1^{\circ}$ C was maintained in the incubators where the

cages were kept. The incubators were standard laboratory floor models. An open dish of water prevented the air from getting dry. The light/dark cycle was controlled by an electric timer set to make the dark period fall between 9 AM and 9 PM. This made it possible to make observations during the time when the crickets were most active (Nowosielski, 1961).

The light source was a 15 watt fluorescent lamp suspended from the top of the incubator.

No attempt was made to control vibratory or chemical stimuli impinging on the animals. Not only did they receive vibrations and air-borne chemicals from a variety of sources, but they were also exposed to sounds and odors arising from other crickets. The opacity of the rearing cages prevented the experimental males from seeing conspecifics other than those in the same cage.

4. Feeding Regimen

Food and a source of water were continually available.

All animals were fed on commercial rabbit food pellets that had been pulverized in a blender and placed in petri dishes.

The house cricket requires a source of free water or a food high in water content (Ghouri and McFarlane, 1958). Although most investigators (e.g., Ghouri and McFarlane; Chauvin, 1958; Alexander, 1961) supply water in inverted vials stoppered with absorbent cotton, this method was found to be unsatisfactory when containers with plastic lids were used because of rapid growth of mold on the rabbit food and the occasional drowning of young nymphs in spilled water. Consequently, in containers with plastic lids pieces of fresh apple were used as the free water source. In stock cages, water vials were inverted on plastic

discs that were covered with filter paper. Food and water were replenished every 2-3 days.

An initial effort to rear the crickets from hatching on an apple diet resulted in retardation of development. After 4-1/2 months on this diet, one animal became a miniature adult. (The typical period for maturation of animals under the given conditions but on a rabbit food diet is two months.) Unfortunately, this animal died a couple of days after ecdysis. Mortality of nymphs on the apple diet seemed to be slightly higher than that of nymphs of the same age reared on rabbit food, but no data were kept.

5. Handling

To reduce the number and kinds of stimuli experienced, the subjects were handled as infrequently as possible. Food was introduced and removed with long-handled forceps. In this manner it was easy to see what was being done and to avoid touching the animals. When it was necessary to transfer animals to another cage, they were either emptied directly from one receptacle to another or picked up in a small vial. The cages were always returned to the incubator as quickly as possible.

6. Cleaning of Cages

When animals were removed, the containers were thoroughly washed with hot water. The containers were then left to air-dry for a minimum of 24 hours, with the usual period being more than 48 hours. Hot water was sufficient to remove any visible dirt and at least some of the chemicals that may have been left by the previous occupants (Sexton and Hess, 1968). Twenty-four hours were deemed sufficient for residual chemicals to reach a concentration as

low as that of the surrounding air.

7. Rearing of Animals

About a week after the final molt, the stock animals were mated in a group cage. Despite Chauvin's observation (1958) on the slower growth rate of the progeny of old mothers, no attempt was made to control parental age. Adults were discarded within 2 months after the final molt because of a scarcity of space.

Eggs were placed singly or in groups of three in moist sand in small vials. These vials were in turn put in well-covered containers and incubated. Within a few days after hatching, nymphs were transferred to the 8 x 8 x 13.5cm containers. In about the penultimate nymphal instar, they were transferred to the larger containers where they were kept until the time of the experiment. The original group size (1 or 3) was maintained as long as indicated by the experimental design. If a group decreased in size (because of a death or removal of a female), it was either again brought up to its original size (3 animals) or discarded.

Observations of growth were made daily at the same time of day. Adult males were deprived from the first day after their imaginal molt. Thus, they were less than 24 hours adult when isolated. When nymphs were isolated, they measured at least 14mm and had well developed wing buds. These characteristics are typical of the final nymphal stadium.

All group reared animals kept together were of approximately the same age.

Females were removed as soon as they were identified (about the 4th

nymphal stadium) to a plexi-glass cage containing only nymphal females. During the 24 hours following emergence as adults, adult females were separated from nymphal females and always kept with at least 2 other females.

8. Observation Incubator and Mating Chamber

In order to observe the animals at rearing temperature, ($34 \pm 1^{\circ} \text{C}$), a Blue M brand bacteriological incubator was used as an observation chamber. The temperature was measured by a thermometer inside the incubator at the level of the mating chamber. The interior of the incubator measured 43 x 47 x 68 cm high. A grid-type shelf, placed 21 cm above the floor of the incubator, supported the mating chamber. A 15 watt fluorescent lamp provided light for the observations which were made through a mirrored one-way glass covering the entire front of the observation chamber.

The experimental mating chambers were commercially obtained, hard, clear, plastic pitchers with a floor area measuring 12 x 13 cm. The bottoms were marked into square centimeters in order that distances between male and female could be approximated. The pitchers were covered with an opaque plastic lid.

9. Observations

Animals selected for testing were of normal size, with all legs, both cerci and at least one antenna intact. No other selection criteria were used. All observations were made during the dark period (the cricket's "night").

The experimental male was removed from the rearing incubator and introduced to the mating chamber directly from the rearing cage. The mating chamber was placed in the observation site 20-30 minutes prior to the beginning

of the observation.

The female was then removed in a shell vial from her rearing chamber and immediately introduced into the mating chamber. The observation period began at this time. At the end of the observation period the pair was discarded.

All females used were 8-15 days adult. The young males were less than 72 and more than 48 hours adult. The older males were 8-15 days adult. None of the experimental animals had had mating experience.

Observation periods were 120 minutes long because preliminary investigations had shown that most old males mate within this period.

10. Data Recording

An Esterline-Angus event recorder moving at the rate of 2.5 mm/min. was used in recording data. The following data were recorded: a) occurrence of any type of stridulation, b) mounts, c) spermatophore transfer, d) observance of a new spermatophore, e) orientation of the male's head with respect to the female, i) loss of spermatophore, j) fate of spermatophore, and k) distance of the male from the female.

11. Definitions of Behavior Items and Measures

Behavior items and measures were defined or identified as follows:

The time of introduction of the female to the test chamber began the first minute of observation.

Latency was timed by noting the first minute in which the item under consideration was noted. The exact latency in minutes and seconds was not recorded.

As it was not always possible for the experimenter to hear the

stridulatory sounds, any wing movement in the manner of stridulation was identified as stridulation.

Any instance of a female climbing on top of a male after approaching him from behind was considered a mount.

Spermatophore transfer and copulation were considered identical. This was considered to have occurred whenever a spermatophore was transferred out of the spermatophore mold during a mount.

Formation or production of spermatophore was identified as the sliding of a newly formed spermatophore into the mold.

A pre-formed spermatophore was defined as a spermatophore present in the spermatophore mold when the observation period began.

Extrusion of a spermatophore was defined as the pushing out of the spermatophore prior to the transfer.

When the distance between male and female was approximately 3 cm or less, the male was designated as being near the female. This was a distance which permitted antennal contact.

The female removed the spermatophore if she pushed it off with her legs or removed it with her palpi. After removal, females sometimes eat spermatophores. Manipulation of the spermatophore with the palpi was considered equivalent to eating it.

12. Abbreviations Used

The following abbreviations were used for the experimental groups:

O - Males observed when 8-15 days adult (O= older)

EO - Older males deprived of social experience from the egg stage

- NO - Older males deprived of social experience from the last nymphal stadium**
- AO - Older males deprived of social experience 2-24 hours after the final molt**
- GO - Group reared older males**
- Y - Males observed when 2-3 days adult (Y= younger)**
- EY - Younger males deprived of social experience for the egg state**
- NY - Younger males deprived of social experience from the last nymphal stadium**
- AY - Younger males deprived of social experience 2-24 hours after the final molt**
- GY - Group reared younger males**

IV. RESULTS

A. MATING BEHAVIOR

1. Typical Mating Behavior

On the basis of the data gathered, the following is a description of the typical mating behavior of the cricket tested at $34 \pm 1^{\circ}$ C. This behavior sequence may be divided into three phases: pre-copulatory, copulatory, and post-copulatory.

a. Pre-copulatory behavior

On introduction to the test chamber in which the male had been for 20-30 minutes, the female rarely remains stationary for more than 10 seconds. She usually begins to walk around immediately. Frequently, the male is also walking at this time. Locomotion of the two crickets most often results in bodily contact in less than 30 seconds after introduction of the female. Subsequent behavior depends upon the responsiveness of both the male and the female.

Stridulation usually does not begin immediately upon contact but generally has a latency of 10 seconds to 3 minutes. Sometimes the first stridulatory sounds are clearly of the calling type and sometimes of the courtship type. At other times it is not possible to distinguish the type of stridulation by the human ear. The first kinds of sound emitted by males old enough to be fully mature seem to bear no relation to either success in copulation or copulation latency. A few young adult males respond to contact with the female by stridulating loudly in the manner of the aggressive song. Occasionally, these males copulate later. Wing movement in the courtship song position (Fig. 1) always

precedes a successful mount (i. e. , copulation). Sometimes wing movement does not produce sound audible to the human ear.

A walking cricket always moves its antennae in such a manner that most objects in front of it will be touched by the antennae. Therefore, the initial contact between the male and female involves antennal contact. The crickets moved backward only after an object was contacted. If the female contacts the male from behind, he usually lowers his body (Fig. 1) from the normal position (Fig. 2) and begins courtship stridulation. If the male contacts the female from behind, he generally moves his antennae over the female's body in an action called "antennation". Following this, the sexually responsive male moves so that the tip of his abdomen is oriented toward the female. He then begins to stridulate with antennae spread and turned lateral (Fig. 1). Head-on contact (Fig. 3) is sometimes followed by a short period when both animals remain still. The male may stridulate at this time. The male then turns to assume the abdomen-to-female (pre-copulatory) position (Fig. 1).

After the male takes the pre-copulatory position, he begins to stridulate, usually maintaining contact with the female. Fig. 4 presents, in diagrammatic form, the flow of pre-copulatory behavioral events .



Fig. 1. Pre-copulatory position. Female has contacted male from behind and has moved slightly to the side. His body is somewhat lowered. Note the spread antennae, the bent thorax, the opened hind wings and the posteriorly pointing cerci.



Fig. 2. Male in normal position. The abdomen tip is raised despite the fact that the spermatophore mold is lowered. The antennae are forward, the cerci held at the usual angle, the hind wings closed and the forewings in resting position.



Fig. 3. Head-on contact. Both animals are temporarily stationary and the male is not stridulating.

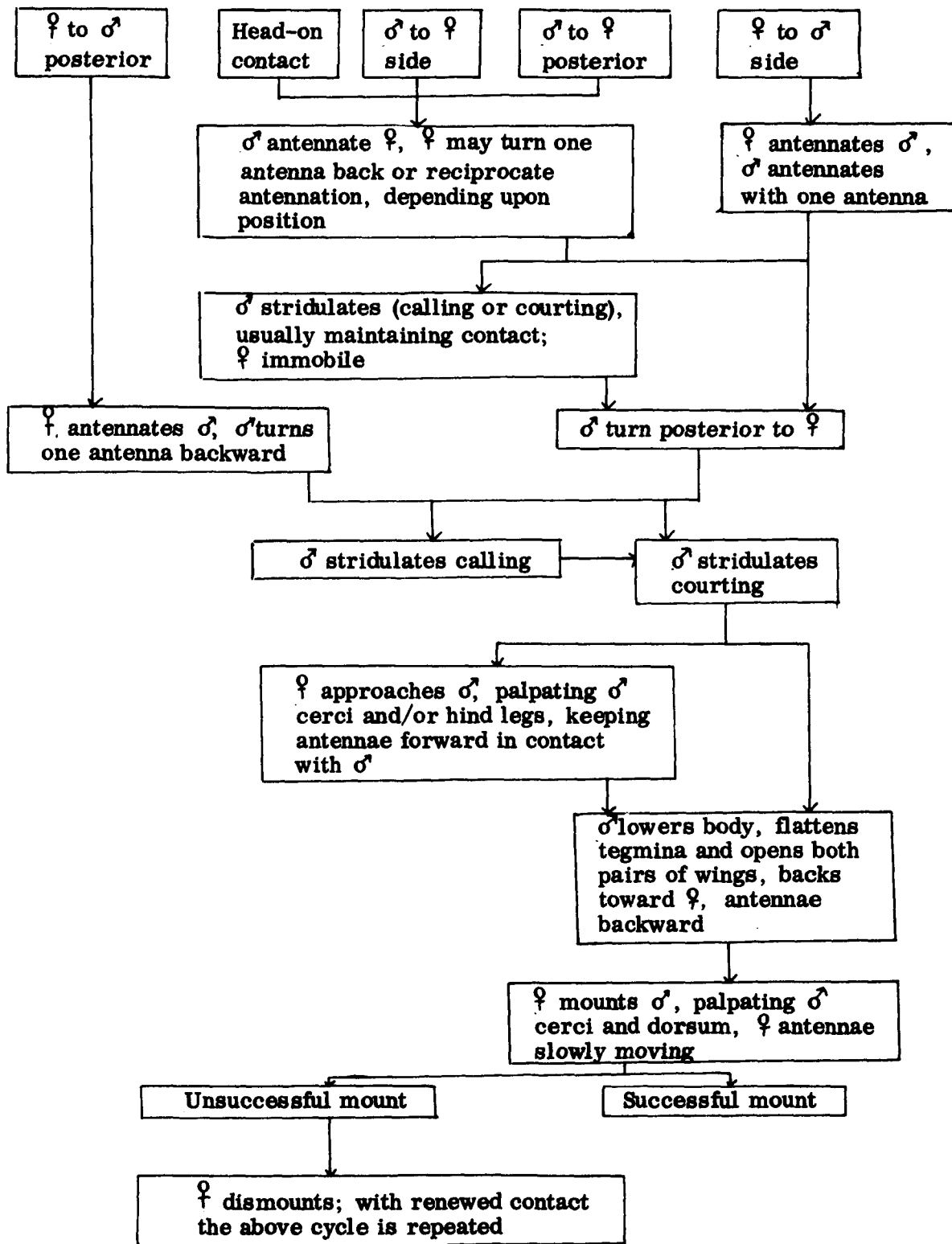


Fig. 4. Pre-copulatory behavior of a sexually responsive pair of crickets.

b. Copulatory behavior

Copulatory behavior occurs when a female starts to mount a male. Although mounts are sometimes unsuccessful, copulatory behavior usually involves spermatophore transfer. The male lowers his body, and the female approaches, palpating his cerci and/or hind legs and keeping her antennae forward and almost horizontal. Occasionally, she antennates the male. As she moves forward (Fig. 5), the male moves his hind wings so that they rest on either side of his body (Figs. 1 and 5). His cerci point straight posteriorly (Figs. 1 and 5) as he moves slowly backward, gently swaying. As the female mounts, she palpates his cerci and dorsum. When the female is about half-way on the male, his abdomen and cerci contact her abdomen and immediately turn upward, exposing the spermatophore. The male then moves backward and side-to-side, and this facilitates engagement of the epiphallic hook with the subgenital plate. Immediately upon engagement of these structures, both animals become immobile while the spermatophore is transferred.

In the copulatory position the male's body almost touches the substrate but the tip of the abdomen is sharply upturned (Fig. 6). His antennae are brought closer together and turned upward, almost forming a 90° angle to the body. The female's head is bent downward and her antennae are spread.

After the spermatophore has been transferred, the male disengages the epiphallic hook, raises his body and returns his abdomen and antennae to a more common position (Fig. 7). The female relaxes her antennae and raises her head. They usually remain in this position for several seconds longer.



Fig. 5. Female beginning to mount male. The female is beginning to palpate the male's dorsum, while holding her antennae forward. His antennae are hold obliquely backward and the wings are open.

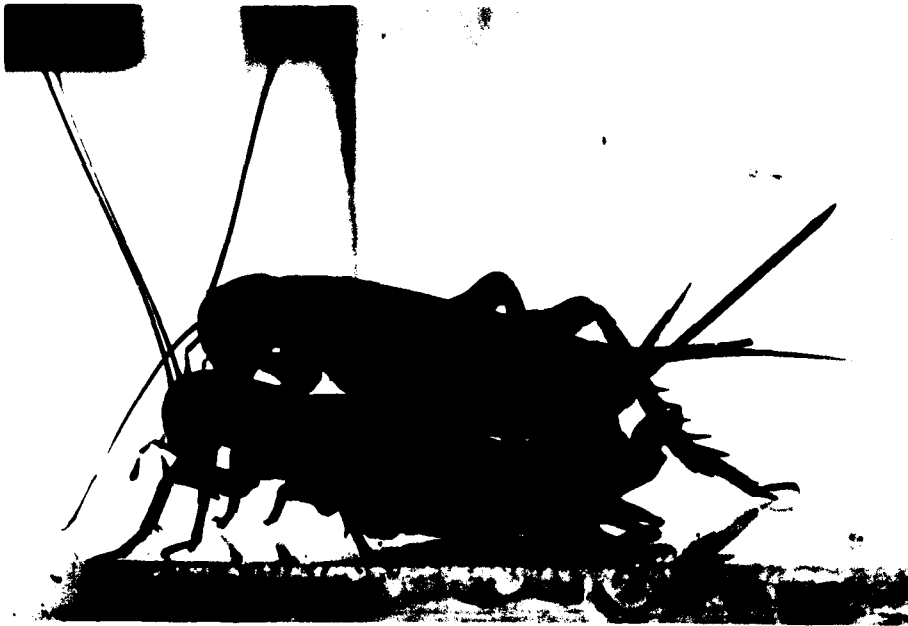


Fig. 6. Copulatory position. The male's mid-abdomen almost touches the substrate and its tip is sharply upturned. The antennae are close together and held erect. Note the extruded spermatophore which is being transferred.

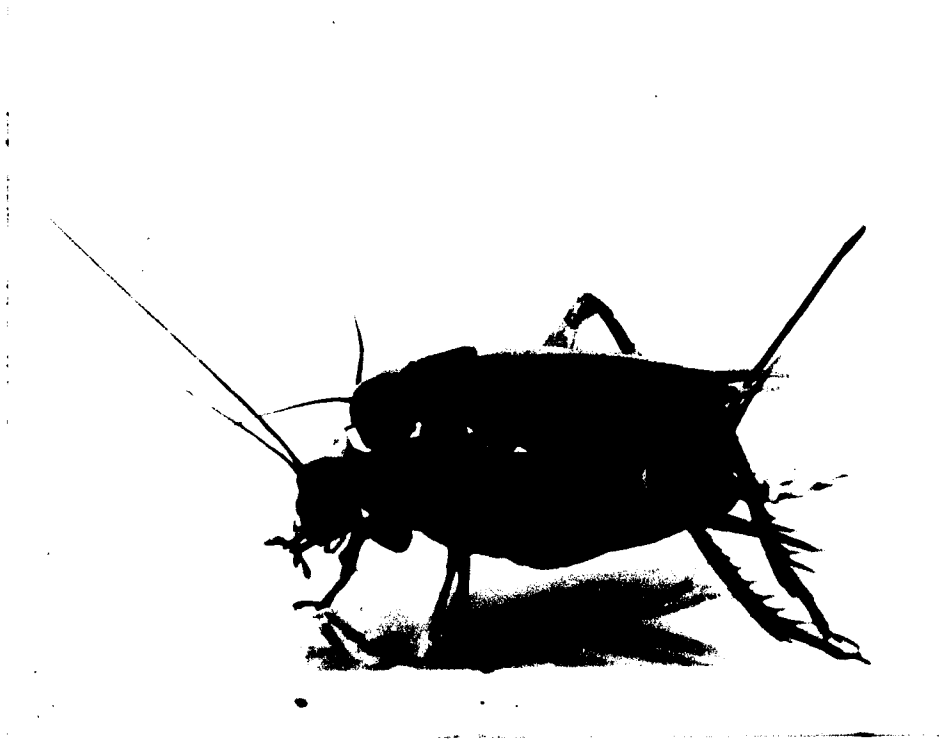


Fig. 7. End of copulation. Although the spermatophore has been transferred, it is not clearly visible. The male has raised his body and returned the antennae to a more common position. The female has not yet raised her head or begun to dismount.

Commonly the female is the first to move away and sometimes even before disengagement. Occasionally, the male walks out from under the female.

Some mounts are abortive because the animals fail to position themselves properly. In such cases the male usually resumes pre-copulatory behavior.

c. Post-copulatory behavior

After a successful mount, the animal which ends the mount usually moves just far enough for the female to no longer be on top of the male. They both then remain stationary. Within a few minutes, the male orients his head toward the female with one antenna resting on the female (Fig. 8). Even if he is parallel to the female similar to Fig. 9, his antenna usually touches her. Although the spermatophore is generally on the female at this time (Fig. 10), this behavior takes place even if the spermatophore is attached to the male's wings. It is also observed before copulation when mature males are tested at 22° C.

About 10 min. following copulation, the male lowers the epiphallus and a newly formed spermatophore slides into the mold (Fig. 11). Orientation toward the female continues for 30 minutes or more. Post-copulatory behavior is followed by another bout of pre-copulatory behavior. The spermatophore is removed by the female using the legs, palpi and mandibles. This occurs either during post-copulatory behavior or while the male is showing pre-copulatory behavior. Sometimes the spermatophore simply is dropped to the substrate (Figs. 11 & 12); at other times it is eaten by the female.



Fig. 8. Post-copulatory orientation toward the female. The male's head is toward the female with the antennae touching the female. The male's wings and cerci are in the usual position.



Fig. 9. Post-copulatory orientation toward the female. Even though the male is not at right angles to the female, his antenna is in contact with her.

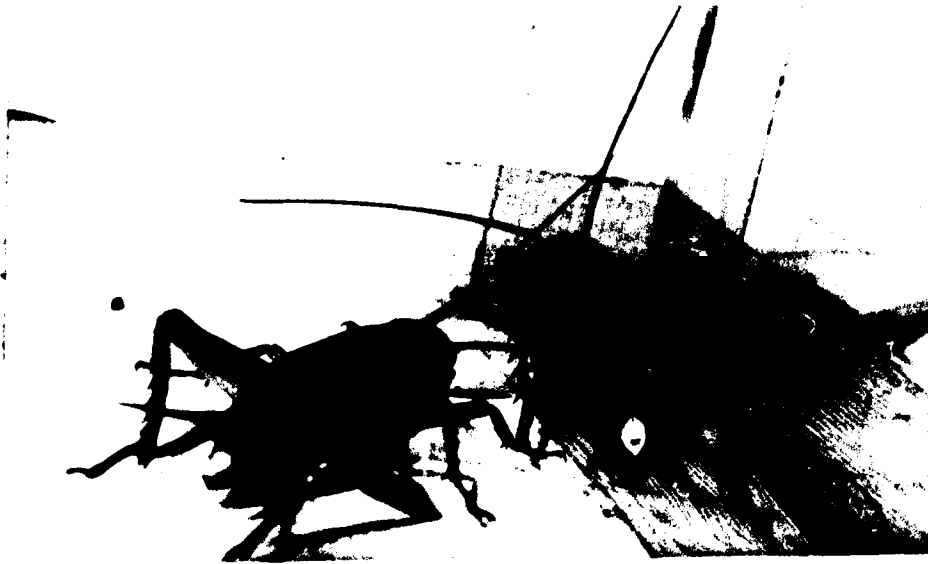


Fig. 10. Spermatophore attached to female. The clearly visible transferred spermatophore is attached to the female. The male, in the post-copulatory position, has formed a new spermatophore but has not retracted it into the body.



Fig. 11. A newly formed spermatophore. The spermatophore has just been formed and projects beyond the spermatophore mold. The female has lost the previously transferred spermatophore which is visible in the foreground.

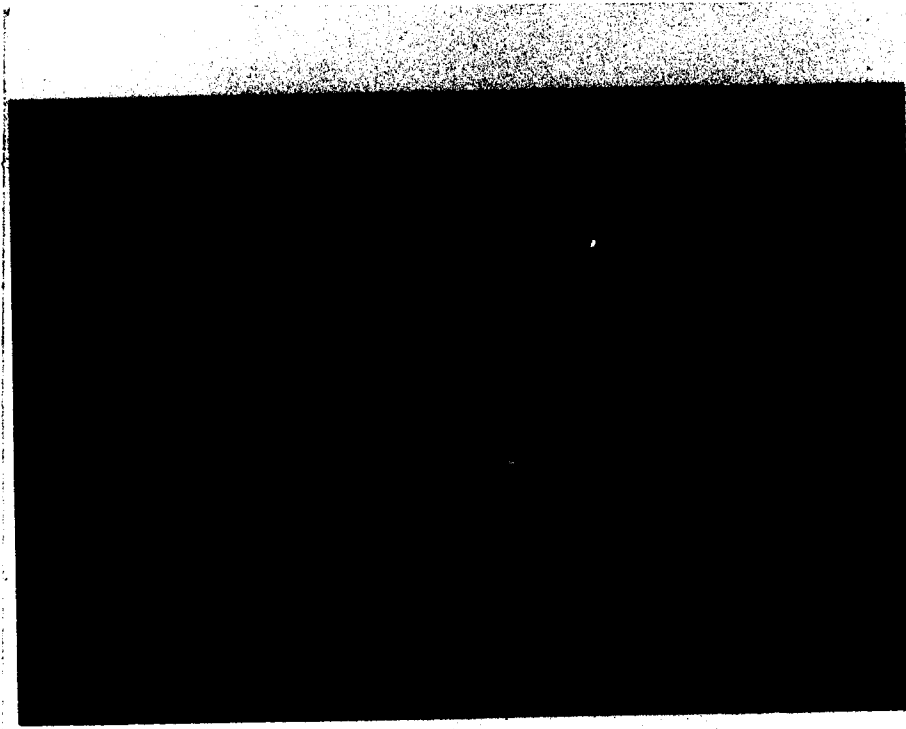


Fig. 12. A spermatophore that dropped to the substrate soon after transfer.

2. Behavior of Males Showing Poor Sexual Response

In the presence of a responsive female, some males initially are sexually non-responsive. This is most often observed in very young adult males. After initial contact, both animals might remain immobile, with or without antennation. If the female begins to mount, the male raises the abdomen very high and/or walks away. Sometimes the female follows the male. At any point either of the animals might become immobile and no further interaction takes place for a while. The male may shift to responsive behavior, or the female may shift to non-responsive behavior. A few males--both younger and older adults--demonstrate no observable mating behavior. The possible interactions between a responsive female and a non-responsive male are shown in Fig. 13.

3. Behavior of Females Showing Poor Sexual Response

Although most females are initially responsive, a few show a poor sexual response. When contact is made, a non-responsive female either remains immobile, or she antennates the male. Whatever the male response, she frequently walks away. Sometimes these females even walk over the males. (Such an approach to the male can be from any angle.) The female may change to responsive behavior if the male is responsive.

If the female remains immobile the male often assumes the pre-copulatory position. Continued non-responsiveness on the part of the female sometimes results in the male also becoming non-responsive. Fig. 14 diagrams the interactions of a responsive male and a non-responsive female. Fig. 15 diagrams the behavior of a non-responsive pair.

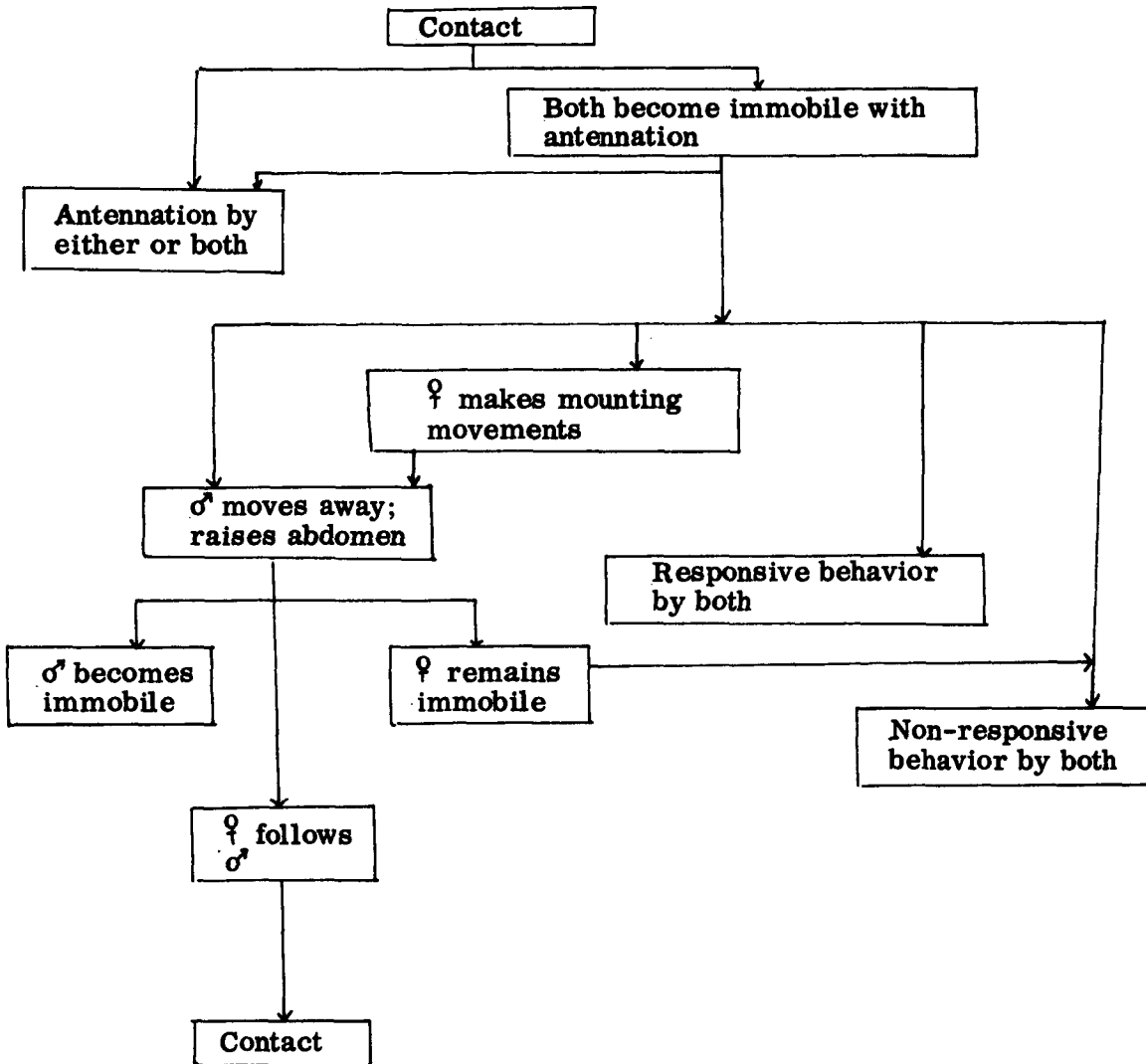


Fig. 13. Behavior of an initially sexually non-responsive male when placed with an initially responsive female.

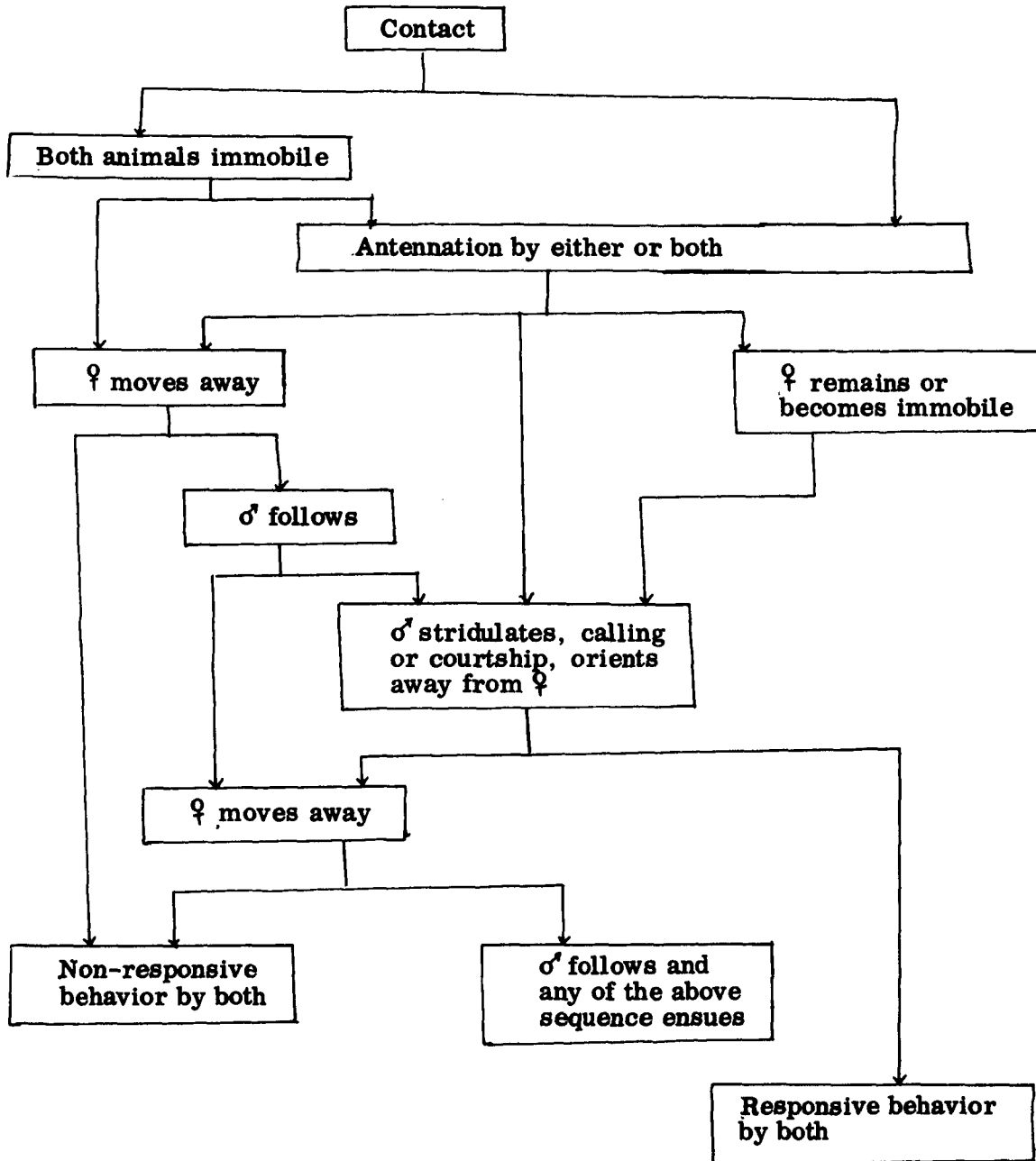


Fig. 14. Behavior of an initially sexually non-responsive female placed with a responsive male.

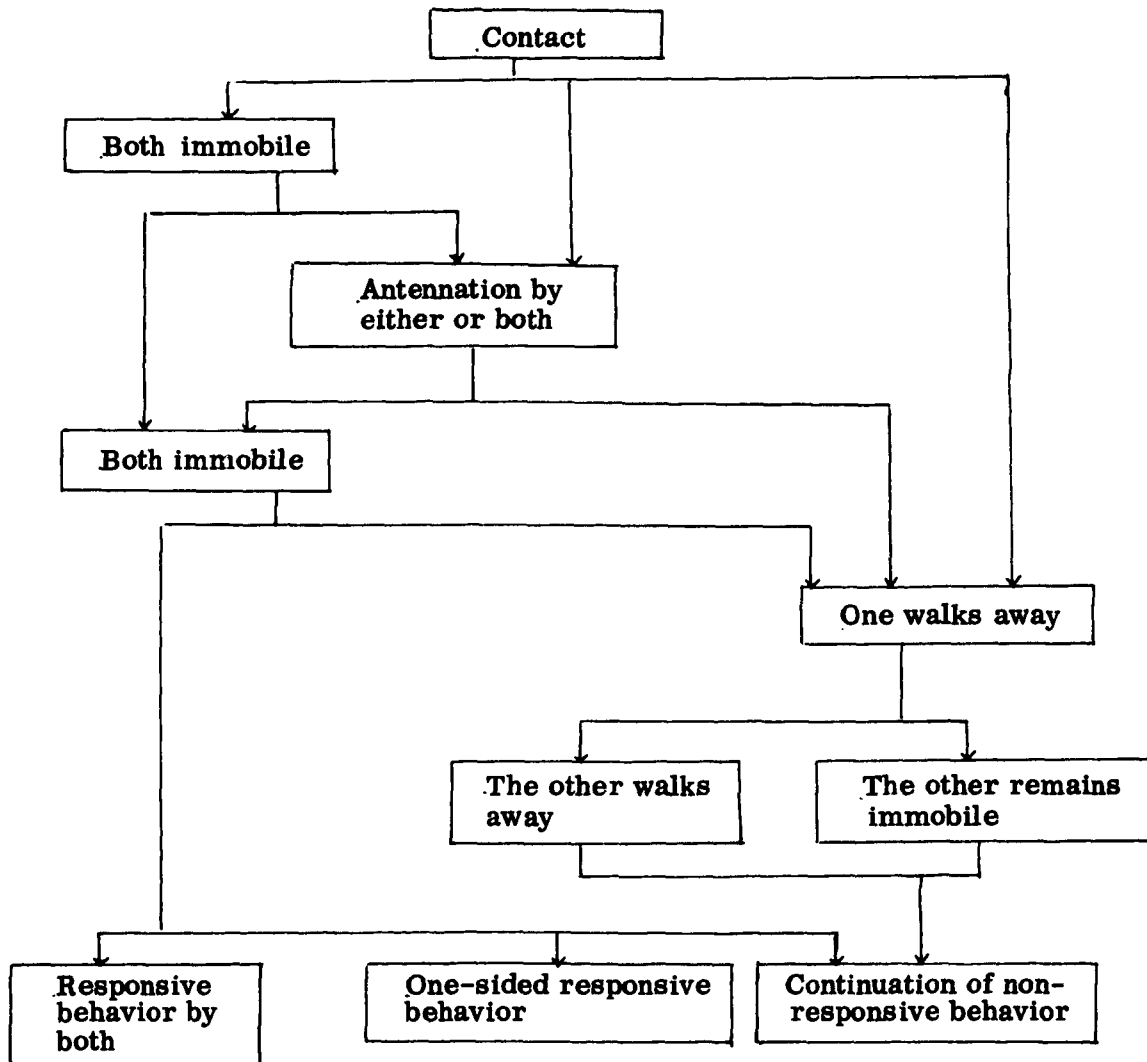


Fig. 15. Behavior of a sexually non-responsive pair.

4. Behavior of Responsive Young Adult Males

Young adult males may respond in the same behavior sequence as the older males do. However, at times the sequence began with post-copulatory behavior instead of pre-copulatory behavior. During the observation period, the pre-copulatory phase may succeed the post-copulatory actions.

B. ANALYSIS OF DATA

1. Treatment of Data

The data were subjected to non-parametric statistical analysis.

Non-parametric techniques were selected in preference to parametric procedures because the data were either ordinal or nominal. These non-parametric tests are distribution free and are simple to compute (Seigel, 1956). The four tests employed were the Kruskal-Wallis Analysis of Variance, the Mann-Whitney "U" test, Chi-Squared, and the Fisher Exact Probability test. The significance level chosen was .05.

The procedure for the analysis of each behavior item was to compare all eight groups first. Regardless of the significance level of the value of the statistic used, the groups involving 8-15 days adult (older=O) males were then compared with each other. The same was done with the groups involving 2-days adult (younger=Y) males. All older groups were combined and compared with all younger groups combined, when both groups showed no differences among the four subgroups (egg, nymph, adult-deprived, and group reared). When a comparison among the older or younger groups resulted in a probability value of .20 or less, appropriate paired-group comparisons among the older groups, among the younger groups and between counterpart groups (groups having received similar treatment, but differing in age) were made. (See Table 1).

Table 1

Procedure for the analysis of each behavioral measure (one example of a nominal measure and one example of an ordinal measure.)

A. A nominal measure

(Frequency of Copulation)

<u>Comparisons of</u>	<u>Test used for nominal data</u>
1. All eight groups	Chi-squared (2x8)
2. All older groups	Chi-squared (2x4)
3. All younger groups	Chi-squared (2x4)
4. Combined older groups versus Combined younger groups	Chi-squared (2x2) (if '2' and '3' did not yield statistically significant results)
5. Within older groups, paired comparisons of each of the four groups with each other	Fisher Exact Probability Test
6. Within younger groups, paired comparisons of each of the four groups with each other	Fisher Exact Probability Test
7. Counterpart group comparisons (EO* versus EY; NO versus NY; AO versus AY; GO versus GY)	Fisher Exact Probability Test

*EO = males isolated as eggs, observed when 1-2 weeks adult (Egg-Older)

NO = males isolated as nymphs, observed when 1-2 weeks adult (Nymph-Older)

AO = males isolated as adults, observed when 1-2 weeks adult (Adult-Older)

GO = group reared males, observed when 1-2 weeks adult (Group-Older)

EY = males isolated as eggs, observed when two days adult (Egg-Younger)

NY = males isolated as nymphs, observed when two days adult (Nymph-Younger)

AY = males isolated as adults, observed when two days adult (Adult-Younger)

GY = group reared males, observed when two days adult (Group-Younger)

Table 1 (continued)

B. An ordinal measure

(Latency to Beginning of First Successful Mount)

<u>Comparisons of</u>	<u>Test used for ordinal data</u>
1. All eight groups	Kruskal-Wallis
2. All older groups	Kruskal-Wallis
3. All younger groups	Kruskal-Wallis
4. Combined older groups versus Combined younger groups	Mann-Whitney "U" (if '2' and '3' did not yield statistically significant results)
5. Within older groups, paired comparisons of each of the four groups with each other	Mann-Whitney "U"
6. Within younger groups, paired comparisons of each of the four groups with each other	Mann-Whitney "U"
7. Counterpart group compari- sons (EO* versus EY; NO versus NY; AO versus AY; GO versus GY)	Mann-Whitney "U"

* See Table 1A for meaning of abbreviations.

2. Groups, Abbreviations and Definitions

Groups and abbreviations used are defined on pages 26-27 and in Table 1A (page 50). Definitions of behavioral measures and items are given on pages 25-26.

C. EFFECTS OF TREATMENT ON MATING BEHAVIOR

The results of the analyses are given in Tables 2-24 and are briefly discussed in this section. Interpretations, and evaluations will be made in the "Discussion" section. Included in the tables are numbers of animals, score ranges, medians, and, where applicable, modes.

1. Number of Copulations

Zero, 1, 2, or 3 copulations per animal took place during the 120 minute observation period (Table 2A). Only two of the 120 males copulated as many as three times. Most older males copulated twice; but few younger males copulated more than once.

A comparison of all the groups showed that occurrence, non-occurrence of copulation varied significantly (Table 2B). While the four older groups were not different in this respect, the four younger groups were. Paired-group comparisons showed that significantly more younger males deprived of social stimulation from the egg stage (EY) copulated than did younger animals that had social experience as adults (AY and GY). But, the number of EY males copulating at least once was not significantly different from that of older males deprived from the egg (EO) stage. Those males deprived as nymphs (NY) did not differ significantly from males of any other younger group nor from males

TABLE 2**Frequency of Copulations****A. Data**

<u>Group</u>	<u>n</u>	<u>Number of Copulations</u>	<u>Mode</u>	<u>Median</u>	<u>No. of males copulating 1 or more times</u>	<u>No. of males copulating 2 or more times</u>
EO*	15	0, 1, 2	1	1	13	6
NO	15	0, 1, 2, 3	2	2	13	10
AO	15	0, 1, 2	2	2	14	11
GO	15	0, 1, 2, 3	2	2	13	8
EY	15	0, 1, 2	1	1	12	2
NY	15	0, 1, 2	0	1	8	3
AY	15	0, 1	0	0	4	0
GY	15	0, 1	0	0	3	0

* See Table 1A for meanings of abbreviations.

TABLE 2 (continued)

**B. Occurrence or non-occurrence of copulation:
statistical analysis of 0 versus 1 or more copulations**

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	X ²	40.8	7	.001
EO,NO, AO,GO*	**			
EY,NY, AY,GY	X ²	13.65	3	.01
All paired comparisons within older groups	**			
EY, NY	Fisher Exact Probability		1	ns
EY, AY	"		1	.01
EY, GY	"		1	.005
NY, AY	"		1	ns
NY, GY	"		1	ns
AY, GY	**			
EO, EY	**			
NO, NY	Fisher Exact Probability		1	ns
AO, AY	"		1	.005
GO, GY	"		1	.005

* See Table 1A for meanings of abbreviations.

** Not different by inspection

N. B. : Comparison of the combined older groups with the combined younger groups could not be made (See Treatment of Data).

TABLE 2 (continued)

C. Number of males copulating:
 statistical analysis of 1 versus 2 or more copulations

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	X ²	***		
EO, NO, AO, GO	"	5.67	3	ns
EY, NY, AY, GY	"	***		
(EO+NO+AO+GO) x (EY+NY+AY+GY)	"	14.30	1	.001
EY, NY	Fisher Exact Probability		1	ns
EY, AY	"		1	ns
EY, GY	"		1	.025
NY, AY	"		1	ns
NY, GY	"		1	ns
AY, GY	**			
EO, EY	Fisher Exact Probability		1	ns
NO, NY	"		1	ns
AO, AY	"		1	.025
GO, GY	"		1	.10

Groups in parenthesis are combined.

* See Table 1A for meanings of abbreviations.

** Not different by inspection

*** Frequency too low for analysis

of the counterpart older group (NO). AY and GY males copulated less frequently than did members of their older counterpart groups, AO and GO.

The probability of intergroup differences in number of males copulating a second time was calculated (Table 2C). It was not possible to make a comparison of all groups because some expected frequencies were too low. The younger groups were not compared for the same reason. The combined older groups copulated two or more times significantly more than did the combined younger groups. Analysis showed EY males to copulate more frequently than GY males, but no other younger intergroup differences were found to be significant. All AY and GY males were unsuccessful in copulating more than one time during the test period.

2. Number of Minutes Elapsing Between Beginning of Observation and First Copulation

Latencies to the beginning of the first successful mount ranged from occurrence in the first minute to occurrence in the 102nd minute (Table 3). The median for all the older groups was 3 minutes while that for all the younger groups was 20 minutes.

Only 2 of 60 older males had latencies to the first copulation of between 6 and 20 minutes; the latencies of 7 younger males were of this length. Younger males copulated either before 38 minutes had elapsed or after 64 minutes had passed; no younger males copulated between 38 and 64 minutes. The EO males had a bimodal distribution of scores with 7 (57%) males having scores close to the older groups' median. Four EO males had longer latencies to first copulation than did males of any other older group. The remaining two animals

TABLE 3

Number of minutes elapsing between start of observation and minute in which first successful mount occurred.

A. Data

Group	n	range	median
EO	13	1-98	5
NO	13	1-27	2
AO	14	1-35	3.5
GO	13	1-42	3
EY	12	1-102	15.5
NY	8	3-79	48.5
AY	4	12-38	20.5
GY	3	8-72	19

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	19.99	7	.01
EO, NO, AO, GO	"	2.7	3	ns
EY, NY, AY, GY	"	0.03	3	ns
(EO+NO+AO+GO) x (EY+NY+AY+GY)	Mann-Whitney	4	1	.0001
All paired group comparisons within older and within younger groups	Not required by above Kruskal-Wallis analysis			
EO, EY	Mann-Whitney	66	1	ns
NO, NY	"	14.5	1	.01
AO, AY	"	3	1	.01
GO, GY	"	9	1	ns

* See Table 1A for meanings of abbreviations.

had scores at or near the median of the younger groups.

A comparison of all groups showed that intergroup differences existed (Table 3). The statistically significant differences found were between older and younger animals that were socially deprived after having had some social experience.

3. Unsuccessful Mounts before First Copulation

Some females mounted males one or more times without copulating. Unsuccessful mounts before the first copulation were more frequent in some groups than in others (Table 4A). Inspection showed that there might be differences in the effects of treatment, so paired group comparisons were made (Table 4B). Females paired with NY males mounted more frequently than did females with EY or AY males, and females with EO males mounted more frequently than did those with males of any other older group. Furthermore, females with EO males mounted more frequently than did females with EY males. The same difference was found between females with NY and NO males.

For easy comparison of the relation between latency to copulation and unsuccessful mounts, three categories of copulation latency were formulated: early (1 to 9 minutes), intermediate (10 to 20 minutes) and late (21 or more minutes) (Fig. 16). Statistical analysis of the time of unsuccessful mounts (early versus late) showed that animals copulating late were partners to unsuccessful mounts significantly more than were those that copulated early ($X^2 = 5.7$, $p = .02$). However, it should be noted that approximately 1/4 of the early copulating males were also involved in unsuccessful mounts.

TABLE 4

Number of unsuccessful mounts prior to first copulation

A. Frequency of distribution of number of females making different numbers of unsuccessful mounts

<u>Group</u>	<u>Number of Animals Copulating</u>	<u>Number of Animals With No Unsuccessful Mounts</u>	<u>Total Number of Animals With One or More Unsuccessful Mounts</u>	<u>Number of Unsuccessful Mounts (Number of Animals)</u>				
				<u>1</u>	<u>2</u>	<u>3</u>	<u>5</u>	<u>10</u>
EO*	13	4	9	4	3	0	1	1
NO	13	12	1	0	1	0	0	0
AO	14	11	3	2	1	0	0	0
GO	13	10	3	1	2	0	0	0
EY	12	11	1	0	1	0	0	0
NY	8	3	5	5	0	0	0	0
AY	4	1	3	1	1	1	0	0
GY	3	1	2	0	2	0	0	0

* See Table 1A for meanings of abbreviations.

TABLE 4 (continued)

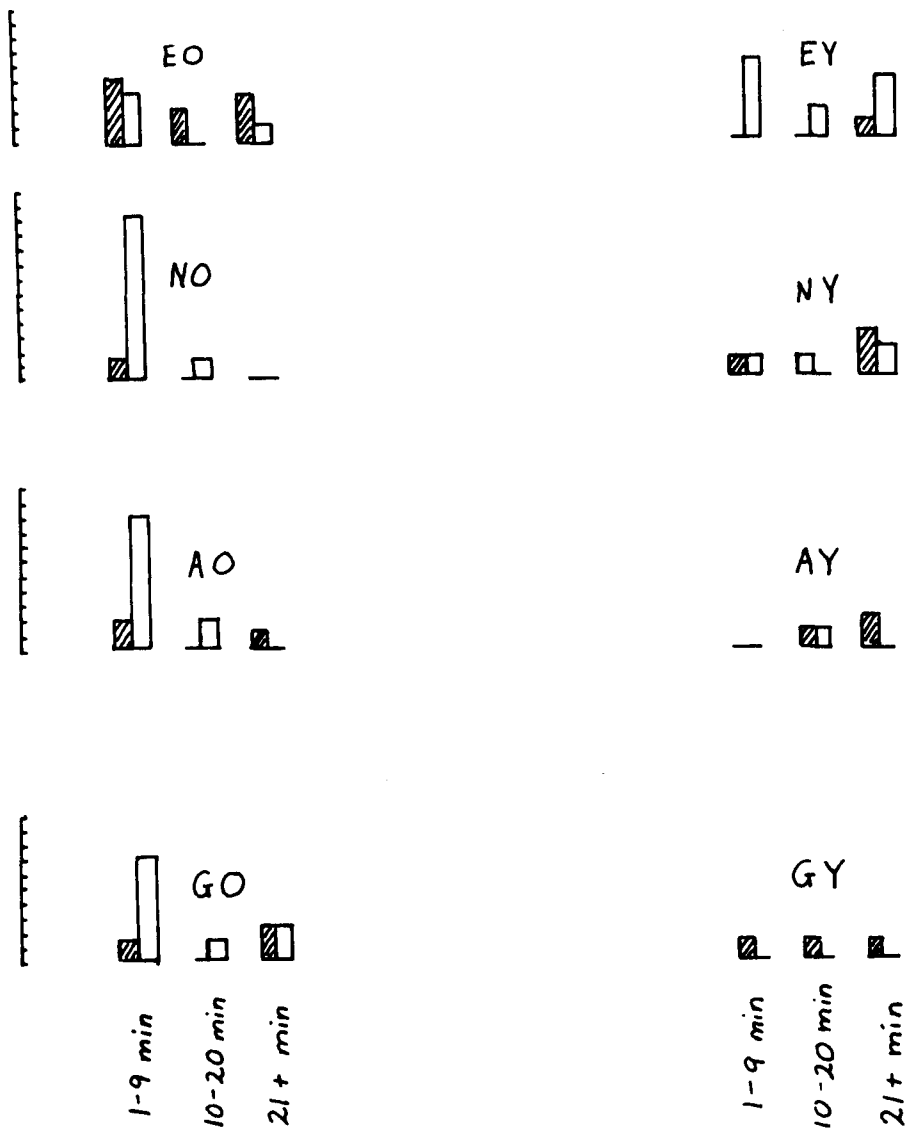
B. Statistical analysis of 0 versus 1 or more unsuccessful mounts prior to first copulation

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	X ²	***		
EO, NO, AO, GO	X ²	***		
EY, NY, AY, GY	X ²	***		
(EO, NO, AO, GO) x (EY, NY, AY, GY)	X ²	*		
EO, NO	Fisher Exact Probability		1	.005
EO, AO	"		1	.025
EO, GO	"		1	.05
NO, AO	**			
NO, GO	**			
AO, GO	**			
EY, NY	Fisher Exact Probability		1	.05
EY, AY	"		1	.05
EY, GY	"		1	ns
NY, AY	"		1	ns
NY, GY	"		1	ns
AY, GY	**			
EO, EY	Fisher Exact Probability		1	.01
NO, NY	"		1	.025
AO, AY	"		1	ns
GO, GY	"		1	ns

* Groups cannot be combined because of differences obvious by inspection

** Not different by inspection

*** Expected frequency too low for comparison



□ = 0 unsuccessful mounts

▨ = 1 or more unsuccessful mounts

Fig. 16. Time of unsuccessful mounts by pairs with short (1 to 9 minutes), intermediate (10 to 20 minutes) and long (21 or more minutes) latency to copulation.

4. Interval between First Copulation and Next Mount of Any Type

The number of minutes elapsing between the first copulation and the next mount of any kind (successful or unsuccessful) ranged from 8 to 105 minutes (Table 5). Female paired with AY and GY males did not mount after the first copulation. Although a comparison of all groups showed no statistical difference, a difference was found between younger males and between the males of EO and EY groups. The scores obtained with EY males were 10 minutes or more longer than any scores obtained with EO males.

5. Number of Unsuccessful Mounts Prior to Second Copulation or End of Observation

Unsuccessful mounts prior to the second copulation were observed in all older groups and in none of the younger groups. Occurrence and non-occurrence of unsuccessful mounts were compared (Table 6). Paired-group comparisons showed that females paired with AO males mounted unsuccessfully in significantly fewer instances than did females paired with EO males. No other significant differences were found.

6. Interval between First and Second Copulations

The interval between the first and second copulations varied from 50 to 102 minutes with the median being 73 minutes (Table 7). No AY nor GY male copulated a second time. Statistical analysis showed that the interval between the first and second copulations was longer for those younger males that did copulate a second time than they were for the older males.

As there were no differences among all older groups nor among all younger groups, the data were combined within each set. Over half of the first

TABLE 5

Number of minutes elapsing between the first copulation and next mount of any type

A. Data

Group	n	range	median
EO*	8	56-78	62.5
NO	12	8-105	69
AO	11	62-95	72
GO	10	59-102	72.5
EY	2	88-93	90.5
NY	4	56-85	74.5

B. Statistical analysis

Groups compared	Statistical test	Value	df	p
All groups	Kruskal-Wallis	7.03	5	ns
EO, NO, AO, GO	"	2.31	3	ns
EY, NY	Mann-Whitney	0		.02
EO, EY	"	0		.02
NO, NY	"	23		ns

* See Table 1A for abbreviations.

TABLE 6

Number of unsuccessful mounts prior to second copulation or end of observation

A. Frequency distribution of number of females making different numbers of unsuccessful mounts

<u>Group</u>	<u>Copulating Once</u>	<u>Number of Unsuccessful Mounts</u>					
		<u>0</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>9</u>
EO*	13	6	3	1	2	0	1
NO	13	7	3	2	0	0	1
AO	14	12	1	0	1	0	0
GO	13	8	2	1	1	1	0

Younger groups are not included because of relatively long latencies to first copulation, and paucity of second copulations.

B. Statistical analysis of 0 versus 1 or more mounts

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All older groups	X ²	5.06	3	ns
EO, NO	**			
EO, AO	Fisher Exact Probability		1	.05
EO, GO	**			
NO, AO	Fisher Exact Probability		1	ns
NO, GO	**			
AO, GO	Fisher Exact Probability		1	ns

* See Table 1A for meanings of abbreviations

** Not different by inspection

TABLE 7

Number of minutes elapsing between the minute in which the first copulation occurred and the minute in which the second copulation occurred

A. Data

<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>
EO*	6	60-78	68.5
NO	10	50-84	70
AO	11	64-95	75
GO	8	59-102	77.5
EY	2	88-93	90.5
NY	3	72-85	81
#			

B. Statistical analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	17.77	5	.01
EO, NO, AO, GO	"	3.25	3	ns
EY, NY	Mann-Whitney "U"	6		ns
(EO+NO+AO+GO) x (EY+NY)	"	2.06		.02
EO, EY	"	0		.036
NO, NY	"	0		.01

* See Table 1A for meanings of abbreviations.

No AY or GY males copulated a second time.

copulations took place within the first 6 minutes. Of the 38 older males copulating within this time, 32 copulated again. Of the 15 older males that copulated after 9 minutes had elapsed, only 3, all AO males, transferred a second spermatophore. There is a significant difference ($p < .001$), thus indicating the likelihood that if a first copulation took place, a second would follow. The same tendency is obvious in the younger males (4 of 7 copulating in the first 6 minutes copulated a second time), although the frequency was too low to permit statistical analysis.

7. Interval between First Copulation and New Spermatophore Formation

Latencies from the first copulation to the formation of a new spermatophore ranged from 8 to 53 minutes, with a median of 14 minutes (Table 8) for all eight groups. Three older groups had median latencies below or at the median for all groups, but the median latency for GO males was well above it. The shortest latency medians (10 minutes) were found with the EO and NO groups.

An all group comparison showed that a significant difference existed. The younger groups were similar in the number of minutes elapsing between the first copulation and the formation of a new spermatophore, but the older groups were not. Further analysis showed that all older groups were different from each other except EO and NO. These latter two groups also had the shortest intervals of all groups between the first copulation and the formation of a new spermatophore.

8. Fate of Spermatophore Transferred during Copulation

Copulating males did not always succeed in transferring the spermatophore to the female (Table 9). In 6 instances the spermatophores were

TABLE 8

Number of minutes elapsing between the minute in which the first copulation occurred and the minute in which the new spermatophore appeared

A. Data

<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>
EO*	13	10-27	10
NO	13	8-50	10
AO	14	9-20	13.5
GO	13	13-53	24
EY	12	15-51	20.5
NY	8	10-37	15.5
AY	3	12-18	16
GY	2	14-45	29.5

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	27.07	7	.001
EO, NO, AO, GO	"	22.23	3	.001
EY, NY, AY, GY	"	3.3	3	ns
EO, NO	Mann-Whitney "U"	71.5		ns
EO, AO	"	42.5		.025
EO, GO	"	7		.001
NO, AO	"	47		.05
NO, GO	"	13		.001
AO, GO	"	13.5		.001
Paired comparisons of younger groups	**			
EO, EY	Mann-Whitney "U"	9		.001
NO, NY	"	20.5		.025
AO, AY	"	9		ns
GO, GY	"	11.5		ns

* See Table 1A for meanings of abbreviations

** Not different by inspection

TABLE 9

Fate of first transferred spermatophore

<u>Fate</u>	<u>Groups</u>							
	<u>EO*</u>	<u>NO</u>	<u>AO</u>	<u>GO</u>	<u>EY</u>	<u>NY</u>	<u>AY</u>	<u>GY</u>
Dropped from ♀	3	0	0	0	0	0	0	0
Removed by ♀ and eaten	8	10	12	9	3	4	2	1
Removed by ♀ and dropped	0	3	2	4	1	1	2	1
Still attached to ♀ at end of observation	2	0	0	0	2	3	0	1
Attached to ♂	0	0	0	0	6	0	0	0
<u>n</u> (first transfers)	13	13	14	13	12	8	4	3

* See Table 1A for meanings of abbreviations.

attached to the tips of the hind wings of the EY males. In all of these cases the spermatophores fell off shortly after transfer. Most spermatophores transferred to the female (77.5%) were removed by the female; some of these (64.1%) were eaten by the female, and the others were dropped to the floor of the chamber. Eight spermatophores were still attached to the female at the end of the observation period. Three of the spermatophores transferred by EO males dropped off the female; these were not subsequently eaten (see Fig. 11).

9. Interval between First Copulation and Removal of Spermatophore by Female

The intervals between the first copulation and the removal of the spermatophore by the female ranged from 1 to 94 minutes (Table 10). Analysis showed no statistically significant differences between any groups or combinations of groups.

10. Interval between Loss of Spermatophore and Second Copulation

In one instance, a spermatophore that had not been removed was removed by a female just before she mounted. All the other females removed the spermatophores before they positioned themselves directly behind the males.

Latencies from removal of the spermatophore to the second copulation ranged from 1 to 90 minutes prior to the mount (Table 11). No statistically significant differences were found between any groups or combinations of groups.

11. Interval between Second Copulation and New Spermatophore Formation

No younger males produced a spermatophore during the test period after the second copulation. Four older males also did not produce spermatophores at this time. In order to determine whether the time remaining was

TABLE 10

Number of minutes elapsing between the minute in which the first copulation occurred and the minute in which the spermatophore was removed by the female

A. Data

<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>
EO*	8	17-71	48
NO	13	37-69	48
AO	14	24-94	55.5
GO	12	1-67	46.3
EY	4	1-71	44.5
NY	5	16-81	38
AY	4	11-76	53.5
GY	2	68-69	68.5

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	6.42	7	ns
EO, NO, AO, GO	"	6.18	3	ns
EY, NY, AY, GY	"	1.6	3	ns
(EO+NO+AO+GO) x (EY+NY+AY+GY)	Mann-Whitney "U"	1.2		ns

* See Table 1A for meanings of abbreviations.

TABLE 11

Number of minutes elapsing between loss of spermatophore from female and second copulation

A. Data

<u>Group</u>	<u>n</u> <u>copulating</u> <u>twice</u>	<u>range</u>	<u>median</u>
EO*	6	11-50	21
NO	10	5-46	25
AO	11	1-51	14
GO	8	2-90	30.5
EY	2	17-77	47
NY	3	4-34	29
Combined young	5	4-77	29

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	2.20	5	ns
EO, NO, AO, GO	"	3.05	3	ns
EY, NY	Mann-Whitney	3		ns
(EO+NO+AO+GO) x (EY+NY)	**			
(EO+NO) x (EY+NY)	**			

* See Table 1A for meanings of abbreviations.

** Not different by inspection

insufficient for these 9 males to produce the second spermatophores, the interval between the second copulation and the end of the observation was determined for each. The difference between this value and the interval from first copulation and new spermatophore formation was then calculated (Table 12). In only one case, an AO male, was the interval to the end of the observation less than the shortest observed latency from a copulation to subsequent spermatophore formation. In three instances, one AO male and two GO males, the latency to the production of the first spermatophore exceeded the amount of time from second copulation to the end of the observation.

The difference between time from second copulation to new spermatophore formation and time from first copulation to new spermatophore formation was determined for those animals producing a second spermatophore (Table 13A). When the number of males showing increases in time taken to produce the second spermatophore were compared to the number of males showing decreases, NO males were found to show more increases (Table 13B). However, the difference was statistically significant only when NO and AO males were compared.

The latencies from second copulation to new spermatophore formation ranged from 8 to 56 minutes (Table 14). Only two animals had latencies greater than 19 minutes; both were EO with latencies of 41 and 56 minutes. The other EO males had latencies of 8 or 9 minutes.

A comparison of all groups showed that intergroup differences existed. The GO males had significantly longer latencies to the formation of the second spermatophore than did NO or AO males, but did not differ from EO males.

TABLE 12

Animals not producing a spermatophore after the second copulation

Difference^z in number of minutes elapsing between the beginning of the second copulation and the end of the observation and number of minutes elapsing between the beginning of the first copulation and spermatophore formation

<u>Difference in number of minutes elapsing</u>	<u>n</u>			
	<u>Group</u>			
	<u>AO*</u>	<u>GO</u>	<u>EY</u>	<u>NY</u>
+5 or more	0	0	2	3
+2	0	1	0	0
-5 or fewer	1	2	0	0

z Number of minutes between 2nd copulation and end of observation
 - Number of minutes between 1st copulation and spermatophore formation
 = Difference

(A minus indicates that the time available after the 2nd copulation was less than the time between the first copulation and formation of the spermatophore.)

* See Table 1A for meanings of abbreviations.

TABLE 13

Animals producing a spermatophore after the second copulation

A. Difference^y in number of minutes elapsing between the beginning of the second copulation and spermatophore formation and number of minutes elapsing between the beginning of the first copulation and spermatophore formation

<u>Difference in number of minutes elapsing</u>	<u>n</u>			
	<u>Group</u>			
	<u>EO*</u>	<u>NO</u>	<u>AO</u>	<u>GO</u>
+5 or more	2	0	0	0
+1 to +4	0	6	1	1
0	0	1	2	0
-1 to -4	4	3	4	1
-5 or fewer	0	0	3	3

^y Number of minutes between 2nd copulation and formation of new spermatophore
 minus
 Number of minutes between 1st copulation and formation of new spermatophore
 equals
 Difference

(A minus indicates that the 2nd spermatophore was produced more quickly than the first.)

* See Table 1A for meanings of abbreviations.

TABLE 13 (continued)

Animals producing a spermatophore after the second copulation

B. Statistical analysis of males producing second spermatophores less quickly than first spermatophores versus those producing spermatophores more quickly

<u>Groups compared</u>	<u>Statistical test</u>	<u>P</u>
All older groups	X ²	***
EO, NO*	Fisher Exact Probability	ns
EO, AO	**	
EO, GO	**	
NO, AO	Fisher Exact Probability	.05
NO, GO	"	ns
AO, GO	**	

* See Table 1A for meanings of abbreviations

** Not different by inspection

*** Frequencies too low for analysis

TABLE 14

Number of minutes elapsing between second copulation and new spermatophore formation

A. Data

<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>
EO*	6	8-56	9
NO	10	8-16	11
AO	10	8-14	11
GO	5	12-19	13

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All older groups	Kruskal-Wallis	12.04	3	.01
EO, NO	Mann-Whitney "U"	31.5		ns
EO, AO	"	25		ns
EO, GO	"	10		ns
NO, AO	"	46		ns
NO, GO	"	7		.025
AO, GO	"	6.5		.025

* See Table 1A for meanings of abbreviations.

12. Interval from First Spermatophore Formation to Second Copulation

The range of time intervals from the first spermatophore formation to the second copulation was from 41 to 77 minutes (Table 15). A comparison of all groups suggested no difference, but further analysis demonstrated that GO males had considerably shorter latencies than did AO males. When all older groups were combined and compared to the combined younger groups, the difference approached significance.

13. Total Minutes near Female

The number of minutes in which the male was near the female (including mount time) ranged from a low of 0 to a high of 120 (Table 16). No statistically significant differences were found.

14. Minutes near Female between First and Second Copulations

The number of minutes in which the males were near the females between the first and second copulations ranged from 37 to 94 minutes (Table 17). No statistically significant differences were found.

15. Total Minutes of Stridulation

Individual males stridulated in from 0 to 110 minutes of the observation time (Table 18). A comparison of all groups indicated that highly significant differences existed between groups. Inspection and further analysis showed that only EY males were different; they stridulated less than any other group.

16. Stridulation Prior to First Copulation

The range of minutes in which stridulation occurred prior to the first transfer was 1-79 minutes (Table 19). An overall comparison did not reveal a significant difference among groups. However, comparison of younger groups

TABLE 15

Number of minutes elapsing between first spermatophore formation and second copulation

A. Data				
<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>	
EO*	6	50-68	57.5	
NO	10	41-76	59	
AO	11	52-77	59	
GO	8	41-69	54.5	
EY	2	68-76	72	
NY	3	49-71	71	

B. Statistical Analysis				
<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	8.8	5	ns
EO, NO, AO, GO	"	5.22	3	ns
EY, NY	Mann-Whitney "U"	2		ns
(EO+NO+AO+GO) x (EY+NY)	"	1.48		.07
EO, NO	**			
EO, AO	**			
EO, GO	Mann-Whitney "U"	16		ns
NO, AO	**			
NO, GO	Mann-Whitney "U"	22		ns
AO, GO	"	14		.01
EO, EY	"	3.5		ns
NO, NY	"	19		ns

* See Table 1A for meanings of abbreviations.

** Not different by inspection

TABLE 16

Total number of minutes in which the male was located near the female

A. Data

<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>
EO*	15	80-120	96
NO	15	39-118	111
AO	15	59-119	111
GO	15	9-120	110
EY	15	85-120	106
NY	15	18-120	102
AY	15	35-119	106
GY	15	0-118	101

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	10.18	7	ns (.20)
EO, NO, AO, GO	"	1.98	3	ns
EY, NY, AY, GY	"	.83	3	ns
(EO+NO+AO+GO) x (EY+NY+AY+GY)	Mann-Whitney	1.27		ns

* See Table 1A for meanings of abbreviations.

TABLE 17

Number of minutes in which the male was near the female between first and second copulations

A. Data

<u>Groups</u>	<u>n</u>	<u>range</u>	<u>median</u>
EO*	6	37-78	62.5
NO	10	46-81	70.5
AO	11	54-94	70
GO	8	51-85	74
EY	2	74-81	77.5
NY	3	69-77	76

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	4.9	5	ns
EO, NO, AO, GO	"	2.9	3	ns
EY, NY	Mann-Whitney	2		ns
(EO+NO+AO+GO) x (EY+NY)	**			

* See Table 1A for abbreviations

** Not different by section

TABLE 18**Total number of minutes in which stridulation occurred****A. Data**

<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>
EO*	15	1-75	19
NO	15	3-110	14
AO	15	3-63	12
GO	15	2-86	18
EY	15	0-35	3
NY	15	0-79	23
AY	15	0-107	18
GY	15	0-38	17

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	22.05	7	.01
EO, NO, AO, GO	"	1.25	3	ns
EY, NY, AY, GY	"	12.17	3	.01
All paired group comparisons within older group	Not required by above Kruskal-Wallis analysis			
EY, NY	Mann-Whitney "U"	43		.01
EY, AY	"	48.5		.01
EY, GY	"	58.5		.01
NY, AY	"	100		ns
NY, GY	"	76		ns
AY, GY	"	83		ns
EO, EY	"	43.5		.01
NO, NY	"	78		ns
AO, AY	"	83		ns
GO, GY	"	100		ns

* See Table 1A for meanings of abbreviations.

TABLE 19

Number of minutes in which stridulation occurred prior to first copulation

A. Data				
<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>	
EO*	13	1-52	2	
NO	13	1-6	1	
AO	14	1-56	2.5	
GO	13	1-40	2	
EY	12	1-9	3	
NY	8	1-79	19.5	
AY	4	12-31	18.5	
GY	3	4-25	7	

B. Statistical Analysis				
<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	10	7	ns
EO, NO, AO, GO	"	1.9	3	ns
EY, NY, AY, GY	"	17	3	.001
All paired group comparisons within older groups	Not required by above Kruskal-Wallis analysis			
EY, NY	Mann-Whitney "U"	10.5		.001
EY, AY	"	0		.01
EY, GY	"	6		ns
NY, AY	**			
NY, GY	**			
AY, GY	Mann-Whitney "U"	9		ns
EO, EY	"	75.5		ns
NO, NY	"	11.5		.01
AO, AY	"	15		ns
GO, GY	"	12.5		ns

* See Table 1A for meanings of abbreviations

showed that they differed significantly. The EY males stridulated significantly less than did NY and AY males, but did not differ from GY males. There were no statistically significant differences among the older groups. NO males stridulated in fewer minutes than did NY males. There were no other differences between paired older and younger groups.

Table 20 shows the relation of relatively long latencies to copulation and amount of stridulation. It can be seen that, except in EO and EY, the amount of stridulation increases in direct relation to increased latency to copulation.

17. Minutes of Stridulation between First and Second Copulations

The range of minutes in which some stridulation occurred between the first and second copulations was 1 to 31 minutes (Table 21). No statistically significant differences were found.

18. Minutes of Stridulation after Change of Orientation Prior to Second Copulation

The range of minutes in which stridulation occurred after change of orientation was from 1 to 31 minutes (Table 22). No statistically significant differences were found.

19. Total Stridulation by Males Copulating Twice

The range of minutes in which stridulation occurred in males copulating twice was 2 to 63 minutes (Table 23). No statistically significant differences were found.

20. Sexual Maturity of Younger Males

Some younger males produced spermatophores before copulation;

TABLE 20

Relation of relatively long latencies to copulation and amount of stridulation

Group

<u>EO*</u>		<u>NO</u>		<u>AO</u>		<u>GO</u>	
<u>cop</u>	<u>min</u>	<u>cop</u>	<u>min</u>	<u>cop</u>	<u>min</u>	<u>cop</u>	<u>min</u>
<u>lat</u>	<u>strid</u>	<u>lat</u>	<u>strid</u>	<u>lat</u>	<u>strid</u>	<u>lat</u>	<u>strid</u>
20	8	27	1	10	1	10	9
21	21			20	20	31	7
52	52			35	32	34	17
61	1					37	37
68	2					42	40

Group

<u>EY</u>		<u>NY</u>		<u>AY</u>		<u>GY</u>	
10	1	11	5	12	1	19	4
18	9	33	15	15	12	72	25
21	3	64	38	26	24		
38	2	68	28	38	31		
69	2	72	23				
75	9	79	79				
86	1						
102	1						

* See Table 1A for meanings of abbreviations.

TABLE 21

Number of minutes in which stridulation occurred between first and second copulations only

A. Data

<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>
EO*	6	6-22	11.5
NO	10	2-26	11.5
AO	11	2-31	7
GO	8	1-19	4.5
EY	2	10-13	11.5
NY	3	3-10	5

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	4.7	5	ns
EO, NO, AO, GO	"	2.24	3	ns
EY, NY	Mann-Whitney "U"	.5		ns
(EO+NO+AO+GO) x (EY+NY)	"	.20		ns
(EO+NO) x (EY+NY)	**			

* See Table 1A for meanings of abbreviations.

** Not different by inspection

TABLE 22

Number of minutes in which stridulation occurred after change of orientation prior to second copulation only

A. Data

<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>
EO*	6	4-21	10.5
NO	10	2-26	11.5
AO	11	1-31	7
GO	8	1-18	4
EY	2	10-13	11.5
NY	3	3-9	5
Combined young	5	3-13	9

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	Kruskal-Wallis	3.41	5	ns
EO, NO, AO, GO	"	2.78	3	ns
EY, NY	Mann-Whitney "U"	0		ns
(EO+NO+AO+GO) x (EY+NY)	"	.04		ns
(EO+NO) x (EY+NY)	"	45		ns

* See Table 1A for meanings of abbreviations.

TABLE 23

Number of minutes in which males that copulated twice stridulated

A. Data

<u>Group</u>	<u>n</u>	<u>range</u>	<u>median</u>
EO*	6	10-32	15.5
NO	10	3-29	13
AO	11	3-63	11
GO	8	2-19	12
EY	2	7-15	11.5
NY	3	14-21	18
Combined young	5	7-21	15

B. Statistical Analysis

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups EO, NO, AO, GO EY, NY	Kruskal-Wallis **	1.83	5	ns
(EY+NY), (EO+NO)	**			
(EO+NO+AO+GO), (EY+NY)	**			

* See Table 1A for abbreviations.

** Not different by inspection

all of these males did not subsequently copulate (Table 24). Other males copulated first and later produced spermatophores as all the copulating older males did. A final group of younger males did not exhibit either one of these kinds of sexual maturity. In production of spermatophores and/or copulation, GY males were found to be less responsive than EY or NY males (Table 24B). When the number of males copulating was compared to the number producing spermatophores only EY males were found to be significantly more active sexually than males of the other groups (Table 24C).

21. Fertility of Younger Males

One female that had copulated twice with a NY male was separated. Two days later an oviposition site was provided. On the fourth day following copulation, her eggs were incubated. Two nymphs were hatched; their development was not followed.

TABLE 24

Copulations and/or production of spermatophores by younger males

A. Data

Group	n	Producing spermatophore only	Spermatophore production followed by copulation	Copulation first, followed by spermatophore production	No spermatophore or copulation
EY*	15	0	4	9	2
NY	15	5	1	7	2
AY	15	6	0	4	5
GY	15	5	1	2	7

B. Statistical analysis of males producing a spermatophore and/or copulating versus neither

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	χ^2	***		
EY, NY	**			
EY, AY	Fisher Exact Probability		1	ns
EY, GY	"		1	.05
NY, AY	"		1	ns
NY, GY	"		1	.05
AY, GY	**			

* See Table 1A for meanings of abbreviations.

** Not different by inspection

*** Frequency too low for analysis

TABLE 24 (continued)

C. Statistical analysis of younger males producing a spermatophore only versus those copulating during the observation period

<u>Groups compared</u>	<u>Statistical test</u>	<u>Value</u>	<u>df</u>	<u>p</u>
All groups	X ²	***		
EY, NY*	Fisher Exact P robability		1	.025
EY, AY	"		1	.005
EY, GY	"		1	.005
NY, AY	"		1	ns
NY, GY	"		1	ns
AY, GY	"		1	ns

* See Table 1A for meanings of abbreviations

*** Frequencies too low for analysis

V. DISCUSSION

A. OVERVIEW

The experimental results obtained indicated that certain types of social experience play a role in the development and/or expression of the mating behavior of house crickets. Both the time at which animals were deprived of social experience and the age at which animals were given the opportunity to mate affected the expression of the behavior. The major finding was the effect of these experiences on the occurrence of copulation (Table 2).

It was to be expected that males observed at later stages of development would be more likely to copulate than males observed at earlier stages of development. Thus, the number of copulating males in the AO and GO groups was greater than the number of copulating males in the AY and GY groups. However, there was no such difference between the EO and EY groups and the NO and NY groups. Rather, males observed at earlier stages of development were as likely to copulate as older males, if the younger males had been deprived of social experience at the egg or nymphal stage. In order of number of males copulating, the groups are ranked as follows:

EO			AY
NO	EY	NY	GY
AO			
GO			
Frequency:	13 or 14/15	12/15	8/15
			3 or 4/15

There were no differences among the older groups, nor among NY, AY

and GY. EY was different from AY and GY but not from NY.

The following sections will explore the relationships of other recorded behavioral items to these differences in the occurrence of copulation.

B. RELEVANCE OF OTHER BEHAVIORAL ITEMS TO THE OCCURRENCE OF COPULATION

Of the behavior items recorded, the following might be related to the occurrence of copulation on the basis of previous work done by other experimenters, or on the basis of their association with copulation:

1. time spent near the female
2. unsuccessful mounts
3. latency to first mount
4. stridulation

Examination of some characteristics of the non-copulating males might be helpful in understanding the relevance of some behavioral items to the occurrence of copulation. Of the non-copulating males, the older ones 1) produced no spermatophores, 2) tended to remain near the female less than other males and 3) tended to stridulate far more than other males (Table 25). These males apparently did not copulate because no spermatophore was formed. However, the fact that one AO male produced a spermatophore several days later when placed with a female shows that at least one male was capable of producing spermatophores. It is not clear from the data which partner was responsible for the distance maintained between the male and female. Nor was it possible in the present experiment to identify the type of stridulation most often produced.

TABLE 25

Profile of the non-copulating male

Group	n	min near female		lat. to spermato- phore production		min. strid.		number of males with un- successful mounts
		range	median	range	median	range	median	
EO*	2	84-90	87	-	-	70-75	72.5	0
NO	2	39-78	58.5	-	-	10-110	60	1
AO	1	103	103	-	-	54	54	1
GO	2	9-116	62.5	-	-	31-86	58.5	1
EY	3	85-97	87	-	-	0-2	1	0
NY	7	18-118	93	36-89(n=5)	65	0-70	18	4
AY	11	35-119	93	49-88(n=6)	69	0-107	12	1
GY	12	0-118	101.5	75-113(n=5)	87	4-38	20	1

* See Table 1A for meaning of abbreviations.

Younger non-copulating males tended to be similar to younger copulating males, except in that they spent slightly less time near the female. Interestingly enough, over half of them produced spermatophores.

When the experimental groups were examined, no group was significantly different from any other group in the number of minutes spent by the male near the female (Tables 16 and 17). Therefore, regardless of its relation to copulation, it was not relevant to the group differentials observed in the occurrence of copulation.

More males in the EO and NY groups were partners in unsuccessful mounts than in the other groups (Table 4), although in both these groups, the number of males achieving copulation was not significantly different from the other older male groups or the EY group. As shown in Fig. 16, there was the tendency for males with long latencies to copulation to be partners in unsuccessful mounts more than those males with short latencies. In the EO group, the median latency to copulation was greater (not statistically significant) than any of the other older groups. The same was true in a similar analysis for NY in the younger male groups. However, there was no correlation between failure to achieve copulation and unsuccessful mounts.

There is also no clear relationship between latency and likelihood to copulate. The latency to first copulation tended to be greater with younger males than with older males ($Y > Q$) (Table 3A), an expected finding. In particular, NY and AY took longer to copulate than did NO and AO respectively (Table 3B). Nevertheless, NY males did not differ significantly from NO males in likelihood to copulate. There were no differences within age groups, however, and the

ranges of the copulation latency periods for groups observed at the same age overlapped considerably.

The remaining item that might be related to the occurrence of copulation is stridulation. Here again, the behavior of the EY group was outstandingly different in quantity from any of the other groups (Table 18). When the amount of stridulation (number of minutes in which it occurred) was related to occurrence of copulation, EY was not different from the older male group (EO), but was different from the NY and AY groups and less than the small GY group (although not statistically significant). EY was thus similar to the older groups in amount of stridulation prior to the first copulation and in likelihood to copulate. On the other hand, NY, which was similar to the older groups in likelihood to copulate, differed significantly in the amount of stridulation before copulation. (Unfortunately, no information is available on the type of stridulation engaged in by any of the animals.) On the basis of the available information, the occurrence of stridulation was not generally helpful in understanding the group differences in copulation.

Is there another behavioral or physiological pattern that may be causally related or concomitantly significant for the copulatory process? Several observations were made regarding spermatophore production and transfer which may be important in explaining the results. Spermatophores are never transferred immediately after production. In 8-15 day adult males observed at $34 \pm 1^{\circ}$ C, the latency from spermatophore production to the second copulation was always in excess of 40 minutes (Table 15). In younger males at the same temperature, these latencies were, except for one animal, in excess of 65 minutes. It can be

inferred, therefore, that a minimum length of time must elapse between spermatophore production and copulation, and this time is greater for younger males than for older males. Most of the older males copulated soon after the female was introduced to the test chamber; one, may, therefore, assume that the older males had produced spermatophores before they entered the test chamber. During the test period 2 EO, 4 EY, 1 NY and 1 GY males produced spermatophores before copulation. The intervals from spermatophore production to copulation were consistent with those quoted above.

In preliminary studies done during the crickets' light phase, the majority of older males had long latencies to the first copulation. Most of those males (6 of 7) having short latencies were group-reared. Nowosielski and Patton (1963) showed that adult male crickets exhibit precopulatory display at highest levels during darkness and just before its onset when on a regular light/dark 12/12 hr. cycle. In light of this finding it is therefore hypothesized that a sexually mature male is usually in possession of a formed spermatophore during the time of greatest sexual activity but not at other times. Since the preliminary studies were done shortly after the onset of the light period, the animals would not be expected to have a formed spermatophore. Early copulation primarily among group-reared animals indicated that social stimulation enhances spermatophore formation during a normally quiescent period.

How are these observations connected with the failure of most younger males with adult social experience (AY and GY) to copulate (Table 2)? Since the younger animals had not yet reached the peak of sexual activity, the intervals between production of spermatophores were relatively long. Now it may be that

when a young adult male is subjected to repeated social stimulation spermatophore formation is induced. The spermatophore, however, becomes non-functional over time. Thus, at least 80% of the younger AY and GY males did not copulate relatively early in the observation period because they did not have formed and functional spermatophores (Table 23). The younger males tended toward longer latencies to copulation than did the older males. Apparently, even in the presence of a formed spermatophore responsiveness to sexual stimuli is lower in the younger males. In addition, forty percent of younger AY and GY males neither copulated nor produced spermatophores (Table 23). Thus it seems the social stimulation may further decrease this already low sexual responsiveness.

The intermediate position of younger NY males with regard to copulatory success indicates that social stimulation begins to have an effect during nymphal stages and that this effect persists into early adulthood.

C. RELEVANCE OF UNSUCCESSFUL MOUNTS TO APPROPRIATE COPULATORY RESPONSES

Appropriate copulatory responses do not seem to be directly related to sexual responsiveness. Many of the EY males did not actually transfer the spermatophore to the female (Table 9). These males exhibited copulatory movements when the female mounted and did not attempt to move out from under the female. EO males, on the other hand, interrupted mounts frequently (Table 4) and always succeeded in transferring the spermatophore to the female. The conclusion can be drawn that, in the absence of social experience, appropriate copulatory responses develop with chronological maturity.

Does the degree of social experience affect the development of appropriate copulatory response? Apparently, the answer is yes. All younger animals having had social experience succeeded in transferring the spermatophore to the female if they copulated at all. Furthermore, practically all of these animals were involved in unsuccessful mounts. The inference is made that social stimulation had provided the experience necessary for some development of the appropriate copulatory response. These younger animals, by virtue of social experience, had reached a stage in the development of appropriate copulatory responses that had been attained in chronological maturation by EO males.

D. MECHANISMS UNDERLYING THE EFFECT OF SOCIAL EXPERIENCE ON MATING BEHAVIOR

The rationale for this experiment was based on an hypothesis that social experience plays a role in the development and/or expression of the species-typical mating behavior of the house cricket. Although the presence of other species members has been shown to affect the growth rate of A. domesticus, there seems to be no effect on shape and function of body structures (Chauvin, 1958; McFarlane, 1962). But there are factors in addition to just morphology that can limit or channel behavior. The modification of the development and/or expression of house cricket mating behavior could happen with no known change in structure.

What other factors controlling or associated with mating behavior could be influenced by social experience? Certain neuroendocrine structures have been shown to affect aspects of mating behavior in the insects. Among these

are the corpora allata which are necessary for the development of sexual glands of female house crickets (Belyaeva, 1966). Mating in female cockroaches (Leucophaea) depends on the presence and activity of the corpora allata (Engelmann, 1960). If the corpora allata of male locusts are removed their accessory glands are rendered inactive (Loher, 1960) and normal sexual activity is prevented (Pener, 1965). However, Roussel (1967) found that Gryllus bimaculatus males allactectomized in the last nymphal instar acted normally, produced spermatophores, fertilized females and their eggs developed. Roussel suggested that the corpora allata have less of a role in sexual development of G. bimaculatus than in some other insects. No data are available on the effect of corpora allata extirpation and implantation in male A. domesticus. However, there is the possibility that these glands govern accessory gland activity in male house crickets as they do in the females of the species and in male locusts.

The corpora allata are innervated by neurosecretory as well as ordinary nerve fibers. Secretions of the median neurosecretory cells are thought to stimulate the development and activity of the c. allata, while conventional innervation from other areas of the protocerebrum transmit inhibitory impulses (Belyaeva, 1966; Hagadorn, 1967).

Stimulation of sense organs usually causes impulses to be transmitted to the brain. If these impulses are then relayed to the areas of the protocerebrum which give rise to the conventional innervation of the corpora allata, corpora allata activity could be inhibited. If these glands in fact control accessory gland activity in male house crickets, low activity of the corpora allata could be related to low activity of the male accessory glands. The same end result

could be obtained by the stimulation of sense organs preventing secretion by the median neurosecretory cells.

Low activity of the male accessory glands would be reflected in a low rate of spermatophore production and perhaps in the incidence of copulation. The experimental results support the hypothesis. Males that had social experience (=stimulation of sense organs) as adults tended toward infrequent copulation when they are young adults (Table 2), and long latencies to spermatophore formation even when the frequency of copulation increased in conjunction with increased age.

It is interesting to note that social deprivation of the normally gregarious cabbage aphid causes hyperactivity of the corpora allata (White, 1968). In the aphid, the hyperactivity was apparent in all the instars except the second. If corpora allata of younger deprived house crickets are also hyperactive, their greater degree of copulatory success can be readily understood.

E. THE DEPRIVATION TYPE EXPERIMENT

The "deprivation" experiment can not deprive the subject of all experience. An organism has experience simply by being (Lehrman, 1953; Schneirla, 1956, 1966; Shaw, 1962; Hinde, 1966). While this type of stimulation may be general, other self-generated stimuli may be specific. Are there specialized, self-generated stimuli that are active in the development of components of mating behavior? Alexander (1968b) states that when he destroyed the tympanic organs of many snowy tree crickets before they became functional, only two crickets were observed to stridulate. The song of one of these two was similar in most

respects to that of an unoperated cricket. (The song of the other cricket was not analyzed.) Alexander concluded that acoustic self-stimulation was necessary for the evocation but not the development of stridulation. It appears that while acoustic self-stimulation by stridulation may not be absolutely essential for the development and performance of a species-typical stridulatory pattern, such self-stimulation does play an important role.

The experimental "deprived" animals were exposed to stridulatory sounds produced by other animals, a situation not unlike that of solitary animals outside the laboratory. It was not expected that these "deprived" animals would produce stridulatory sounds atypical of the species. However, the context in which a particular stridulatory sound is produced may be affected by social experience. Unfortunately, the experimental procedure was not such that the type of sound being produced could be identified. So despite the absence of differences in total amount of stridulation among most groups, or the similarity of EY to older groups in the amount of stridulation before the first copulation, no conclusion can be drawn as to the quality of the stridulation.

Another source of self-stimulation that may be important is the pattern in which crickets frequently rub the cerci with their hind legs. Stimulation of the cerci can elicit movements facilitating a mount by a female (Huber, 1955). Cercal contact with the cricket itself (or with other objects) could provide a cricket with the experience necessary for the development of mating behavior.

The kind and frequency of stimulation are probably important in the development of mating behavior, while the actual source of the stimulation is probably of lesser importance. This means that deprived crickets could get

enough self-induced stimulation to, for example, cause hypoactivity of the accessory glands. It also means that it should be experimentally possible to make a completely socially deprived male act like a group-reared one. Norris (1962) did this by experimentally causing socially deprived male locusts to become more active physically, similar to group-reared males. These same animals exhibited slow sexual maturation--this also being a characteristic of group-reared males.

F. SOCIAL DEPRIVATION AND SEXUAL BEHAVIOR IN VERTEBRATES

It is of some interest to compare the effects of social deprivation on cricket behavior with those on the behavior of higher organisms.

Shaw (1962) studied the effects on platyfish of physical and visual deprivation. Four of her experimental groups corresponded with the experience groups employed in the present work. She found that the number of fish displaying sexual behavior increased with an increase in social experience. These results were exactly the opposite from those I obtained with younger crickets: more EY and NY displayed sexual behavior than did AY and GY. However, she noted that deprivation during the juvenile stage resulted in a disruption of positional orientation. NY males were apparently affected in a similar way since they were involved in more unsuccessful mounts than were other younger males. There must also have been a disruption of positional orientation of the EY males because they were frequently unsuccessful in transferring the spermatophore to the female.

Deprivation has been found to enhance male sexual behavior by

androgen-injected turkey poults (Schein and Hale, 1959). The experience groups were similar to those of Shaw (1962) and to those used in the present work. Again, however, the results do not parallel those obtained with crickets. Poults that were group kept and subsequently isolated responded to models in a sexual manner more than did isolated or group kept poults. Isolated poults held an intermediate rank while group kept poults ranked last. The investigators suggested that their results were not due to "prolonged differential social experiences". Subsidiary tests had indicated that continued exposure to sexual stimuli depressed sexual responses. The conclusion was drawn that the frequency or level of sexual responses were modified primarily by the "transient effects of continuous stimulation" (i. e., contact with other poults just prior to testing). Is this conclusion applicable to the outcome of the cricket experiments? There were no differences between AY and GY or AO and GO despite the fact that adult isolates had a "recovery" period. On the contrary, the short latencies to copulation by group kept animals in preliminary investigations indicate that there may be transient effects at certain periods of the day.

The dependence of adult mating behavior of male rats on presence of littermates during infancy also has been studied (Hard and Larsson, 1968). The rats were removed from littermates at two days of age but stayed with the mothers until weaning. Other males were reared with one littermate. Most peer deprived males did not mate until they had relatively long periods of contact with females while a few never mated. Peer-experienced males were highly successful in copulating and did so after shorter periods of contact with females. The tendency to approach and make contact was the same in all groups. The authors

stated that the retarded sexual development of the restricted males was basically due to deficiencies in the orientation of males and not due to incapacity to perform thrusting and intromission. Interestingly, once a deprived male copulated successfully, the normal mating pattern became established.

The restriction of social interaction of Rhesus monkeys from one month of age results in little sexual behavior (Mason, 1960). Furthermore, there are gross deficiencies in the organization of this behavior. On the basis of the data obtained, Mason suggested that the components of the male copulatory pattern are differentially dependent upon social experience. All restricted males approached the partner and attempted to mount. However, there was an absence of efficient and appropriate postural orientation with regard to the sexual partner.

From the studies cited, it seems that difficulties in positional orientation during mating behavior may be a general occurrence among socially deprived animals. In younger crickets, the adjustment in response to difficulties was dependent upon the extent of deprivation. Younger males with no social experience apparently did not attempt to compensate for improper orientation during a mount and therefore were frequently unsuccessful in transferring the spermatophore to the female. Younger males with experience in nymphal stages (NY) seemed to compensate by terminating a mount. The behavior of EO males demonstrated a persistent effect on positional orientation. Nevertheless, the increase in age was accompanied by the development of adjustment movements. These males were involved in more unsuccessful mounts and always succeeded in transferring the spermatophore to the female. However, the compensation was not fully effective as several animals did not satisfactorily attach the

spermatophore to the female.

With the crickets as well as with platyfish, rats and monkeys, deprivation did not affect approach to the partner. The amount of time spent near the female did not differ significantly among any of the cricket groups. It is therefore concluded that social experience has differential effects on the components of the male cricket's copulatory behavior pattern just as it does in the other animals.

This type of deprivation effect has been found to extend to other social behavior. For example, previously isolated kittens nuzzle a female's abdomen, but have difficulty in localizing a nipple (Schneirla and Rosenblatt, 1961).

The above discussion does not assume that the male's behavior is independent of that of the female. Social behavior by definition involves responses to other animals (Etkin, 1967). Adjustments in positional orientation, then, are adjustments to the mate. What role does female experience play in copulatory success of deprived animals? Mason (1960) found a striking increase in sexual responsiveness of restricted males when placed with socially experienced females. However, their sexual performance remained poorly integrated. The female crickets of the present work were all socially experienced with other females. Would male responsiveness (not performance) have been difficult had the females been socially inexperienced? Perhaps, but this question can not be answered now. The work by Sexton, et al., (1968) on the aggregation of crickets near "conditioned" paper is suggestive of a basic cricket tendency to respond positively to other crickets. Group kept females carry more of the conditioning agent than isolated females, thus enhancing the probability of "aggregation" in the mating situation. This kind of effect may explain why no group differences

were found in the number of minutes that the male spent near the female.

G. SOCIAL DEPRIVATION AND POPULATION SIZE

It is important to study the effect of social experience on mating behavior in an attempt to gain an understanding of the relationship between population density and population growth rate. Such a relationship has been demonstrated in many organisms (Allee, et al., 1949, pp. 349-355; Wynne-Edwards, 1962). In insects the cause of this relationship has generally been attributed to the availability or utilization of the food supply (Andrewartha and Birch, 1954). However, the behavior of animals reared at high densities is often different from that of those reared at low densities. For example, young adult Schistocerca gregaria males have a different activity pattern when crowded than when kept singly (Norris, 1962). Furthermore, social stimuli affect the developmental rate of mating behavior in locusts (Norris, 1954). It seemed possible that the behavior of house crickets might be altered if the type of social stimuli experienced at a particular stage of development were varied.

It has been proposed that self-limiting homeostatic methods of population density are present in practically all species of animals (Wynne-Edwards, 1962). Does the experiment reported herein support the hypothesis that "the actual regulation of population density is largely a matter of exercising control over recruitment and loss in the population" (Wynne-Edwards, 1962, p. 15)? Younger singly reared males copulated in more cases and more frequently than younger males with social experience as adults. On the other hand, group-reared males have more opportunities to copulate if females are present in the group.

Individual rearing is analogous to low population density. Early maturation of individually reared animals thus provides a mechanism for rapidly increasing the population density (i. e. , recruitment of new individuals). High density may delay recruitment by delaying sexual maturation.

However, singly reared males were notably deficient in transferring the spermatophores to the female. Does this deficiency cancel the impact of early maturation? Probably not since the crickets tend to remain together over several matings which increases the chance of eggs being fertilized. The important thing under low density conditions is to be sexually mature if and when a female is encountered. Any success at all in copulation enhances the probability of survival of the species and of increasing population size. Since EY males did copulate in greater numbers, copulate more frequently and have more success than did other younger males, this experiment provides partial support to Wynne-Edwards hypothesis.

H. SIGNIFICANCE OF THE STUDY

The significance of this study is severalfold. Primarily, it demonstrates that social experience can influence the development and expression of mating behavior of the male house cricket. Deprivation of social experience results in apparent acceleration of sexual development and difficulties in executing the mating act. The age of the crickets at the time of observation was shown to be important. Had two age groups not been studied, the impermanent effect of deprivation would not have been observed. Furthermore, although the study was horizontal, the duration of the observation period allowed some animals to

mate two or more times. This made it possible to make some longitudinal observations. Results of such longitudinal observations (Tables 2, 3, and 15) indicate that deprivation throughout adult life did not result in one step maturation. Younger males did not copulate as often per individual as did older males.

The importance of the time of experience is also demonstrated. The effects of deprivation were most pronounced in males deprived from the egg stage. The decrement in copulatory success from "totally" deprived to adult experienced males, combined with the relatively high incidence of unsuccessful mating or mounting by two deprived groups, has an important implication. The growth dependent processes of maturation operate simultaneously with social experience in the development of cricket sexual behavior. This concept was developed and discussed by Schneirla (1956, 1966).

Finally, the study indicates that the cricket mating pattern does not develop as a unit, all parts of which are affected equally by experience. Instead, it seems that the stridulatory mechanism can develop well ahead of sexual maturation. In turn, sexual maturation and positional orientation are not developed as a unit. Even positional orientation must have its subunits, as evidenced by the behavior of EY and EO males in regard to attachment of spermatophore and unsuccessful mounts. Attraction of individuals also is something different from sexual maturation.

I. IMPLICATIONS FOR FURTHER RESEARCH

The interpretation of the experimental results can not be ascertained as correct without further research. It was hypothesized that social deprivation

acted internally by affecting corpora allatal activity. If this is true, the corpora allata of younger deprived animals should be more well developed than those of socially experienced ones. Histological study would ascertain whether they are well developed. In conjunction with a histological study, the contents of the accessory glands should be examined to find out if corpora allatal activity is associated with production of spermatophore material.

The results concerning the number of unsuccessful mounts in different groups need to be re-examined. At the same time special attention should be given to the behavioral adjustments during mounts and the ultimate way in which the spermatophore is attached. It could then be determined if social experience actually improves the chances of insemination by improving positioning of the male.

The kind of stridulation performed during the observation needs to be carefully observed since there is the likelihood that the type of social experience affects the type of stridulation in a given situation.

Finally, experiments of the type reported herein ought to be done using female subjects and using both male and female subjects. It is highly likely that experimentation with socially deprived females would yield similar results. The mating of socially deprived animals of both sexes may lead to highly significant findings related to regulation of population size.

TABLE 26**Summary of results of statistical analysis**

<u>Table</u>	<u>Abbreviated title</u>	<u>Comparisons made</u>	
		<u>All groups</u>	<u>All old groups</u>
2B	Freq. Cop. (0 vs 1 or more cops.)	.001	--
2C	Freq. Cop. (1 vs 2 or more cops.)	--	--
3	Latency to 1st cop.	.01	--
4	Unsuccess. Mounts (Ovs 1 or more)	--	--
5	1st cop. to next mount	--	--
6	Unsuccess mounts before 2nd cop.	--	--
7	Interval from 1st to 2nd cop.	.01	--
8	Min from 1st cop to new spermato.	.001	.001
9	Fate of spermato.	-----	
10	1st cop to remov of spermato.	--	--
11	Loss of spermato. to 2nd cop.	--	--
13	Incd. time from 2nd cop to spermato	--	--
14	Min from 2nd cop to new spermato	--	.01
15	Min from 1st spermato to 2nd cop.	--	--
16	Min near female	--	--
17	Min near female between 1st & 2nd cops	--	--
18	Total min strid.	.01	--
19	Strid prior to 1st cop	--	--
21	Stridu between 1st and 2nd cop	--	--
22	Strid after change of orient prior to 2nd cop	--	--
23	Tot strid for males cop 2 times	--	--
24B	Cop and/or spermato by younger ♂	--	--
24C	Spermato prod vs cop for younger	--	--

TABLE 26

Table	Comparisons made																	
	Young grps	Ovs Y	EO NO	EO AO	EO GO	NO AO	NO GO	AO GO	EY NY	EY AY	EY GY	NY AY	NY GY	AY GY	EO EY	NO NY	AO AY	GO GY
2B	.01	--	--	--	--	--	--	--	--	.01	.005	--	--	--	--	--	.005	.005
2C	--	.001	--	--	--	--	--	--	--	--	.025	--	--	--	--	--	.025	.10
3	--	.0001	--	--	--	--	--	--	--	--	--	--	--	--	--	.01	.01	--
4	--	--	.005	.025	.05	--	--	--	.05	.05	--	--	--	--	.01	.025	--	--
5	.02	--	--	--	--	--	--	--	.02	--	--	--	--	--	.02	--	--	--
6	--	--	--	.05	--	--	--	--	--	--	--	--	--	--	--	--	--	--
7	--	.02	--	--	--	--	--	--	--	--	--	--	--	--	.036	.01	--	--
8	--	--	--	.025	.001	.05	.001	.001	--	--	--	--	--	--	.001	.025	--	--
9	-----																	
10	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
11	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
13	--	--	--	--	--	.05	--	--	--	--	--	--	--	--	--	--	--	--
14	--	--	--	--	--	--	.025	.025	--	--	--	--	--	--	--	--	--	--
15	--	.07	--	--	--	--	--	.01	--	--	--	--	--	--	--	--	--	--
16	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
17	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
18	.01	--	--	--	--	--	--	--	.01	.01	.01	--	--	--	.01	--	--	--
19	.001	--	--	--	--	--	--	--	.001	.01	--	--	--	--	--	.01	--	--
21	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
22	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
23	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
24B	--	--	--	--	--	--	--	--	--	--	.05	--	.05	--	--	--	--	--
24C	--	--	--	--	--	--	--	--	.025	.005	.005	--	--	--	--	--	--	--

VI. SUMMARY

1. Some literature pertaining to the biology of the house cricket was reviewed.
2. A 2 x 4 factorial design, with the variables of age and social experience, was used in an attempt to alter the mating behavior of male house crickets.
3. Experimental males were observed in a mating situation at the age of 2-3 days adult or 1-2 weeks adult. They were either socially deprived from the egg stage, socially deprived from the last nymphal instar, socially deprived on the first day of adulthood or group-reared throughout life.
4. The mating sequence was observed and described.
5. Statistical analyses were done for a number of aspects of the mating sequence. (For summary, see Table 25).
6. Younger adult males socially deprived throughout life were found to copulate significantly more frequently than those with social experience as adults.
7. Younger adult males socially deprived throughout life had shorter latencies to the first copulation than did those deprived of social experience during the adult stage.
8. The intervals between the first and second copulation were longer, in general, for younger males than for older males.
9. The interval from first copulation to spermatophore formation increased with increasing social experience.
10. Younger males socially deprived from the egg stage stridulated much less than any other younger group. They differed from their older counterpart group in the total minutes of stridulation but not in the amount of stridulation

before the first copulation.

11. The rationale for the experiment was discussed.

12. Deprivation and the kinds of stimuli available to the deprived animal were discussed.

13. The hypothesis was formulated that social experience affects the mating behavior of male house crickets by affecting corpora allata activity which in turn acts on the accessory to control spermatophore production.

14. Effects of deprivation on house crickets and select vertebrates were compared. The conclusion was drawn that deprivation adversely affects positional orientation during the mating sequence.

15. The data seemed to indicate that social experience is not an important force in the regulation of the density of cricket populations.

16. A discussion was given on the significance of the study.

17. A brief discussion was devoted to the kinds of research that would be desirable to follow up this experiment.

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Autobiography

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