

FOOD AND WATER DEPRIVATION EFFECTS ON REPRODUCTION
OF FEMALE Blattella germanica (L.)

by

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INTRODUCTION

The German cockroach, Blattella germanica (L.), has been the focus of numerous studies due to its importance as an insect pest in many areas of the world. Although its status as a carrier of human disease may be questionable, there is little doubt that this cockroach species is a nuisance in homes, restaurants, hospitals, on ships and in numerous other places (Mallis, 1969).

This cockroach is found in warm, moist environments with dark hiding places such as cracks and crevices (Cornwell, 1968). The German cockroach may be active at any time of the day but peak activity occurs during periods of darkness. The activity patterns of B. germanica may be associated with the need for food and water since these basic necessities cannot be present in all harborages. Indeed, Ebeling et al. (1966) caught more cockroaches in food-baited traps when there was no food in the area for the previous two days.

Food availability is closely associated with the development and reproduction in the German cockroach. Since food consumption during the reproduction is cyclic (Cochran, 1983), the effects of food stress depend on when in the reproductive cycle food is unavailable. Food is necessary for mating in B. germanica (Roth and Stay, 1962). Starvation will lead to delays in the production and hatch of viable oothecae (Kunkel, 1966).

Although crucial for survival, the importance of water to normal reproductive processes of the German cockroach has not been

well-studied. The basic water requirements of the female during reproduction have been reported (Cochran, 1983). The needs of the female are high during periods of reproduction since she has to meet the demands of both her metabolism as well as those of the developing oocytes (Roth and Willis, 1955a).

Since the basic patterns of food and water consumption have been reported, this study was undertaken to examine the effects of food and water stress on the reproduction of the German cockroach. Food and water were deprived for various periods of time following landmark events in the female reproductive cycle.

The main objectives of this study were:

- (1) to gather additional information on the basic biology of the German cockroach;
- (2) to verify the results of previous studies in regard to the food and water requirements of the female during reproduction;
- (3) to study the effects of food deprivation at different periods of the reproductive cycle in order to determine whether starvation will delay reproduction, decrease fecundity, or increase mortality of the female;
- (4) to study the effects of water deprivation at different periods of the reproductive cycle in order to determine whether the absence of water will delay reproduction, decrease fecundity, or increase mortality of the female;
- (5) to determine the relative importance of food versus water in regard to reproduction and survival of the female.

The results of these temporary food and water deprivations, as well

as additional information about the basic food and water requirements of the female during reproduction are presented here.

LITERATURE REVIEW

General Biology of the German Cockroach

Cockroaches, in general, are influenced by environmental factors such as light, temperature, and humidity. They prefer warm, moist environments (Cornwell, 1968; Gunn, 1935; Gunn and Cosway, 1938; Fleet, et al., 1978) although humidity preferences aren't as important if water is available (Gunn, 1935). Cockroaches depend on their environment to warm or cool their body to an extent. Gunn (1935) reported that Blattella germanica prefers temperatures between 24-33°C. He also observed that B. germanica will move to areas of higher humidity when they are desiccated. Haber (1926) reported a temperature preference of 20.6°C with 75 per cent relative humidity for B. germanica. Temperature may exert even more of an influence on cockroach activity. Warm temperatures increase activity whereas cooling inhibits activity. Mellanby (1939) observed that cold causes cockroaches to be immobile and in a "chill-coma." At the other extreme, respiratory water loss is the major deterrent to survival at high temperatures (Gunn, 1933). Cornwell (1968) states that the upper temperature limit is fixed by the rate of desiccation. Ramsey (1935) showed that evaporation increases with high temperatures (above 30°C) but much of the loss is through the body surface rather than through respiratory movements.

B. germanica exhibits a daily activity pattern with peaks at dawn and dusk (Sommer, 1975; Dreisig and Nielsen, 1971) although in

heavy infestations they may be active at almost any time. The latter concluded that this is an endogenous rhythm, not depending upon environmental stimuli. However, Sommer (1975) reported that activity increases in females following water deprivation and Harker (1958) observed that food limitation may also be important in establishing the rhythm phases. Van Herrewege and David (1974) suggested that food and water searches were the causes for the daily activity patterns. Ebeling et al. (1966) caught more cockroaches in food-baited traps when food was unavailable in the area for the previous two days. From these studies, it would appear that food and water availability are important in determining activity.

Water

As in many other organisms, water is one of the most important factors limiting B. germanica populations. Water balance is intimately associated with the temperature and humidity preferences of the cockroach. Since B. germanica lives in a warm microclimate, it must find ample water in order to prevent desiccation.

Willis and Lewis (1957) found that adult female German cockroaches survived approximately 12 days without water at 40 per cent humidity but 42 days with only water. At 70 per cent relative humidity, survival without water increased to 18 days but 28 days with water only. Maluf (1939) reported survival of the Oriental cockroach at room temperature without food or water to be 20-60 days whereas Haydak (1953) found two females which survived 11 and 12 days at the same conditions. The latter is in closer agreement with the findings

of Willis and Lewis (1957) for the same species.

Mueller (1978) reported that a regular water supply is necessary for normal development of B. germanica and that water deprivations lead to delays in reproduction and increased mortality. Cochran (1983) showed water consumption by the female to be greatest following the molt to adulthood and prior to oothecal formation. Oothecal hatch is dependent on the water content of the ootheca (Cornwell, 1968). Approximately 60-65 per cent of a newly formed ootheca with eggs is water in those cockroaches which drop their oothecae soon after formation (Roth and Willis, 1955b). These oothecae are usually tough and water-impermeable. The German cockroach, on the other hand, forms an ootheca which is soft and permeable at its anterior end which remains attached to the female. Through the loss of dry matter and the uptake of water from the female, the oothecal water content increases from 62 to 76 per cent by the time hatching occurs (Roth and Willis, 1955b).

In female Leucophaea maderae, daily water consumption is greatest shortly after parturition (Scheurer and Leuthold, 1969). These authors reported that large amounts of water are transferred to developing eggs in the ootheca twenty days after ovulation but there is little change in the hemolymph volume. It would seem that water deprivation then would have little effect on water transfer to the eggs since the necessary water would be withdrawn from the fat body.

Verrett and Mills (1973, 1975, 1976) have studied the water relations of Periplaneta americana during reproduction. They found that female consumption of water is greatest during the first two days of the six-day vitellogenic cycle, with consumption peaks occurring on

days 2 and 5. They postulated that the first peak coincided with the peak in food consumption and the second peak was related to the needs of the ootheca. Total body water of the female was greatest the first two days of the vitellogenic cycle, then declined. The amount of tissue water followed the same pattern although the hemolymph volume remained constant. They concluded that there was water storage in some other tissue besides the ovarioles. They also looked at the effects of removing the frontal ganglion. Removal impaired water ingestion to an extent; however, they were still able to drink. Frontal ganglionectomy led to 35 per cent mortality in 5 days mainly through water loss due to transpiration. Oocyte maturation was also inhibited due probably to a lack of hemolymph water. It also is possible that the corpora allata have an influence on cockroach drinking behavior since the corpora allata influence water uptake and balance in other insects (Pfeiffer, 1945; Strong, 1965).

Cockroaches have become successful at solving the water problems associated with oothecal hatch. Many species, such as the Oriental cockroach, have a hardened ootheca covered with a waxy material to prevent water loss (Cornwell, 1968). Hatching will occur from oothecae held in completely dry air, and there is little additional water loss when temperatures are increased to 40°C (Cornwell, 1968). However, damage to the ootheca leads to an increase in water loss.

The German cockroach protects its ootheca from desiccation by formation of an ootheca with differing amounts of sclerotization. Roth and Willis (1955a) observed that the posterior end of the ootheca is heavily sclerotized and impermeable compared to the anterior end.

They also showed that age of the ootheca at detachment, temperature, and humidity are all important factors in whether a prematurely detached ootheca will hatch. Although Ross (1929) reported that oothecae detached nine days after formation will hatch if kept moist, the water content of the newly formed ootheca is enough to allow the eggs to hatch without additional water from the mother (Cornwell, 1968). The amount of water lost from an ootheca depends more on its age than on the humidity with evaporation losses being the greatest 4-6 days after oothecal formation (Roth and Willis, 1955b).

Nutrition

Cockroaches are capable of surviving on many different foods, even those of poor quality in small quantities (Gordon, 1959). Evidence for this comes from the multitude of diets used to rear them. Combinations of many different food items have been used--skimmed milk and whole wheat; sugar, salt, casein and starch in various combinations with cod-liver oil and dried yeast; linseed oil meal; protein, yeast and lettuce are only a few of the diets studied (Chauvin, 1949; McCay, 1933; McCay, 1938, Melampy and Maynard, 1937). The requirements of insects for certain nutrients depend on the species.

Proteins and amino acids are essential for development and reproduction (Johansson, 1964). Haydak (1953) reported longevity of adult female B. germanica to be greatest on a 11-24 per cent protein diet. Longevity in this species decreased as the protein was increased above that level. Other species such as Blatta orientalis and Periplaneta americana can develop on a high protein diet but the German cockroach

cannot. Johansson (1964) reported that carbohydrates are necessary to maintain life in insects and this is true for the German cockroach (Gordon, 1959). Little is known about the requirements for dietary fat (Guthrie and Tindall, 1968) although if either glycerol or fatty acids are missing, B. germanica can synthesize the absent one to form the fat (Haber, 1926). Gordon (1959) also reported the need for magnesium and other trace minerals. Dadd (1960) reported that insects require dietary sterols for survival and Chauvin (1949) observed the need for sterols in B. germanica in order to reproduce.

The association between nutrition and the reproduction of insects is well known (Grisson, 1958; Wigglesworth, 1960; Slansky, 1980a,b). Emery (1896) spoke of "alimentary castration" whereas Marchal (1897) used the term "nutritional castration" to describe the relationship of food and reproduction. Johansson (1964) reported that diet plays an important role in egg production and Chapman (1971) concluded that protein is important for yolk production.

Van Herrewege (1969) found food consumption to be greatest in B. germanica prior to each molt. Kunkel (1966) observed that the interval between nymphal molts increased when food was deprived. If food was not regularly available, nymphs developed slower and mortality increased (Mueller, 1978). Noland, et al. (1949) found development of B. germanica to be faster on a synthetic diet but a dog biscuit diet led to better reproduction. Haydak (1953) reported that adult females consume between 1.4 - 2.3 mg. of food daily depending on the protein present in the food.

Starvation Effects

Starved adult female B. germanica can survive 41.9 days if water is available but only 12.8 days without food or water (Willis and Lewis, 1957). Starvation has a tremendous impact on reproduction but these effects vary with the insect species. Starvation greatly decreases the fecundity of Agrotis segetum but only slightly reduces fecundity of Pyrausta nubialis (Kozhantshikov, 1938). Blake (1961) observed an increase in the number of eggs produced by a Dermestid beetle held without food or water. Johansson (1964) reported that if an insect adult requires food for egg production, then for continuous egg production constant access to food is necessary. Egg production will cease if food is removed following an initial feeding period. Females which lay their eggs in batches usually must feed to produce their next batch of eggs. Starvation may indirectly affect reproduction by influencing the corpora allata (Johansson, 1964). Engelmann and Rau (1965) reported that starvation reduced hemolymph protein levels in Leucophaea maderae but feeding replenished them. Cochran (1983) found food consumption by B. germanica to be cyclic in association with the reproductive events. Under periods of food stress, German cockroaches produce fewer, smaller oothecae (Mueller, 1978) and the reproductive cycle is delayed (Kunkel, 1966). Starvation does not seem to influence mating of Nauphoeta cinerea (Roth, 1964) but German cockroaches held without food will not mate (Roth and Stay, 1962). Engelmann and Rau (1965) reported the association between feeding and reproduction in L. maderae with food necessary for oocyte maturation (Scharrer, 1946).

Food consumption is necessary for oothecal formation in both Blattella and Periplaneta (Kunkel, 1966). Blattella females use up to 90 per cent of their food reserves, accumulated during the preovipositional period, to produce a single ootheca. Additional oothecae are produced only after subsequent feedings. Kunkel (1966) found that Periplaneta females continued to produce oothecae even following starvation. They formed 4-5 additional oothecae; however, these oothecae were smaller than usual. Weaver and Pratt (1981) reported that an ootheca of this species represents 7 per cent of the weight of an unstarved female so that only a limited number of oothecae can be produced from food reserves during starvation. During starvation, most of their females produced only 1 or 2 additional oothecae. Bell (1971) found that oothecal production in P. americana fell after starvation began. All females produced one ootheca besides the one they were forming when starvation started but only 32 per cent produced a third one. Mills et al. (1966) observed that P. americana females feed only the first 2-3 days of the oocyte maturation period. Weaver and Pratt (1981) suggested that starvation leads to a decrease in oocyte growth such that the oviposition cycle is lengthened leading eventually to the shutoff of corpora allata activity. If starvation continues, then reproduction is stopped. When food becomes available, endocrine activity resumes and reproduction follows. The authors suggest that juvenile hormone production is altered by the corpora allata during periods of food stress.

Mating Behavior

In some species, volatile sex attractants are produced by the female, sensed by the male at a distance and the two begin their characteristic mating behavior actions (Barth, 1962). However for the German cockroach, physical contact between the two sexes is necessary to start the male courting behavior. A non-volatile sex attractant is produced on the female integument (Roth and Willis, 1952). The male and female make antennal contact, during which the male picks up the attractant from her and courtship begins.

When the male German cockroach has been sexually stimulated, he raises his wings to expose the openings to two pairs of dorsal abdominal glands. These glands produce a secretion which the female is attracted to. Access to these glands is impossible when the male is at rest so the wings must be raised and the abdomen extended in order to allow courtship to continue. The female mounts the dorsum of the male to feed on these secretions; the male then pushes his abdomen under the female and clasps her genitalia. If successful at genital coupling, the male then twists his abdomen such that the two sexes are end to end. A successful copulation will last an hour or more (Roth and Willis, 1952).

These authors made a detailed study of the mating behavior of B. germanica. They found that males can distinguish between sexes by antennal contact since they fail to begin courtship behavior after contact with another male. Physical contact is required to elicit the behavioral response of the male. A male may be stimulated right after maturation and even by ootheca-bearing females although copulation

will not occur.

Receptivity of the female to mating may depend on several factors, one of which is her nutritional state. In the cockroach Bysotria, a small meal increased receptivity even though the meal was inadequate for vitellogenesis (Roth and Barth, 1964). These authors suggested that food intake triggered functioning of the neurosecretory system. The effects of starvation on mating of B. germanica and N. cinerea were discussed earlier. Chapman (1971) found that oocyte maturation was not necessary for mating of locusts to occur. Engelmann (1960) reported that removal of the ovaries of L. maderae did not eliminate the female response to males.

Evidence that mating is under endocrine control came from observations of L. maderae by Engelmann and Barth (1968). Allatectomized females were more sluggish than normal females in responding to the courting actions of males. Eventually up to 50 per cent of these allatectomized females mated whereas 100 per cent of allatectomized L. maderae were observed to mate in studies by Roth and Barth (1964). In some species it would appear that mating is under endocrine control but in the cockroach Diploptera punctata (Engelmann, 1959) and the cricket Gryllus it is not (Roussel, 1967).

Reproductive Cycle

Shortly after the molt to adulthood, the female B. germanica becomes sexually receptive. The period until mating may be 4-6 days (Ueda et al., 1969), 8-14 days (Roth and Stay, 1962), or about 10 days (Cochran, 1983). This time period may be related to the conditions

under which rearing took place. Females may mate more than once although one mating is enough to fertilize all of the eggs produced in a lifetime (Woodruff, 1938; Cochran, 1979).

Following mating, the female cockroach undergoes a sequence of events leading to the formation and eventual hatch of the ootheca. The first process, that of oocyte formation and maturation, may occur prior to mating in some species. Amerson and Hays (1967) followed oocyte development in German cockroach nymphs. The oocytes are well-developed but still immature by the final nymphal stage. Shortly after maturation, the female has mature eggs present. Roth and Stay (1962) reported that the oocytes were 0.5 mm less than 1 day after emergence but reached 2.7 mm by oviposition. The eggs are usually fertilized as they pass from the common oviduct toward the ootheca (Cornwell, 1968). Unmated B. germanica females may produce oothecae but these will not hatch. Parthenogenesis is known for several cockroach species (Roth and Willis, 1954; Willis, Riser, and Roth, 1958) but not for B. germanica.

The ootheca is formed 2-4 days after mating (Haber, 1919) or after 4.1 days (Cochran, 1983). The ootheca is completely formed approximately 15-24 hours after it is first visible protruding from the abdomen. Unlike many cockroach species, B. germanica females carry the ootheca until just before the eggs hatch although sometimes hatching occurs while she is still carrying the ootheca. Roth and Willis (1955) reported the period until hatch to be 17 days, Cochran (1983) found it to be 27 days and Rau (1944) observed it to be between 6 and 16 days with an average of 10 days. Although there no doubt are

individual variations, these differences are probably due largely to temperature differences. Indeed, Gould (1941) reported that the incubation period was shortened from 28 to 17 days by raising the temperature from 25-30°C. After the ootheca hatches, it is usually a week to ten days before the second ootheca is formed (Cochran, 1983). This ootheca is carried the same length of time as the first. Hatching may occur at any temperature between 15-35°C (Ross, 1929). After the third or fourth ootheca, the number of eggs hatching begins to decrease (Willis et al., 1958). The average number of nymphs emerging is variable; Cochran (1983) reported 36 nymphs hatching from 42 egg compartments, Willis et al. (1958) counted 28 nymphs emerging from 37 eggs whereas Woodruff (1938) observed 32 nymphs emerging.

Endocrine Control of Reproduction

The cyclical nature of cockroach reproduction suggests that reproduction is under endocrine control. Wigglesworth (1936) reported that a hormone from the corpora allata controlled yolk deposition in Rhodnius. Since then hormonal control of oocyte development has been found in all cockroaches studied (Cornwell, 1968). Oocyte maturation and corpora allata activity parallel each other in L. maderae (Luscher and Engelmann, 1955). The gonadotrophic hormone does not affect the ovaries of P. americana until after molting such that inhibition of oocyte growth can occur before yolk is deposited (Girardie, 1962).

In B. germanica, egg maturation in the ovary is very slow while the female is carrying an ootheca (Roth and Stay, 1962). These authors also found that oocytes increase greatly in size during production of

the next ootheca. Oocyte production may be quickened by removing an ootheca before it is ready to hatch (Parker and Campbell, 1940). The attachment of the ootheca to the female apparently inhibits release of the gonadotrophic hormone from the corpora allata. Roth and Stay (1962) suggested that hormonal activity resumes following hatch or experimental removal of the ootheca. The corpora allata increase in size during periods of yolk deposition (Luscher and Engelmann, 1955). They also reported that the volume of the corpora allata changes in cycles. The glands are activated following mating, inactive during pregnancy, and active again after the ootheca hatches. The relationship between mating and corpora allata activity is important. For P. americana, mating increases the total number of eggs laid by accelerating egg maturation (Griffiths and Tauber, 1942; Roth and Willis, 1955). Engelmann (1960) and Roth (1964) reported the same to be true for L. maderae and N. cinerea respectively. It logically follows that mating stimulates the corpora allata since egg maturation is under hormonal control for some species (Scharrer, 1946; Girardie, 1962; Roth and Stay, 1962). Mating accelerates egg maturation in B. germanica by two days although the mechanism by which mating stimulates endocrine activity is unknown (Roth and Stay, 1962).

Inhibition of the corpora allata has been reported to occur in one of two ways (Engelmann, 1964). Roth and Stay (1959, 1961, 1962) suggested that nervous stimuli inhibit the corpora allata whereas Engelmann (1964) proposed a humoral mechanism between the genitalia and the central nervous system. Allatectomized mated female B. germanica have inhibited oocyte development; implantation of the corpora

allata leads to oocyte maturation and oothecal production (Roth and Stay, 1962). Following experiments with artificial oothecae and B. germanica, these same authors believed that the inhibition of oocyte development while the ootheca is being carried is due to nervous involvement resulting from oothecal pressure on the genital chamber. As the ootheca increased in size, it stimulated stretch receptors leading to nervous inhibition of the corpora allata. If the nerve cord is cut, nervous impulses fail to reach the brain and corpus allatum activity continues as does egg maturation. Morphological evidence for the stretch receptors is lacking (Cornwell, 1968). If the ootheca was replaced with glass beads or an artificial ootheca, egg maturation continued to be inhibited (Roth and Stay, 1959). Engelmann (1964), however, reported that inhibition of oocyte development was caused by a chemical agent from the ootheca which acted on the nerve cord. He postulated that the eggs or the distended brood sac released this substance which then acted on receptors in the abdominal ganglia and the brain. No extracts from the ootheca or brood sac have been found which inhibit the corpora allata of cockroaches. It is evident that the nervous and endocrine systems control oothecal development. Nevertheless, the pathways leading to cyclic activity of the corpora allata remain unknown.

Oocyte Resorption Under Stress

Oocytes in the ovarioles may be destroyed and their contents resorbed in many insect orders such as Diptera, Hemiptera, Coleoptera, Hymenoptera, Orthoptera and Dictyoptera (Chapman, 1971). The terminal

stages of oocyte development are most subject to resorption although all stages of oocytes may undergo resorption. The follicle cells break down the yolk and then are digested themselves. The nutrients may be used by the mother for her needs (King and Hopkins, 1963). Hopkins and King (1964) reported that resorption occurs under conditions of stress such as starvation. Chapman (1971) observed that the lack of fertilization causes resorption in some insects. For Schistocerca, the presence of a hormone and blood protein availability are influential (Highnam, Lysis, and Hill, 1963). Scharrer (1946) found that the removal of the corpora allata during vitellogenesis leads to oocyte degeneration and yolk resorption in L. maderae. Bell (1971) reported that, in P. americana, oocyte resorption begins 7-10 days after starvation. Blood protein synthesis decreases while vitellogenic blood protein concentrations increase. Oocyte resorption is a result of the inhibition of juvenile hormone secretion, a paucity of yolk precursors or a combination of the two. For Blatta orientalis, Sams (1975) reported that starvation leads to vitellogenic arrest but resorption does not immediately follow; rather, the oocytes remain in a minimal metabolic state.

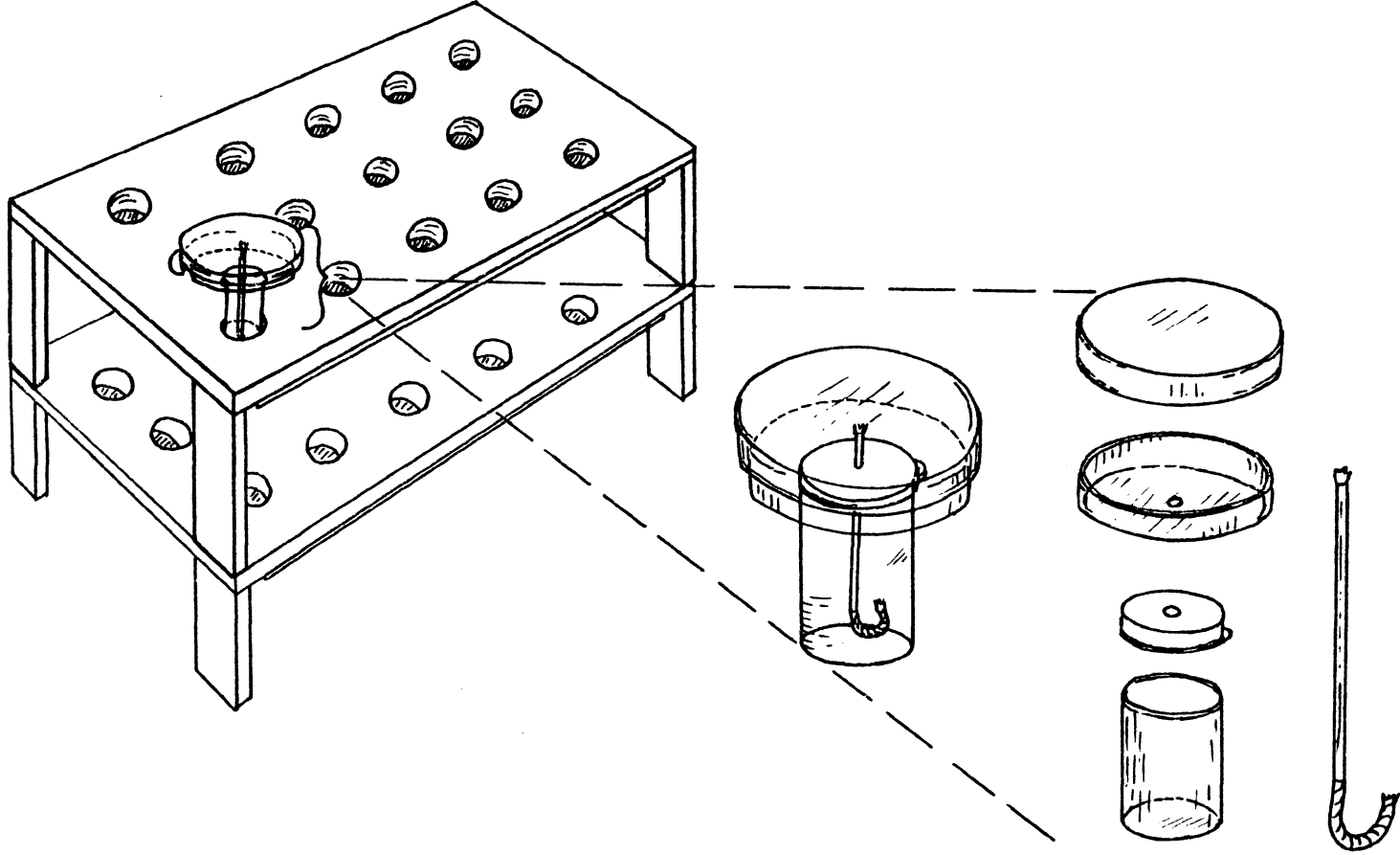
MATERIALS AND METHODS

The German cockroaches, Blattella germanica (L.), used in this study were from stocks maintained by the Department of Entomology, Virginia Polytechnic Institute and State University. The VPI-normal strain, maintained in culture since 1947, was used. This strain was reared in battery jars having fiberboard spacers. A double layer of cheesecloth served as a cover. A Petri dish containing a damp sponge, and a paper cup filled with dry dog food were included in each jar. Rearing took place in a room where the temperature ranged from 21-25°C with the humidity and photoperiod being ambient.

Late-instar nymphs were removed from these stocks and reared to adulthood in similar battery jars in a modified environmental chamber located in an adjacent room. The temperature in this chamber was held between 25-27°C with a photoperiod of 14 D:10 L. A constant relative humidity of 40-50 per cent was maintained using a saturated salt-sugar solution (Winston and Bates, 1960). A Bristol's Thermo-Humidigraph recorded the temperature and humidity continuously.

Upon reaching adulthood, males and females were removed daily from the battery jars; males were placed in a different battery jar, whereas females were placed in individual rearing chambers like those described by Cochran (1983). These chambers (Fig. 1) consisted of a plastic water vial and a covered Petri dish which fit on top of the vial. A small glass tube, inserted through the lid of the vial, extended nearly to the bottom of the vial. A cotton wick was pulled

Figure 1. German cockroach rearing apparatus



through the tube to extend out both ends of the tube. This arrangement produced a column of water when one end of the wick was submerged in the water within the vial. When the Petri dish was placed on the water vial to allow the insect to drink, the water tube extended into the dish through a small hole in the dish bottom. A filter paper circle was cut to fit the Petri dish and served as a liner. The circle also had a hole cut in its center to allow the water tube to pass through the dish without the filter paper absorbing water. A stainless steel planchet containing a dry dog food pellet was included in each chamber along with a small, black construction paper harborage. Fifteen of these rearing chambers fit on each specially constructed wooden tray.

Food and water consumption were measured daily except during deprivation periods. The planchet with food was weighed on a Mettler Gram-matic balance accurate to ± 0.05 mg. Food consumed per day was considered to be one meal. Water consumption was more difficult to quantitate due to evaporation. Evaporation losses over a twenty-four hour period were large in comparison with the small amounts drunk over the same period. For this reason, the method of Cochran (1983) was used. This method consisted of removing the water vial for 23 of every 24 hours. Water was available for one hour daily. Each water vial was weighed before and after the one hour period. The amount of water which evaporated during the hour was determined from control vials and was used as a correction factor. That factor, based on 80 observations, was $10.8 \pm 0.2 \mu\text{l}$ per hour (mean \pm S.E.M.) (Cochran, 1983). This method of providing water did not seem to hinder reproduction or to affect the longevity of the insects.

A special procedure was followed for mating the females as necessary. Daily, beginning with the fifth day after the females reached adulthood, a VPI-strain adult male was placed into each chamber for the purpose of mating. The chambers were observed at half-hour intervals for approximately three hours. Successful matings take an hour or more (unpub.) so more frequent checks were unnecessary. After the three hour period had elapsed, males were removed and returned to their battery jar. This procedure was repeated daily until all females had mated. One mating per female was shown to be adequate for reproduction to occur in most females (Cochran, 1979). Each male was used for one mating only.

When an ootheca hatched, the number of nymphs hatching and the number of compartments in the ootheca were counted and recorded. The nymphs were then discarded. Each experiment was continued until the second ootheca had hatched.

Careful records were kept for each female. These records included the day each landmark event of the reproductive cycle occurred--adult maturation, mating, oothecal production and hatch--and the periods between these events. Individual records of food and water consumption were kept and the amounts consumed during each period were calculated. Data on mortality were collected and any abnormalities in development or reproduction were noted.

Deprivation Experiments

Post-Maturation

After molting to adults, sixty females were placed into individual rearing chambers (4 trays of 15 chambers per tray) for this water deprivation study. Food was available continuously. The control females were allowed access to water for one hour daily. Water was taken away from the other females on the day they became adults. The water was unavailable to these three groups of females for 3, 7, or 12 days. Water was then returned to each female for one hour daily until hatch of the second ootheca. All surviving females were given the opportunity to mate beginning five days after maturation.

For the food deprivation study, another sixty females were placed into individual rearing chambers following their molt to adulthood. Water was available for one hour daily. Food was available continuously to the control group of females. Food was unavailable to the other three groups of females for 3, 7, or 12 days following their maturation. Food was returned the day after each deprivation period and was available continuously until the second reproductive cycle was completed. All the females had an opportunity to mate beginning five days after they matured.

Post-Mating

For this study, ninety adult, virgin females were placed in individual rearing chambers with food and water available. The females were allowed to mate. There were six groups of fifteen females per group. The first three groups of females to mate were deprived of

water for 3, 7, or 12 days after which the water was available for one hour daily. Food was available continuously to these females. The final three groups had water available for one hour daily but food was unavailable for 3, 7, or 12 days following mating. After each deprivation period was over, the food was returned to all survivors and remained available until the second ootheca hatched.

After First Oothecal Hatch

Ninety females carrying their first oothecae were placed in individual rearing chambers; six trays of fifteen females each were set up. Each female had food and water available continuously until her ootheca hatched. The number of nymphs that hatched and the number of oothecal compartments were counted and recorded for each female. Water was taken away from the females on the first three trays the day the ootheca hatched but food remained available. Fifteen females were deprived of water for three days; fifteen females were held without water for seven days while a third group of fifteen females had no water for twelve days. Water was returned to all survivors the day following the deprivation for one hour daily until the second reproductive cycle was completed. The females on the other three trays were kept without food following the oothecal hatch. Water was available for one hour daily. The females on one tray had no food for three days while the females on the final two trays were deprived of food for seven or twelve days each. Food was returned and available continuously following the deprivation periods.

While Carrying First Ootheca

Newly emerged adult females were placed in a battery jar containing males. Food and water were available continuously in the jar. The jar was checked daily and any female carrying an ootheca was removed and placed in an individual rearing chamber. Forty-five of these chambers were set up, 15 on each of three trays. The females in the first two trays were given access to water for five days after they produced their oothecae. On the sixth day, the water was taken away from the females on one tray for 7 days; the other group had no water for ten days. Water was returned to any survivors for one hour daily following the deprivation period. Food was available continuously throughout the study. Only these two lengths of deprivation were chosen since earlier results indicated the ability of some females to survive more than five days without water during the incubation period with no obvious ill effects.

The third group of fifteen was held without food for the entire incubation period although water was available continuously. Based on previous results, three, seven, or twelve days without food during this period did not reduce hatch or increase mortality of the female. Some females did not feed or fed only once while carrying an ootheca. Food was withheld until the ootheca hatched and was available continuously for the rest of the study.

Statistical Analysis

The statistical analysis of this experiment was completed with the aid of Dr. G. I. Holtzman of the VPI&SU Statistics Department.

An Analysis of Variance procedure with the Duncan's Multiple Range Test was performed on the data. Means \pm the standard deviation of the mean were calculated for the data.

RESULTS

Controls

The general food and water requirements of the female during reproduction are shown in Table 1. Food consumption was greatest following the molt to adulthood prior to production of the first ootheca. The large amount of food consumed was probably necessary to meet both the basic metabolic needs of the female as well as the needs of the maturing oocytes. The cyclic pattern of food consumption is shown in Figure 2. Approximately one day after maturation feeding begins at a high level. Nearly all females fed for the next 3 days and over 80 per cent of the females fed every day until mating. The latter also consumed greater than normal amounts of food during this period. They ate between 5-10 mg. of food per day until mating occurred. Once a female had mated the amount of food consumed per day dropped sharply. The low level of feeding continued through the incubation period. During this time less than 1 mg/day was eaten by each female; each female also fed very infrequently. On the day that the first oothecae hatched, more than 60 per cent of the females fed but they consumed only small amounts of food. The next three days all females fed as food consumption peaked at over 10 mg/day on the second day following oothecal hatch. Food consumption and the percentage of females feeding then declined steadily until the second oothecae were produced. Reduced feeding (less than 1 mg/day) continued through the second incubation period. The general pattern of food consumption

Table 1. Calculations on food and water consumption of control females.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Food Eaten per Day (mg) ^b	Total Water Drunk (μl)	Total Drinks	Water Drunk per Day (μl) ^b
A-M	45.3±7.3 ^c	5.1	136.2±42.2 ^c	6.7±1.9	15.5
M-EC1	8.1±2.9	2.1	51.7± 8.9	2.6±0.8	13.3
EC1-ECH1	16.6±4.1	0.8	102.3±23.5	7.6±3.6	5.2
ECH1-EC2	35.7±6.1	5.6	122.4±17.2	5.4±0.7	19.1
EC2-ECH2	15.8±3.5	0.8	108.6±18.9	6.7±1.4	5.2

^aAbbreviations: A = maturation, M = mating, EC = oothecal production, ECH = oothecal hatch

^bThe intervals for these calculations are shown in Table 2.

^cMean ± standard deviation.

Figure 2. Food and water consumption by control Blattella germanica during reproduction: first reproductive cycle.

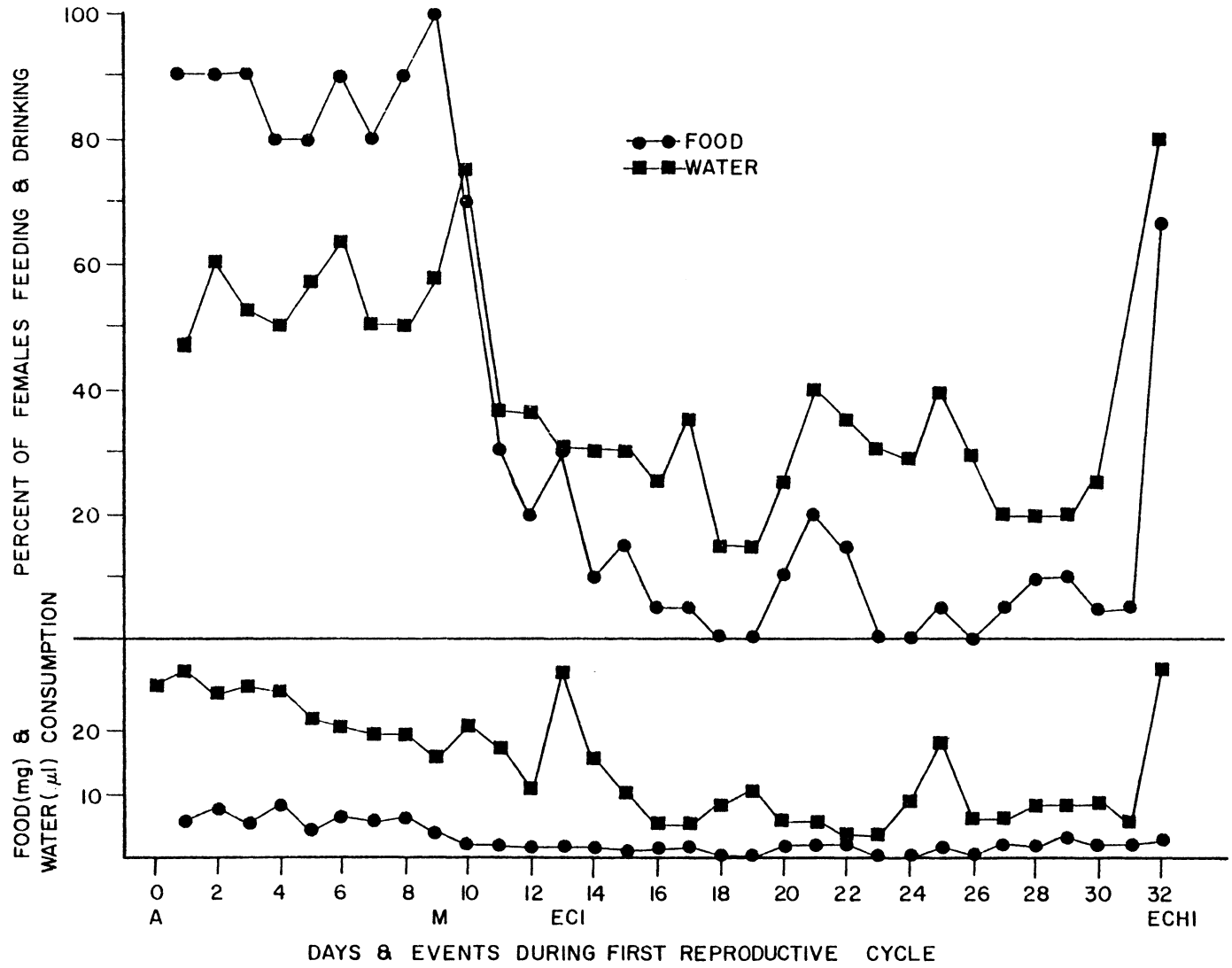
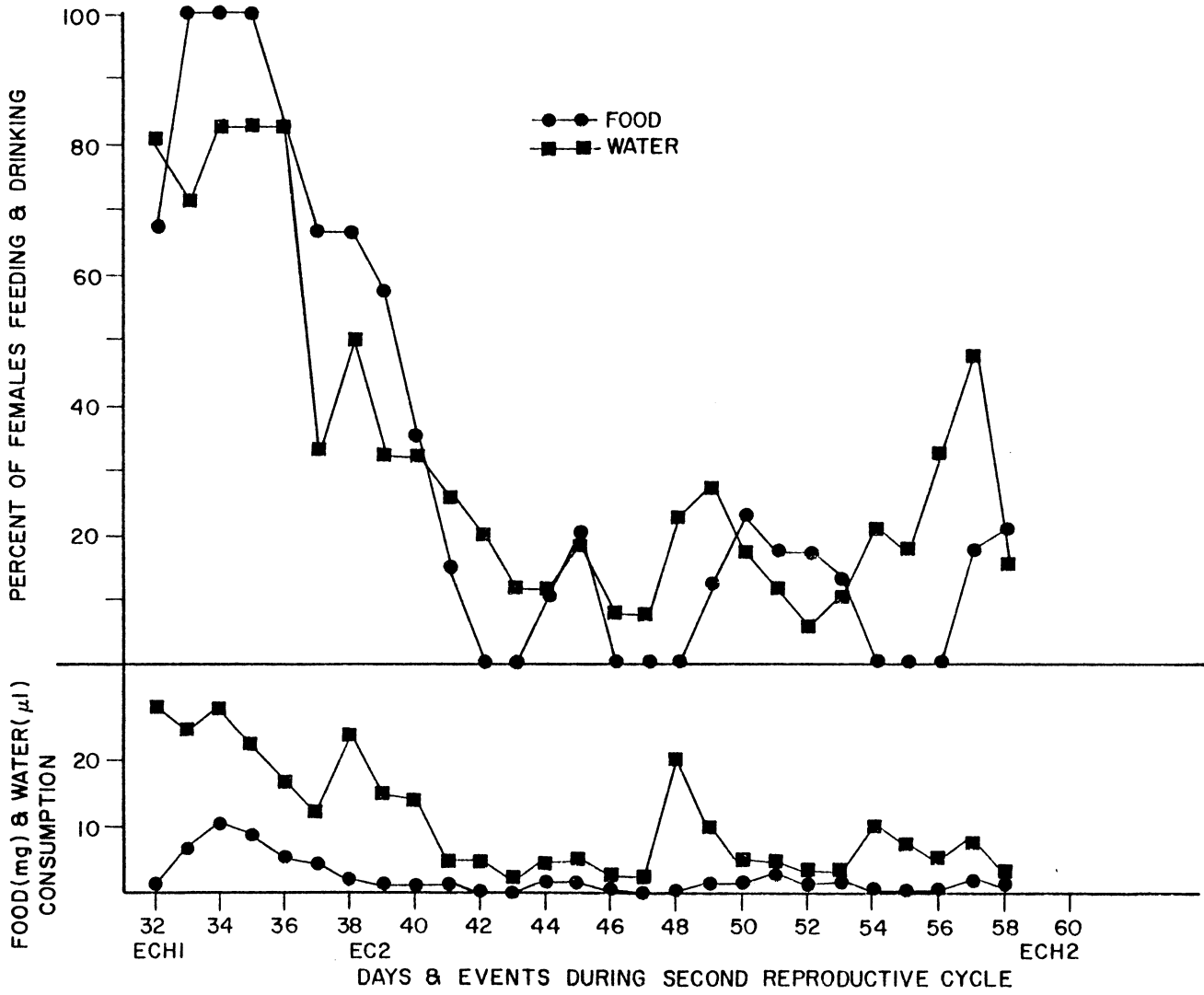


Figure 2 (cont.). Food and water consumption by control Blattella germanica during reproduction: second reproductive cycle.



during reproduction as reported here agrees with that observed by Cochran (1983). The numbers are similar and differences in the total amounts consumed during each period may be due to variation in the experimental conditions as well as biological variation.

The cyclic patterns observed in regard to water consumption resembled those associated with food consumption (Fig. 2). Again water consumption is greatest following maturation but, unlike food consumption, drinking continues at a high level until the first ootheca is formed although the percentage of females drinking begins to drop 1-2 days after mating. Water consumption is low during the incubation period but on the day of the oothecal hatch most of the females take a large drink. The females continue to consume large quantities of water until the second oothecae are formed, although the amounts consumed show a general decrease. The second incubation period also is marked by reduced water consumption. From Table 1, it is seen that water consumption per day was lowest during the incubation period and greatest during the formation of the second ootheca. The female needs more water during periods of oocyte maturation in order to meet the demands of the developing embryos. Roth and Willis (1955a) reported that the female must supply the developing embryos with water so they can develop although the present results seem to show that water is drunk and possibly stored before and during oothecal production rather than during the incubation period. The females drank most often during periods of oothecal production; they drank almost daily while forming the oothecae but only every 3-4 days while carrying the oothecae (Table 1).

The number of days between events of the reproductive cycle are shown in Table 2. The time between maturation and mating was similar to that found by other authors. Roth and Willis (1955), Ueda et al. (1969), and Cochran (1983) all reported similar figures depending upon the experimental conditions. These results were most comparable to those of Cochran (1983) since the experimental setup was very similar. The females in this study mated a day earlier on the average (Table 2) than did those of Cochran (1983). The higher temperature during this study is the most likely explanation for the difference since temperature is known to affect the length of other phases of the reproductive cycle. The period between mating and production of the first oothecae was consistent for these females, usually between 3-5 days (Table 2). The incubation period was approximately 20 days (Table 2). This phase of the reproductive cycle seemed to be the most affected by temperature. Cochran (1983) reported an incubation period of one week longer whereas Tsuji and Mizuno (1972) observed an incubation period of 20 days at a temperature of 27°C which was the approximate temperature throughout this study. Temperature seems to be the apparent explanation since Gould (1941) reported a shorter incubation period with increasing temperature. A 5-7 day interval occurred between hatch of the first oothecae and formation of the second oothecae (Table 2). This is earlier than the 9.1 days reported by Cochran (1983) due again most likely to temperature. The second incubation period was very similar to the first one.

The percent hatch of the oothecae (Table 3) was similar to, although slightly higher than, that observed by Cochran (1983). First

Table 2. Reproductive cycle of the German cockroach.

Group	Days Between Landmark Events				
	A-M ^a	M-EC1	EC-ECH1	ECH1-EC2	EC2-ECH2
Controls	8.8±2.4 ^d	3.9±0.7	19.7±0.4	6.4±0.9	21.0±0.7
No Water Post-A ^a 3 days	10.0(7.0) ^b ±1.6	3.2±1.2	19.0±1.7	6.8±1.3	21.0±1.0
No Water Post-ECH1 3 days	---	---	---	13.6(10.6) ^b ±8.1	19.7±1.0
No Food Post-A 3 days	14.6(11.6) ^c ±4.7	3.3±0.7	22.1±0.9	7.3±1.3	21.0±1.0
7 days	16.6(9.6) ^c ±1.9	3.2±1.1	21.8±1.1	7.4±1.4	19.3±0.9
12 days	21.0(9.0) ^c ±2.0	3.3±0.5	22.0±0.0	9.0±0.0	20.0±0.0
No Food Post-M 3 days	10.2±2.4	3.4(0.4) ^c ±0.7	21.3±0.5	7.3±1.0	20.8±0.8
7 days	9.6±2.5	3.4(0.0) ^c ±0.9	21.2±0.9	7.3±1.0	20.6±0.5
12 days	9.5±1.6	3.4(0.0) ^c ±1.0	20.6±1.1	6.9±0.7	20.3±0.5
No Food Carrying EC1	---	---	20.8±0.9	7.8±1.0	20.4±0.7
No Food Post-ECH1 3 days	---	---	---	9.6(6.6) ^c ±2.0	20.3±1.0
7 days	---	---	---	7.4(0.4) ^c ±1.3	18.8±1.4
7 days	---	---	---	21.5(14.5) ^c ±3.8	20.7±1.4
12 days	---	---	---	6.4(0.0) ^c ±1.1	21.5±0.5
12 days	---	---	---	26.5(14.5) ^c ±3.2	20.8±0.6

^aLetters represent: A = maturation, M = mating, EC1 = first ootheca produced, ECH1 = first oothecal hatch, EC2 = second ootheca produced, ECH2 = second oothecal hatch

^bDays after water returned ^cDays after food returned ^dMean ± standard deviation of mean

and second oothecae were not significantly different in size ($p \leq .05$) (Table 3). Tsuji and Mizuno (1972) reported 35 nymphs hatched from an ootheca whereas Willis et al. (1958) observed 27 nymphs emerging from 32 eggs. Some of this variation no doubt is due to rearing conditions as well as true biological differences. One additional note about the control females is necessary. One ootheca hatched from a female that had died three days prior to the hatching. The ootheca was of normal size, 42 eggs, but only 31 nymphs emerged for a 74 per cent hatch which is less than normal.

Water Deprivations

Depriving females of water during the reproductive cycle had a tremendous impact on survival (Fig. 3). Since the lack of water had such a great influence on survival, the effects on reproduction itself are not totally clear. However, it logically follows that increasing mortality will eventually lead to decreased reproduction of the species. The effects of water deprivation varied with the time that water was unavailable (Fig. 3). For example, no females ($n = 45$) survived to reproduce following water deprivation for any of the three deprivation lengths after mating whereas some females survived up to 9 days without water during the incubation period (Fig. 3).

Post-Maturation

All of the females ($n = 30$) held without water for 7 or 12 days after they became adults died before mating (Fig. 3). One female died after 1 day without water; this was unusual and most likely not the result of the deprivation. These females survived 5.0 ± 1.2 days

Table 3. Hatch per ootheca of German cockroaches.

Group ^b	HATCH PER OOTHECA							
	EC1				EC2			
	# Hatch	# Eggs	%	n ^a	# Hatch	# Eggs	%	n ^a
Controls	38.3±3.7 ^c	42.0±2.0	91	45	37.8± 3.1 ^c	41.4±2.8	91	30
No Water Post-A 3 days	36.4±5.9	42.0±4.7	87	5	36.8± 2.4	41.2±2.7	89	5
No Water Post-ECH1 3 days	--	--	--	--	28.7± 4.9	31.8±5.3**	90	10
No Food Post-A 3 days	34.5±3.4	39.6±2.3	87	11	33.1± 7.0	38.9±6.7	85	11
7 days	30.7±6.8	37.8±5.8	81	10	37.7± 4.5	42.9±4.6	88	10
12 days	39.3±6.0	44.0±4.0	89	3	34.3± 2.5	40.0±2.0	86	3
No Food Post-M 3 days	36.3±4.8	41.9±3.0	87	14	37.7± 2.8	42.5±2.8	89	14
7 days	37.3±3.8	41.6±3.0	90	10	38.9± 2.4	43.3±2.4	90	10
12 days	37.3±4.1	43.3±1.5	86	8	39.4± 1.6	44.3±1.4	89	8
No Food Carrying EC1	38.7±2.9	43.3±2.4	89	15	38.4± 2.9	43.3±2.4	90	15
No Food Post-ECH1 3 days	--	--	--	--	29.3± 7.4	34.5±7.3*	85	11
7 days	--	--	--	--	26.4± 9.7	31.8±9.2**	83	8
7 days	--	--	--	--	28.7±13.7	32.7±9.2**	84	3
12 days	--	--	--	--	24.5± 0.7	30.0±0.0**	82	2
12 days	--	--	--	--	36.6± 1.5	40.8±1.8	90	5

^aNumber of observations

^bAbbreviations as in Table 2

^cMean ± standard deviation

*Statistically different from controls at p = .05 level

**Statistically different from controls at p = .01 level

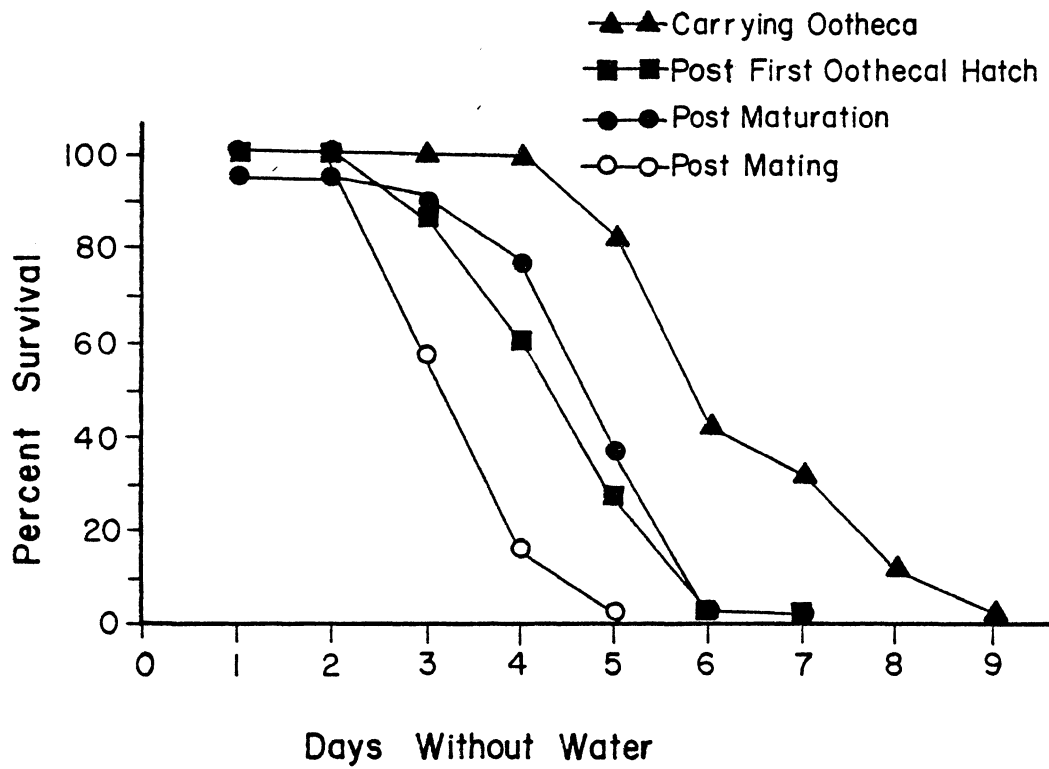


Figure 3. Survival of water-deprived females.

(mean \pm S.D.) (Fig. 3). Females were able to survive 3-4 days without water but on subsequent days survival dropped sharply until there were no survivors after 7 days (Fig. 3).

Of the females deprived of water for three days following maturation ($n = 15$), ten (67%) died before mating. Mating was slightly delayed in these females (Table 2) although still within the range of normal females. All other periods in the reproductive cycle occurred without additional significant delays (Table 2). These females consumed more food and water during most period of the reproductive cycle than did control females (Table 4). These females may have been compensating for the slow start due to the water deprivation, however their oothecae were not significantly different from those of the controls (Table 3). The percent hatch of the first oothecae was slightly lower than that of the second one or those of the controls (Table 3). This may have been the result of the water deprivation although it is within the range for normal females.

Post-Mating

The females deprived of water following mating survived an average of 3.7 ± 0.8 days (mean \pm S.D., $n = 45$) without water (Fig. 3). There was 100 per cent mortality before oothecae were formed or hatched. The females survived 3-6 days without water (Fig. 3). The females deprived of water after mating did not survive as long as those deprived after maturation. This was somewhat unusual since control females drank less water following mating than they did before mating (Fig. 2). One possibility is that, even though less water is

Table 4. Food and water consumption of females deprived of water for three days after maturation.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μl)	Total Drinks	Amount Drunk Per Day (μl) ^b
A-M	62.8±19.1 ^c	6.3	162.7±24.5 ^c	5.8±1.6	16.3 (23.2) ^d
M-EC1	8.5± 7.0	2.7	41.2±15.6	2.2±0.8	12.9
EC1-ECH1	12.2± 9.2	0.6	146.2±22.3	10.8±1.6	7.7
ECH1-EC2	42.8± 3.0	6.3	173.8±24.0	6.2±1.3	25.6
EC2-ECH2	13.0± 5.2	0.6	134.6±30.8	10.0±2.6	6.4

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean ± standard deviation.

^dWater consumption per day after water became available again.

consumed during this period, the water is important at the time since a high percentage of control females did drink following mating (Fig. 2).

Post-First Oothecal Hatch

Of the females held without water for 7 or 12 days after their first oothecae had hatched ($n = 30$), none survived long enough to produce a second ootheca. The females survived between 3-9 days with an average of 4.9 ± 1.4 days (mean \pm S.D.) (Fig. 3).

There was 33 per cent mortality during the deprivation period of those females held without water for three days after they hatched their first oothecae ($n = 15$). The remainder of the reproductive cycle was greatly affected. Production of the second ootheca was delayed up to 28 days for these females with the average being nearly 11 days after water was returned (Table 2). The total amount of food consumed was higher than normal but daily consumption was less than normal (Table 5). Water consumption varied greatly ranging from 27-295 μ l. Water consumption appeared to depend on the number of days that the second ootheca was delayed although on the average, daily water consumption during the period was below normal (Table 5). During the incubation period, females drank fewer times than normal (Table 5). Oothecal size was reduced, thus reducing the number of nymphs hatching; however, the percentage hatching was very normal (Table 3) approximating 90 per cent. All of the females which survived the deprivation produced and hatched second oothecae.

Table 5. Food and water consumption of females held without water for 3 days after hatch of the first ootheca.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μ l)	Total Drinks	Amount Drunk Per Day (μ l) ^b
A-M	---	---	---	---	---
M-EC1	---	---	---	---	---
EC1-ECH1	---	---	---	---	---
ECH1-EC2	46.8 \pm 11.1 ^c	3.4	149.2 \pm 81.3 ^c	7.6 \pm 6.5	10.8 (13.8) ^d
EC2-ECH2	8.7 \pm 6.1	0.4	78.1 \pm 21.5	4.3 \pm 1.5	4.0

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean \pm standard deviation.

^dWater consumption per day after water became available.

While Carrying First Ootheca

Water deprivation during the incubation period was less harmful than at any other time. Other studies have shown females during this period to survive a week without water and not be greatly affected. None of the females deprived of water for either 7 or 10 days survived to hatch their oothecae. They lived an average of 5.7 ± 1.4 days (mean \pm S.D.) with a range between 4-9 days (Fig. 3). From these results it seems apparent that a week without water generally led to mortality.

Food Deprivations

Water deprivations were shown to have a large affect on survival of the female German cockroach. On the other hand, food deprivations do not cause mortality as quickly but directly affect reproduction. Removal of food usually led to a delay in the reproductive cycle. Mortality was much lower than in the water studies.

Post-Maturation

The females deprived of food for 12 days following maturation ($n = 15$) were affected greatly by the absence of food with 12 (80%) not surviving to mate. Those that died were able to survive an average of 10.4 days without food. The survivors mated in 21.0 ± 2.0 days (mean \pm S.D.) (Table 2). This was longer than normal but was only 9 days after their food was returned. The latter compares favorably with the controls. Food consumption per day was higher than normal possibly in order to compensate for the earlier lack of it (Table 6). Daily water consumption was much less than normal (Table 6) throughout the cycle. Through the rest of the reproductive cycle daily food

Table 6. Food and water consumption of females deprived of food for 12 days following maturation.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μ l)	Total Drinks	Amount Drunk Per Day (μ l) ^b
A-M	58.0 \pm 8.0 ^c	2.8 (6.4) ^d	138.8 \pm 14.9 ^c	7.8 \pm 1.0	6.6
M-EC1	10.0 \pm 2.7	3.0	17.3 \pm 12.3	1.0 \pm 0.8	5.2
EC1-ECH1	16.3 \pm 5.5	0.7	70.3 \pm 14.2	4.7 \pm 2.1	3.2
ECH1-EC2	53.0 \pm 6.2	5.9	144.3 \pm 6.8	6.0 \pm 0.0	16.0
EC2-ECH2	9.7 \pm 1.5	0.5	59.3 \pm 9.9	3.7 \pm 1.2	3.0

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean \pm standard deviation.

^dDaily food consumption after food was returned.

consumption was close to normal (Table 6). The first oothecae were formed on schedule but there were minor perturbations later in the reproductive cycle. These females carried their first oothecae 1-2 days longer than control females did and 2 days longer than they carried their second (Table 2). Production of the second oothecae was also delayed 1-2 days (Table 2). The second oothecae of these females were somewhat smaller than the first ones although both were in the range of normal oothecae and had a high per cent hatch (Table 3).

Females kept without food for seven days after maturation ($n = 15$) survived much better; 13 (87%) survived the deprivation period with 10 of those mating and producing oothecae. Mating was delayed again in this group. These females mated an average of 16.6 ± 1.9 days (mean \pm S.D.) after maturation but 9.6 days after food was returned (Table 2). This is comparable to the figure for normal females. Food consumption was normal for the entire reproductive cycle although daily water consumption was less than normal (Table 7). These females also drank less often through the cycle (Table 7). The incubation periods were of normal length with the first period two days longer than the second one (Table 2). Production of the second oothecae was slightly delayed as well (Table 2). The first oothecae were smaller than normal, fewer nymphs hatched, and the percentage hatch was nearly ten per cent below normal (Table 3). The second oothecae were slightly larger than the controls although not significantly larger (Table 3).

Of the females deprived of food for three days after maturation ($n = 15$), 13 (87%) survived to mate. Two females mated but failed to produce oothecae. Mating was delayed an average of 14.6 ± 4.7 days

Table 7. Food and water consumption of females deprived of food for 7 days following maturation.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μl)	Total Drinks	Amount Drunk Per Day (μl) ^b
A-M	54.3±9.0 ^c	3.3 (5.7) ^d	160.9±24.9 ^c	7.1±2.4	9.7
M-EC1	9.1±4.7	2.8	32.6±16.3	1.2±0.6	10.2
EC1-ECH1	15.3±5.8	0.7	74.5±21.3	4.0±2.2	3.4
ECH1-EC2	49.2±4.8	6.6	125.8±26.4	4.7±1.3	17.0
EC2-ECH2	12.4±7.7	0.6	72.3±19.4	3.7±1.2	3.7

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean ± standard deviation.

^dDaily food consumption after food was returned.

(mean \pm S.D.) after maturation or 11.6 days after the food was returned (Table 2). This was longer than normal although not outside of the range reported by Roth and Stay (1962) of between 8-14 days. Total food and water consumption during the reproductive cycles were normal although daily consumption of both was below normal between maturation and mating (Table 8). The first incubation period was 1 day longer than the second even though both were comparable to those of control females (Table 2). Both oothecae were smaller than normal although not significantly smaller and both had over 85 per cent hatch (Table 3).

Post-Mating

Of the females deprived of food for 12 days after mating ($n = 15$), eight (53%) survived to hatch the first oothecae. Production of the first oothecae was not delayed (Table 2) even though there was no food available between mating and oothecal production. The remainder of the reproductive cycles progressed without delay (Table 2). Especially interesting was the fact that the first incubation period was not characterized by the increased food consumption that might be expected in order to compensate for the deprivation period (Table 9). Both oothecae were larger than those of normal females although not significantly different (Table 3). The percentage hatching from the first oothecae was slightly lower than that of the second oothecae or those of controls.

Thirteen (87%) of the females deprived of food for 7 days following mating ($n = 15$) survived to hatch the first oothecae. Three females survived but failed to produce or hatch oothecae. Again,

Table 8. Food and water consumption of females deprived of food for 3 days following maturation.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μl)	Total Drinks	Amount Drunk Per Day (μl) ^b
A-M	51.2±18.4 ^c	3.5 (4.4) ^d	127.0±37.2 ^c	5.0±2.2	8.7
M-EC1	9.2± 3.8	2.8	24.8±14.6	1.2±0.7	7.5
EC1-ECH1	16.7± 6.0	0.8	68.7±14.6	3.4±1.2	3.1
ECH1-EC2	43.6±10.3	6.0	110.6±25.7	4.1±1.2	15.2
EC2-ECH2	12.1± 8.2	0.6	70.4±15.7	3.4±2.2	3.4

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean ± standard deviation.

^dDaily food consumption after food was returned.

Table 9. Food and water consumption of females deprived of food for 12 days following mating.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μl)	Total Drinks	Amount Drunk Per Day (μl) ^b
A-M	41.8±3.1 ^c	4.4	119.0±26.9 ^c	7.2±1.0	12.5
M-EC1	0.0±0.0	0.0	15.2± 3.9	1.2±0.7	4.5
EC1-ECH1	15.5±5.6	0.8	82.1±27.5	8.4±2.7	4.0
ECH1-EC2	40.7±6.8	5.9	104.6±11.9	5.0±0.0	15.2
EC2-ECH2	16.9±3.9	0.8	84.0±31.5	7.9±1.9	4.1

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean ± standard deviation.

the first oothecae were produced without delay (Table 2) even though food was unavailable after mating. The incubation period was of normal length (Table 2) with food consumption during the period at 1.1 mg/day (Table 10). This was greater than normal; although only somewhat higher than usual, it may be attributed to the earlier deprivation. Water consumption was close to normal except between mating and oothecal formation when it was greatly reduced (Table 10). The second incubation period was also normal (Table 2). Oothecal hatch was close to that of normal undeprived females although the first oothecae were slightly smaller than the second ones (Table 3).

Over ninety per cent of the females held without food for the three days after mating survived to form and hatch an ootheca ($n = 15$). None of the events of the reproductive cycle were delayed (Table 2). Food consumption during the first incubation period was greater than normal (Table 11) although food and water consumption for the rest of the reproductive cycles were nearly normal. Oothecal hatch was not greatly affected although once again the first oothecae were smaller than the second ones and had a lower per cent hatch (Table 3).

Post-First Oothecal Hatch

Only 7 (47%) of the females deprived of food for 12 days following hatch of their first oothecae survived to produce a second one ($n = 15$). This period for food deprivations led to surprising results. Whereas Kunke1 (1966) reported that females had to feed to produce their second oothecae, these results showed that to be not completely true. Two patterns emerged for the production of second oothecae by

Table 10. Food and water consumption by females deprived of food for 7 days following mating.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μl)	Total Drinks	Amount Drunk Per Day (μl) ^b
A-M	42.4±9.0 ^c	4.4	130.1±27.4 ^c	6.1±2.0	13.6
M-EC1	0.0±0.0	0.0	19.9± 6.4	2.0±0.6	5.9
EC1-ECH1	24.1±6.0	1.1	79.1±12.8	5.7±1.7	3.7
ECH1-EC2	38.9±4.9	5.3	122.0±21.9	5.1±1.1	16.7
EC2-ECH2	18.5±4.4	0.9	89.3±25.5	7.9±1.4	4.3

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean ± standard deviation.

Table 11. Food and water consumption by females deprived of food for 3 days following mating.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μl)	Total Drinks	Amount Drunk Per Day (μl) ^b
A-M	41.8±6.6 ^c	4.1	148.6±35.2 ^c	8.1±2.4	14.6
M-EC1	0.0±0.0	0.0	23.1± 6.1	2.1±0.8	6.8
EC1-ECH1	21.7±13.0	1.0	93.5±30.7	7.9±2.4	4.4
ECH1-EC2	39.7± 8.7	5.4	115.2±27.9	5.4±0.7	15.8
EC2-ECH2	14.2± 4.8	0.7	89.8±21.6	7.6±1.5	4.3

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean ± standard deviation.

these females. One group of females ($n = 2$) produced their second oothecae in 6.4 ± 1.1 days (mean \pm S.D.) (Table 2) which is almost six days before they had access to food. Water consumption during this time was also well below normal (Table 12) as these females drank less than $40 \mu\text{l}$. The incubation period of these females was of normal length (Table 2) but food consumption was much greater than normal (Table 12) possibly in compensation for the earlier starvation. The oothecae suffered greatly due to this deprivation. They were much smaller than normal and per cent hatch was reduced significantly (Table 3). The other group of females ($n = 5$) waited to feed before producing their second oothecae. Oothecal production was delayed an average of 26.5 ± 3.2 days (mean \pm S.D.) or 14.5 days after food was returned (Table 2). Food and water consumption were much greater than normal although daily consumption was below normal for the most part (Table 13). The second incubation period was of normal length (Table 2) with food and water consumption at the same level as controls (Table 13). These oothecae were less affected by the food deprivation. Oothecae were slightly smaller on the average but per cent hatch was high (Table 3).

The females deprived of food for 7 days after their first oothecae hatched responded like those starved for 12 days. Eleven (73%) of these females survived to form a second oothecae. The first group of females ($n = 8$) formed their next oothecae an average of 7.4 ± 1.3 days (mean \pm S.D.) (Table 2) after their first oothecae hatched or 0.4 days after food was once again available. Essentially these females did no feeding and water consumption was below normal

Table 12. Food and water consumption by females deprived of food for 12 days following hatch of the first ootheca: females formed second ootheca before food was returned.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μ l)	Total Drinks	Amount Drunk Per Day (μ l) ^b
A-M	---	---	---	---	---
M-EC1	---	---	---	---	---
EC1-ECH1	---	---	---	---	---
ECH1-EC2	0.0 \pm 0.0 ^c	0.0	36.4 \pm 14.2 ^c	3.4 \pm 0.9	5.7
EC2-ECH2	39.5 \pm 0.5	1.8	98.0 \pm 12.0	5.5 \pm 0.5	4.6

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean \pm standard deviation.

Table 13. Food and water consumption by females deprived of food for 12 days following hatch of the first ootheca: females formed second oothecae after food returned.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μl)	Total Drinks	Amount Drunk Per Day (μl) ^b
A-M	---	---	---	---	---
M-EC1	---	---	---	---	---
EC1-ECH1	---	---	---	---	---
ECH1-EC2	65.2±16.0 ^c	2.5 (4.5) ^d	205.7±38.3 ^c	11.3±2.8	7.8
EC2-ECH2	20.0±15.6	1.0	65.6±14.2	4.6±0.8	3.1

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean ± standard deviation.

^dFood consumption per day food was available.

during the oothecal production period (Table 14). The incubation period was nearly normal (Table 2) as were food and water consumption during it (Table 14). Oothecae were significantly smaller than controls with a reduced per cent hatch (Table 3). The other group of females ($n = 3$) waited until food was returned before producing their second oothecae. Oothecal production was delayed an average of 21.5 ± 3.8 days (mean \pm S.D.) (Table 2) or 14.5 days after food was once again available. This figure of 14.5 days is identical to the number obtained in the 12 day deprivation study above. Oothecae, however, were slightly larger than those of the females that had not fed before producing the second oothecae in this study (Table 3). The small number of observations may be partially responsible for these results.

Three days without food following oothecal hatch was not critical to survival since 11 (73%) of the females survived to produce second oothecae. Production of the second oothecae was delayed. The oothecae were formed in an average of 9.6 ± 2.0 days (mean \pm S.D.) (Table 2) or 6.6 days after food was again available; this is comparable to the period required by controls. Food and water consumption were below normal (Table 16). Oothecae were smaller than normal with reduced per cent hatch (Table 3).

While Carrying First Ootheca

All females ($n = 15$) deprived of food for the entire first incubation period survived to hatch their first oothecae. The first oothecae were slightly larger than normal (Table 3). It seems obvious that the female does not need to eat during the first incubation

Table 14. Food and water consumption by females deprived of food for 7 days after hatch of the first ootheca: females formed second oothecae before food was returned.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μl)	Total Drinks	Amount Drunk Per Day (μl) ^b
A-M	---	---	---	---	---
M-EC1	---	---	---	---	---
EC1-ECH1	---	---	---	---	---
ECH1-EC2	0.6±0.9 ^c	0.1	66.6±42.2 ^c	4.4±1.9	9.0
EH2-ECH2	15.6±5.5	0.8	66.5±15.4	5.0±1.6	3.4

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean ± standard deviation.

Table 15. Food and water consumption by females deprived of food for 7 days following hatch of the first ootheca: females formed second oothecae after food returned.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μ l)	Total Drinks	Amount Drunk Per Day (μ l) ^b
A-M	---	---	---	---	---
M-EC1	---	---	---	---	---
EC1-ECH1	---	---	---	---	---
ECH1-EC2	60.0 \pm 6.5 ^c	2.8 (4.1) ^d	163.5 \pm 33.3 ^c	9.5 \pm 2.4	7.6
EC2-ECH2	15.6 \pm 5.5	0.8	66.5 \pm 15.4	5.0 \pm 1.6	3.4

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean \pm standard deviation.

^dFood consumption per day food was available.

Table 16. Food and water consumption by females deprived of food for 3 days after first oothecal hatch.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μ l)	Total Drinks	Amount Drunk Per Day (μ l) ^b
A-M	---	---	---	---	---
M-EC1	---	---	---	---	---
EC1-ECH1	---	---	---	---	---
ECH1-EC2	32.1 \pm 10.8 ^c	3.3 (4.9) ^d	88.3 \pm 33.5 ^c	4.8 \pm 1.3	9.2
EC2-ECH2	14.2 \pm 6.4	0.7	61.8 \pm 14.0	4.4 \pm 1.2	3.0

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean \pm standard deviation.

^dDaily food consumption after food was returned.

period. Production of the second oothecae may have been delayed slightly (Table 2) although this did not appear significant. Food consumption was higher than normal during oothecal formation although normal amounts of water were consumed (Table 17). The second oothecae were of normal size and per cent hatch (Table 3).

Table 17. Food and water consumption by females deprived of food for the complete first incubation period.

Event ^a	Food Consumption		Water Consumption		
	Total Food Eaten (mg)	Amount Eaten Per Day (mg) ^b	Total Water Drunk (μl)	Total Drinks	Amount Drunk Per Day (μl) ^b
A-M	---	---	---	---	---
M-EC1	---	---	---	---	---
EC1-ECH1	0.0±0.0 ^c	0.0	---	---	---
ECH1-EC2	50.3±9.7	6.5	119.3±24.5 ^c	5.9±1.1	15.3
EC2-ECH2	15.5±4.6	0.8	96.2±17.6	7.1±1.4	4.7

^aAbbreviations as in Table 1.

^bIntervals for these calculations are shown in Table 2.

^cMean ± standard deviation.

DISCUSSION

From the results presented, it is evident that food and water consumption by the female are closely associated with reproduction of the German cockroach. The cyclic pattern of food and water consumption, in relation to the reproductive cycle reported by Cochran (1983), was confirmed by these results. In addition, other results from this study merit further discussion.

Additional information about the basic biology of the B. germanica reproductive cycle was gathered. It appears that environmental conditions have a great impact on the development and reproduction of this species. The constant rearing temperature for the study was near the optimum temperature for reproduction, which caused an acceleration in the reproductive cycle (Table 2). The incubation period was shortened the most by the warmer temperature confirming the results of Gould (1941). Other periods of the reproductive cycle were slightly shorter than those reported by Cochran (1983) for this same strain of B. germanica. These differences, although small, could be attributed to the temperature differences of the two studies.

The female, following the molt to adulthood, consumes large amounts of food and water for approximately 10 days. Roth and Stay (1962) found that, during this period, the oocytes matured and increased greatly in size. Late in this period, the female mates and forms an ootheca. Although mating is not a requirement for oothecal production, it is necessary for a fertile ootheca. Since mating

accelerates oocyte maturation by only a short period (Roth and Stay, 1962), there must be other more important factors for oocyte maturation.

Food would seem to be a very important factor since the female eats such a large amount prior to oothecal formation. Starvation, indeed, does delay the reproductive cycle (Kunkel, 1966) and seems to inhibit mating (Roth and Stay, 1962). One of the most interesting results of this study was the effect of starvation following hatch of the first ootheca. Whereas Kunkel (1966) reported that a female must feed before producing a second ootheca, this study demonstrates that this is not always true. As shown in Table 2, some females produced the second ootheca before food was available following hatch of the first. These oothecae were slightly smaller than normal (Table 3). A possible explanation might be that a few females had enough food reserves to produce a second ootheca but not enough to produce one of normal size. This may be an adaptation which has an increased survival value. Multiple reproductive strategies during times of stress would aid the female in reproduction efficiency.

Females in this study did not survive as long without food or water as did those of Willis and Lewis (1957). The decreased longevity of these deprived females may be due to the extra metabolic demands placed on them during reproduction. These demands appear to be greatest during periods of oothecal production since that is when the largest amounts of food and water are consumed. Females survive longest without food or water during the incubation period, when metabolic demands are less. Oocytes are not really maturing at this time, thus lowering the amount of food needed. The female should have

a somewhat reduced metabolic rate and she should be able to prevent excessive water loss during this relatively inactive period by staying in a harborage with a higher humidity. The female carrying an ootheca should need to leave the harborage only 3-5 times to find water and the little food that may be required. Indeed, females with oothecae are not often trapped away from the harborage (Ross, unpub.).

The relative significance of food versus water deprivation effects on reproduction is important. Water availability is directly associated with survival of all organisms and B. germanica is no exception. If water is not available in large enough quantities to allow survival of the female, then it is fairly obvious that she will be unable to reproduce. Females survive longer without food than they do without water. The lack of food delays reproduction but does not greatly increase mortality except after extremely long periods without food. Since the German cockroach is an opportunistic feeder, the chances are slim that it will not find food before starvation leads to death. Rather it appears that these females have become well adapted to surviving temporary food shortages by delaying reproduction until conditions become suitable again. Although food limitation may affect reproduction directly, it appears that water is the main limiting factor. Starvation may delay or decrease the size of one or two oothecae but once food becomes available reproduction continues relatively unaffected. However if the lack of water kills the female the total loss to reproduction of the species is much greater. By having a reproductive cycle where certain periods are more important than others in terms of nutritional requirements the female may be able

to reproduce more efficiently. Since the periods of oocyte maturation are the most important and occur at the beginning of each reproductive cycle, if food and water are not immediately available, the female can delay reproduction until the conditions are more suitable.

Deprivations have the greatest affect on the ootheca being produced at the time of the deprivation especially if food or water are absent for long periods. Some females appear to compensate for the deprivation by consuming larger amounts of food or water than undeprived females. The relatively high percentage hatch, greater than 80 per cent (Table 3), of the oothecae of deprived females is interesting. If food or water are lacking, the impact seems to be mainly on oothecal size. The strategy seems to be one in which the ootheca is smaller so that there are enough resources to allow a high percentage of the embryos to hatch insuring that they can open the ootheca.

Mueller (1978) also reported that oothecal size was reduced following temporary food and water deprivations. He reported that each deprivation reduced the size of the ootheca by approximately 33 per cent. The results of this study are not as dramatic; only deprivations following the first oothecal hatch led to significant reductions in size of the second ootheca. Smaller oothecae were the result of both food and water deprivations following first oothecal hatch. However, these results confirmed those of Mueller (1978) in regard to percent hatch. Both studies showed that percent hatch was high for oothecae from both control and deprived females.

The results of this study differed from those of Mueller (1978) in regard to survival of deprived females. Mueller (1978) reported that survival was reduced most by food deprivation; whereas, in this study, water deprivation caused greater mortality during all periods of the reproductive cycle. Mueller (1978) also found that deprivations had a greater impact on oothecal formation than they had on survival. The majority of females in this study produced oothecae if the deprivation period was survived.

Females may use all of their food and water reserves in order to survive until food and water become available rather than producing oothecae. Then when the resources are available reproduction starts again. However, once a female produces an ootheca her strategy may change. If food and water are limited during the incubation period, the female may use her nutrient reserves to insure hatch of the ootheca even though she may die. Females have been observed to die just prior to or shortly after the hatch of viable oothecae (Cochran, Durbin, unpub.). There appears to be some point at which hatch of the ootheca becomes more important than survival of the female when resources are limited.

These studies show what a female in the field may have to cope with. Food is not continuously available in all harborages in the wild so the female must be able to survive without it for short periods. At other times food may be available but limited in quality and quantity. In these studies food was either present or absent but not limited in quantity when available. When food was available, the female could consume as much as she desired in order to compensate for

the period of deprivation. Since the basic food requirements and consumption patterns were reported by Cochran (1983) and confirmed in this study, several points need further investigation. One study could look at the effects of limited food availability; not totally limited for a certain length of time but a limited quantity over a long period. This would help to ascertain whether there is a threshold amount of food which must be consumed before reproduction will proceed normally or whether the feeding process itself stimulates the reproductive cycle. A similar study carried out with water could also yield interesting results. Limited water quantities would no doubt enable a female to survive but may not be enough to allow her to reproduce. The information resulting from studies of this type would be important in justifying the continued use of sanitation for cockroach control.

Sanitation may be the most important method of controlling the buildup of cockroach populations. Sanitation includes the elimination of food, water, and harborages. The elimination of all harborage areas might be successful if it were possible but the small size of B. germanica makes almost any crack, crevice, or dark space a suitable hiding place. Caulking and other techniques have been tried with limited success (Farmer, unpub.). Harborage elimination does not appear to be a good method for control when used alone.

The other aspects of sanitation, food and water availability, then become the most important. This study shows that food and water availability have a great impact on survival and reproduction of the female German cockroach. Much of the success of this species is due to its versatility in regard to food requirements. The close

association between this species and man makes the elimination of all food and water sources almost impossible. However, limitation of these resources is possible and reasonable. With respect to the reproductive cycle, the timing of food and water availability appear to be the most crucial. Limitation of these resources during critical periods in the cycle would seem to be an effective means of controlling the populations. Since cockroach populations at any one time may contain females in all reproductive states, the emphasis must be on limiting food and water at all times through sanitary measures. By limiting the availability of these resources it may be possible to impair the reproduction of the population. Used alone, sanitation probably is only slightly effective in controlling cockroach populations but when used with other control measures it should prove to be successful.

The idea that cockroach reproduction is under endocrine control has been reported previously (Engelmann, 1970; Cochran, 1983). The factors responsible for the cyclic processes of reproduction are not well known for B. germanica. Information is available from studies using other cockroach species such as Periplaneta americana (Tobe and Stay, 1982). These authors reported that activity of the corpora allata (CA) is the most important internal factor in cockroach reproduction. Engelmann (1970) found that the CA may be inhibited by the presence of an ootheca in the uterus of certain cockroach species. Roth and Stay (1962) confirmed this for the German cockroach carrying an ootheca. Food and mating are important external factors controlling reproduction (Kunke1, 1966; Engelmann, 1970). The effect of mating on reproduction is most important during the first reproductive cycle

while food is important during all of the cycles. However, the first reproductive cycle is different from the following ones. The first cycle may be triggered by intense feeding by final instar nymphs which then molt into adults (Kunkel, 1966). There is no immediate period of intensive drinking (Cochran, 1983) although food and water consumption increase rapidly shortly after the molt into adulthood. Oocytes are maturing at a rapid rate during this period also (Roth and Stay, 1962). These authors reported that mating has little effect on oocyte maturation since B. germanica mates late in the oocyte maturation period. The mechanism for CA activation is unknown. Feeding or drinking may be responsible or possibly initiation of CA activity is related to the molting process (Cochran, 1983).

Later reproductive cycles are characterized by a large number of females drinking on the day the oothecae hatch. These females drink a larger than normal amount that day also. There is a one day delay before the feeding cycle begins. The increased food and water consumption continues until just before the next ootheca is formed. Cochran (1983) suggests that enough food and/or water are consumed during this brief period to stimulate any stretch receptors involved in CA activation. The results of Kunkel (1966) seem to support this idea.

Cochran (1983) proposed a possible scheme of events leading to CA activation. An ootheca in the genital chamber of female B. germanica inhibits food and water consumption and possibly CA activity as well. When the ootheca hatches, the inhibition stops, food and water consumption increase greatly and the reproductive cycle begins

anew. If food and water are available then the females consume them and initiate the hormonal mechanism for oocyte development. If these resources are not available, the female may delay the reproductive cycle until resources become available again. It is probable that in most cases the female can find food and/or water before mortality occurs. This system would appear to be an efficient one for an opportunistic feeder like the German cockroach.

Conclusions

The results of this study show that the German cockroach is a highly adaptive insect. Its reproductive cycle is patterned with characteristic feeding and drinking cycles in relation to the events of reproduction. The cyclic patterns reported by Cochran (1983) were confirmed by this study. After maturation the female feeds and drinks nearly every day until an ootheca is produced. Food and water consumption are minimal while she carries the egg-case but increase greatly after it hatches. This pattern is repeated for each reproductive cycle.

Food and water availability are critical for survival and reproduction of B. germanica. The effects of food and water deprivations are dependent upon when the resources are unavailable during reproduction and the length of the deprivation. Starvation will delay the reproductive cycle, decrease oothecal hatch, or even lead to increased mortality of the female if food does not become available. For the most part, females survive food deprivations longer than water deprivations. The absence of water for short periods of time leads to

mortality and also is detrimental to reproduction. The female is very susceptible to water deprivations so water availability appears to be more critical than food availability in regard to survival, although reproduction may be delayed by the lack of either resource.

Finally since these results suggest that reproduction of the German cockroach may be affected by the absence of food or water, it appears that sanitation may be very important. Population growth may be inhibited by limiting access to food and water especially during certain periods of the reproductive cycle.

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FOOD AND WATER DEPRIVATION EFFECTS ON REPRODUCTION
OF FEMALE Blattella germanica (L.)

by

Edward John Durbin

(ABSTRACT)

The food and water requirements of the female German cockroach for reproduction as well as the effects of food and water deprivations during the reproductive cycle were studied. The data obtained are useful both in advancing our knowledge about the basic biology of this species, in addition to determining whether sanitation should continue to be stressed in cockroach pest management programs.

Experimental animals were reared under constant humidity and temperature with a controlled photoperiod. Females were deprived of food or water following maturation, mating, first oothecal hatch, or during the egg-case carrying period. Effects on survival and reproduction were noted.

Water deprivation increased mortality at all periods of the cycle tested, with additional effects on the reproductive cycle. Females survived food deprivations much better although direct effects on reproduction were observed. There were delays in the reproductive cycle along with decreased oothecal hatches. Females carrying oothecae survived the deprivations better than females in other reproductive states.

It appears that female B. germanica can survive without food or water for short periods although, normally, reproduction will not

occur in the absence of either. The effects of food and water deprivations vary greatly with both the length of time the resource is unavailable and the period of the reproductive cycle during which the resource is unavailable. Since food and water seem to be critical to reproduction of the German cockroach, a continued emphasis on sanitation appears justified.