GROUP FORMATION AND DISPERSAL IN THE GERMAN COCKROACH, *Blattella germanica* (L.) (Dictyoptera: Blattellidae)

by

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To My Parents -

whose love and encouragement
are greatly appreciated.

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INTRODUCTION

Cockroaches comprise one of the oldest groups of insects, dating back 250 million years to the Carboniferous Period (Cornwell 1968). Of over 3,500 extant species that have been described, only a handful are domestic pests. These species have adapted well to Man's environments. Infestations of domestic cockroaches are psychologically distressing to most people. However, their esthetic and psychological damage often overshadows their medical importance. Cockroaches have been shown to be both experimental and natural vectors of medically important viruses, bacteria, fungi, protozoans, and helminths (Roth and Willis 1957, 1960). The close association between cockroaches and man is reason for concern about the transmitance of pathogens to humans. Some of the pathogens shown to be carried by cockroaches include the dysentery protozoan *Entamoeba histolitica*, the poliomyelitis virus, and several species of bacteria such as *Salmonella*, *Shigella*, *Staphylococcus*, and *Streptococcus* (Roth and Willis 1957, 1960; Rueger and Olson 1969; and Alcamo and Frishman 1980).

Cockroach control has primarily relied on the use of insecticides. Rigorous control regimes emphasizing insecticides have been proposed and tested for the complete

eradication of cockroaches and other urban pests. Serious problems have arisen from this dependency on chemical control. Some chemicals have been shown to be highly repellent to cockroaches, limiting their effectiveness in the field (Ebeling et al. 1966,1967). Even more disconcerting is the development of resistance, cross-resistance, and multiple resistance to several chemical compounds (Grayson 1966, Van den Heuvel and Cochran 1965). Consequently, researchers are looking toward other means of control. The impact of the Integrated Pest Management philosophy is being felt in urban entomology as people begin looking for multi-disciplinary means of controlling cockroach populations. However, more basic biological, behavioral, and physiological work is required to provide the necessary foundation of information upon which future control programs can be built. The work presented here is an effort toward that end.

The specific objectives of this research were to determine whether, and in what manner, the reproductive state and the density of adult female cockroaches within a group might affect group formation within a harborage and the dispersal of a group from a harborage. The results of these studies are presented in two parts, the first dealing with group formation and the second with dispersal.

PART I - GROUP FORMATION

INTRODUCTION

The German cockroach, Blattella germanica (L.), is a world-wide pest in urban environments and on ocean-going vessels. Pest management schemes have so far relied heavily on pesticides, although research on alternate control methods is underway at VPI & SU and elsewhere. Unfortunately, improvement of conventional techniques and advances in new approaches are hampered by a lack of basic information on cockroach group behavior as was evident in an earlier experiment on genetic control (Ross et al. 1981). Much of the earliest work on cockroaches involved physiological studies or pesticide evaluations. Only within the past decade has there been much work on behavior.

German cockroaches are gregarious animals. Therefore, most of the behavioral work has centered around attempts to unravel the factors involved in their gregarious nature and elucidate social interactions. Pettit (1940) was one of the first to demonstrate the effects of gregariousness on the growth rate of the German cockroach. He found that nymphs in

groups grew faster than solitary nymphs. Chauvin (1945) showed the opposite, an increase in crowding decreased the growth rate of nymphs. However, Chauvin also found that if excreta were allowed to build up in the cages along with an increase in population density, the growth rate did increase. Subsequent workers have verified that nymphs reared together develop sooner than isolated nymphs (Willis et al. 1958; Ishii and Kuwahara 1967; Izutsu et al. 1970; Ishii 1971). Finally, Ledoux (1945) explained group formation in the German cockroach as a social phenomenon due to the interattractions of thigmotaxis, positive hygrotaxis, and a positive chemotaxis to their own odors.

Possible hygroreceptors were identified in the German cockroach by Roth and Willis (1952b). Gunn and Cosway (1938) showed the effects of humidity and temperature on the growth rate of Blatta orientalis. Other investigators have studied the optimal temperature ranges for Blattella germanica as well as for other species (Gunn 1933, 1934, 1935; Gould 1941). The upper limit where German cockroaches stayed was 33° Celcius. The range was 21-33°C with over 67% remaining at temperatures between 25°C and 30°C (Gunn 1935). Some Periplaneta species have been shown to aggregate at higher temperatures (27°C) but separate at lower temperatures (15°C) (Ono and Tsuji 1974). This relationship was not seen in Blattella germanica.

The thigmotaxic behavior of cockroaches has been reported by several investigators. Berthold and Wilson (1967) quantified it and found that German cockroaches favor resting spaces of 3/16 inches high when given choices of 1/16 inch increments from 3/16 to 1/2 inch. They also confirmed the hypothesis that cockroaches prefer sites previously soiled by other cockroaches. Given a choice between shelters 1/2 cm or 1 cm high, adult *Blattella germanica* select 1/2 cm heights (Mizuno and Tsuji 1974; Sommer 1975b).

The factor responsible for the chemotactic response in German cockroaches is an aggregation pheromone produced in the rectal pad cells and excreted with the feces (Ishii and Kuwahara 1967, 1968). This pheromone is primarily responsible for the aggregation of early instar German cockroaches and appears to be responsible for adult aggregations as well. Other species also produce aggregation pheromones, most notably *Periplaneta americana* (Burk and Bell 1973; Bell, *et al.* 1973). Aggregation pheromones do not appear to be species specific in cockroaches (Ishii 1970; Bell, *et al.* 1972). This could only be advantageous for species that essentially share the same ecological niche and require the same habitat characteristics. Only in a few cases did nymphs of one species actually avoid paper contaminated by another species

(Roth and Cohen 1973). This avoidance can also be seen within the same species. Beyond certain densities, aggregation effects of nymphs are replaced by repulsive behavior. This repulsive or dispersal inducing effect was found to be due to oral secretions from adults (Suto and Kumada 1981). These clear, watery droplets are only produced at high densities or under stressed conditions. The advantages of increased density, such as increased developmental rates, are concomitant with certain disadvantages. German cockroaches reared under high density conditions have a decreased birth rate, greater wing and antennal damage, and shorter life spans (Komiyama and Ogata 1977) as well as a higher mortality rate (Ebeling and Reierson 1970).

Another chemical stimulus in cockroaches is the sex pheromone produced by females. The female sex pheromone of the German cockroach appears to be composed of two distinct compounds (Nishida et al. 1975). These compounds are non-volatile (Nishida et al. 1975) and must be detected by direct antennal contact (Roth and Willis 1952a; Ishii 1971, 1972). Although produced only by females, the chemicals can be rubbed off on other members of the population. Thus, an adult male can be sexually stimulated by fully grown male and female nymphs as well as other adult males if they have been in contact with sexually receptive adult females (Roth

and Willis 1952a). Furthermore, the production of female sex attractants is cyclic and is controlled by the corpora allata. Production of sex pheromone is greatest in virgin females, decreases sharply after mating, and ceases until the female is again sexually receptive (Roth 1967).

Aggregation behavior in cockroaches is clearly dependent on a wide variety of factors. Temperature, humidity, the presence of food and water, the availability of suitable spaces, and the production of chemical cues are all important. Environmental heterogeneity and physiological responses contribute to the tendency of cockroach populations to aggregate in harborages. The social relationships inherent to the particular species also play a vital role.

Cockroaches fall into three categories of behavior (Bell _et al_. 1979). The most highly evolved category of behaviors is exemplified by dominant/subordinant displays involving dominance hierarchies and territoriality. A second and less evolved category of behaviors includes aggressiveness but lacks dominance hierarchies and territoriality. _Blattella germanica_ belongs in the third category as it is a species that has little or no agonistic behavior. No territoriality seems to occur and even intra-male fighting does not seem important to mating fitness (Breed _et al_. 1975).

The behavioral characteristics of German cockroaches can not be applied equally to all members of a population. Differences in behavior occur among the components of a population. The behavioral repertoire of females often differs from the other social components of the population. Female behavior changes with respect to reproductive state and may even influence certain behaviors of the other members of a population. Female Blattella germanica aggregate more than adult males (Sommer 1975b). There appears to be no significant difference in the level or frequency of agonistic encounters of males and females, yet females with egg cases are more aggressive than those without (Breed et al. 1975). This may be an attempt to protect the egg case, and therefore a form of parental care. The reproductive state of females may even affect their circadian cycle. Virgin Leucophaea maderae females have a locomotor activity superimposed on their ovarian cycle (Wiedenmann and Martin 1980). Five classes of circadian locomotor activity exist in Blattella germanica. Differences occur between males, females with oothecae, females without oothecae, fifth-sixth instars, and second-third instars (Sommer 1975a). The behavior of female Nauphoeta cinerea changes according to their reproductive state (Ewing 1973). Sexually receptive females are more active than one day old unreceptive females. The females

affect the behavior of the males in that territorial males form dominance hierarchies in the presence of females. Population density has even been shown to affect the spatial patterns and behavioral interactions of cockroaches such as Byrsotria fumigata (Breed and Byers 1979).

The extent to which female German cockroaches influence other members of a population is unknown. Most behavioral work has concentrated on developmentally and sexually homogenous laboratory populations. Combined components have usually been confined to male-female studies. The work reported here simulates a population as it might exist in a natural harborage in order to study all the components and their interactions. The dispersion, or spatial distribution, of the cockroaches within the harborage is examined. This should not be confused with the dispersal, or emmigration, of cockroaches from a harborage.

MATERIALS AND METHODS

The experiments were conducted using glass aquaria measuring 32 cm x 22 cm x 21 cm. Each aquarium was covered with a screen lid and coated with a film of petroleum jelly on the inside walls. These precautions minimized the chances of escape. Four shelters, 10 cm x 4 cm x 1 cm were placed side by side in each aquarium. The 4 cm x 1 cm sides were open. The shelters were made from black construction paper and served to partition each harborage into four homogenous areas. A small, mixed population of VPI strain *Blattella germanica* (L.) was released into each harborage. A base population of 4 adult females, 4 adult males, 16 medium-size nymphs (third to fourth instar), and 16 small nymphs (first to second instar) was used. Using 4 males and 4 females allowed them to space themselves evenly in each shelter if that was their nature. Throughout the experiment, multiples of four were used since that was the number of shelters available. Sixteen medium and 16 small nymphs were used since an adult:nymph ratio of 1:4 (80% nymphs) is commonly observed in cockroach populations. Ono and Tsuji (1972) found populations in a state of equilibrium consisted of 80% nymphs. Ross and Wright (1977) found populations in apartment complexes ranged from 68% to 92% nymphs.

Variations of the experiment involved using females in three stages of reproductive development: Females without oothecae, females with young, immature oothecae, and females with older, more mature oothecae. Two of the thirteen stages of oothecal development described by Tanaka (1976) were used. Females with oothecae in the first stage of embryological development and females with oothecae in the ninth to tenth stages of embryological development represented the young and the older oothecae. The density of the females was also varied. Densities of 4, 8, and 16 female cockroaches were studied. The number of males and nymphs was kept constant at the densities stated above. Five to eight replicates of each variation were performed.

Each experiment was run for two days. Food and water were provided for the first day while the cockroaches became acclimated to their environment. The food and water were removed after the first day to prevent its use as a harborage site. At the end of the second day, the shelters were sealed off to prevent further movement between them. The cockroaches were anesthetized with carbon dioxide and each shelter censused. No cockroaches were reused for any of the experiments. New shelters were made for each experiment. Aquaria were washed thoroughly after each use.

The statistical analysis was done with the help of Dr. Golde I. Holtzman of VPI & SU's Department of Statistics.

A new application of Morisita's dispersion index was devised (Morisita 1959, 1962). The index gives a delta value between 0 and 1. A delta value of 0.25 indicates a random distribution among the four shelters. If delta is significantly greater than 0.25, over-dispersion or aggregation occurs. If delta is significantly less than 0.25, then under-dispersion or random dispersion occurs. Significance levels depend on the variability of the replicates and the number of observations. Thus, 0.35 may be significantly higher than 0.25 for one component of the population but not for another. An alpha level of less than 0.10 was used for significance. The methods of calculation are summarized in the Appendix. A more detailed explanation of the statistic is being prepared for publication (Holtzman, Bret, and Ross, unpublished).

RESULTS

The distribution of each component within the four shelters can be visualized in Figures 1 and 2. Figure 1 summarizes the % of each component in shelters 1 to 4, and those outside the shelters, according to female density. Figure 2 summarizes the same information according to female reproductive state. These graphs show a bimodal distribution between shelters 1 and 4. This bimodal distribution is misleading. In actuality, most cockroaches were found in one, not both, of the outermost shelters. The next largest number of cockroaches was just as often in an inner shelter as in the other outer shelter. In order to eliminate the false bimodal distribution, and elucidate more information about the behavioral associations within each population, the shelters were re-numbered. The shelter containing the most females was arbitrarily labelled number 1. The shelter with the second most females was labelled number 2, and so on until number 4. The other components were then recorded in the appropriately re-numbered shelter.

The new system is shown in Figures 3 and 4. It is clear that most of the cockroaches were located in only one of the four shelters. Relatively few cockroaches were outside the four shelters, with the exception of the small nymphs. Only 2.1 to 8.7 % of the females, males, and medium nymphs were

found outside the shelters. This is in contrast to 28.3 to 36.1 % of the small nymphs. Many small nymphs aggregated between the shelters, in the corners of the aquaria, or occasionally escaped.

Figures 3 and 4 give a general picture of within-harborage distribution, but they do not reveal whether the apparent relationships are statistically significant. A special dispersion statistic was used to study the distribution of the cockroaches among the four shelters (Holtzman et al. unpublished). The dispersion statistic, delta, provided a test of the statistical significance of inter- and intra- component aggregation as well as of population aggregation. In addition, it revealed trends toward less or more intense aggregation that are especially important in studying the combined effects of the two variables -- female density and female reproductive state. Three reproductive states at three densities resulted in nine different experiments, each involving the four sex/age class components. Results were analyzed first with respect to female density and then reproductive state in order to have numbers large enough to show statistical significance. In Section I, the results are examined when arranged by the three densities of females. Delta values and significance levels for these are presented in Table 1. In Section II, the results of the experiment are examined as arranged

according to the three reproductive states of the females. Delta values and significance levels are in Table 2. Biological significance emerges only when the combined effects of the two variables are considered. The data, arranged acording to the combined effects of density and reproductive state, are presented in Section III. These affect the interpretation of the data presented in Sections I and II, and consequently are described in more detail. Delta values are given in Tables 3, 4, and 5 for populations containing non-egg case bearing females, females with early stage egg cases, and females with late stage egg cases, respectively. Statistical significance cannot be shown at this level but behavioral patterns and trends can be seen.

Section I - Female Density

When the data were analyzed according to female density, regardless of reproductive state, the number of females in a population appears to have influenced the aggregation behavior of the population and its components. With only four females present (Table 1:4♀), significant levels of aggregation occurred for the individual components and for the population as a whole. The males aggregated least and the nymphs aggregated most.

Doubling the number of females (Table 1:8♀) resulted in greater dispersion. The population as a whole was less aggregated. This was due to the dispersion of the individual

components. Females no longer aggregated together ($d_{♀}$ = 0.36, $p>0.10$) and neither did males ($d_{♂}$ = 0.30, $p>0.10$). However, there was an association between the two as they did aggregate together. Female-male aggregation remained significant ($d_{♀♂}$ = 0.33, $p<0.05$) although less so than at the lower density ($d_{♀♂}$ = 0.44, $p<0.001$). The small nymphs continued to aggregate by themselves (d_S = 0.43, $p<0.01$). Medium nymphs also aggregated by themselves (d_M = 0.36, $p<0.01$).

These trends continued as the density of females was increased to sixteen (Table 1:16♀). Again, neither females nor males aggregated among themselves ($p>0.05$). However, female aggregation was significant at $p<0.10$. Male-female aggregation no longer occurred at this density ($p>0.10$). Small nymphs still aggregated with each other (d_S = 0.60, $p<0.001$), as did medium nymphs (d_M = 0.45, $p<0.001$).

Inter-component aggregation of medium and small nymphs was significant at each of the female densities. Similarly, medium and small nymphs aggregated with the females in every case but one. Medium nymphs and females did not significantly aggregate at the female density of eight ($p>.05$). However, this is significant at $p<.10$.

Section II - Female Reproductive State

Other patterns emerged when the data were summarized as to the reproductive state of the females, regardless of

density (Table 2). Females did not aggregate together when they lacked egg cases ($d_{♀}$ = 0.25, $p>0.10$). Males in such populations were also randomly dispersed ($d_{♂}$ = 0.35, $p>0.05$) although aggregation was significant at $p<0.10$. Males and females did not aggregate by themselves, but they did aggregate with each other ($d_{♀♂}$ = 0.31, $p<0.01$). Significant intra-component aggregations were found only among small and medium nymphs (d_S = 0.44 and d_M = 0.41).

This pattern was altered when females bearing young oothecae were present in the population (Table 2:B). The females were highly aggregated ($d_{♀}$ = 0.53, $p<0.001$), in contrast to the randomness seen among the non-gravid females (Table 2:A). Only the males remained randomly dispersed ($d_{♂}$ = 0.32, $p>0.10$). The aggregation response of the medium and small nymphs increased (d_M = 0.47 and d_S = 0.53).

A further change occurred when the females of the population were carrying mature oothecae (Table 2:C). The females still aggregated together ($d_{♀}$ = 0.39, $p<0.05$), but less so than when the egg cases were immature. The males were again randomly distributed within the harborage. This was stronger than in the other experiments ($d_{♂}$ = 0.26 vs $d_{♂}$ = 0.32 and $d_{♂}$ = 0.35). Medium and small nymphs again aggregated by themselves (d_M = 0.40 and d_S = 0.49). As with the females, aggregation was less intense than when the females carried immature egg cases.

Inter-component aggregation between small and medium nymphs was significant regardless of the female reproductive state. Inter-component aggregation between the nymphs and the females was also significant for each of the female reproductive states but was more intense with the gravid females than the non-gravid females.

Section III - Density and Reproductive State Combined

Significant differences in aggregation were shown when the data were examined according to female density and female reproductive state (Sections I and II). Nevertheless, the aggregation behavior could not be attributed solely to one or the other factor. Indeed, when the data are considered with respect to possible inter-relationships between these variables, they suggest that the reproductive state of the females influences the density effects. Figure 5 illustrates the combined effects of density and reproductive state. The symbols indicate the relative delta values. Four symbols indicate the highest aggregation, no symbols indicate no aggregation. The corresponding delta values for the nine combinations of density and reproductive state are presented in Tables 3-5.

Population aggregation depends on the combined effects of female density and reproductive state. An inverse relationship between density and degree of aggregation occurred in populations with non-gravid females (Table 6:4A

and Table 3). At low densities, populations with non-egg case bearing females (A) displayed strong aggregation behavior. At the higher densities, very little, if any, aggregation occurred. On the other hand, a direct relationship between density and aggregation occurred in populations with gravid females (Table 6:B & C and Tables 4 and 5). In general, as the density of the females increased, the aggregation response of the population increased. Only two exceptions to this were noted. The aggregation response of the males did not change much. Secondly, aggregation between males and females decreased as the density of females bearing mature egg cases increased. Another trend occurred in the experiments using gravid females. Populations with early-stage oothecae aggregated more than populations with females carrying late-stage oothecae. This trend occurred regardless of the density of the females.

These aggregation patterns of the populations are merely responses to under-lying relationships between and among the populations' components. Behavioral changes in one or more of those components are reflected in the differences between the various populations.

As already seen, populations were highly aggregated at low densities of non-gravid females. This was due to the unique behaviors of the components of those populations (Table 3). The females themselves displayed a high degree

of aggregation ($d_{♀}$ =.44). Within the non-gravid experiments, this only occurred at low female density. At the higher densities, the non-gravid females were randomly dispersed. A special characteristic of this experiment was the aggregation of the males. In no other experiment were the males aggregated. Only at low densities of non-gravid females were males aggregated instead of being randomly distributed ($d_{♂}$ = .50 vs. $d_{♂}$ =.27 and $d_{♂}$ = .30). Inter-component aggregation was also very strong at the low female density. Delta values for each combination of components were greater than or equal to .50. This was especially notable for the males. In no other instances were inter-component aggregations involving males this intense.

At the highest density of non-gravid females (16:A), the random distribution of the entire population was due to a complete lack of aggregation in both the adult females ($d_{♀}$ =.24) and males ($d_{♂}$ =.30) and a very low level of aggregation among the medium and small nymphs. Even the inter-component aggregations were very low for each combination of components as seen in Table 3 ($d_{♀♂}$ =$d_{♀S}$ =$d_{♂M}$ =$d_{♂S}$ = .28, $d_{♀M}$ =.29, d_{MS} =.32).

Aggregation responses in populations of gravid females (B and C) were also mediated by the components (Tables 4 and 5). Populations were highly aggregated at the highest density of females with immature oothecae (16:B). The basis

for this differs from that of the high aggregation seen in the low density non-gravid female populations (4:A). The males were not aggregated as before, but instead were randomly dispersed. However, the females were highly aggregated ($d_{♀}$ =.56), more so than in any other experiment. Likewise, the small nymphs aggregated more in 16:B than in any other experiment, as evidenced by an extremely high delta value (d_S = 0.77). Inter-component aggregation between medium and small nymphs and between females and nymphs was also greatest in this experiment. Thus, the strong aggregation behavior of the population at the high density of females bearing immature oothecae (16:B) was primarily due to the females and the nymphs while at the low density of non-gravid females (4:A) it was due largely to the males.

That certain components exhibited different responses under different conditions shows that 1) females, males, medium nymphs, and small nymphs do not have the same behavioral responses, and 2) these components of the population are influenced, in varying degrees, by the density and reproductive states of the females. The aggregation response of the females was the most varied, from random dispersion to a high degree of aggregation. Their reproductive states and consequent density effects were the major factors responsible for the observed

aggregation patterns of the females themselves, and of the relationships between and among the other components of the population. The adult males were the most consistent. In all but one case, they displayed very little or no aggregation. A drastic switch was seen in populations with low numbers of non-gravid females. As already discussed, males did aggregate under, and only under, those circumstances. The medium and small nymphs were variable. Their aggregation behavior was closely aligned with the females' behavior. If female aggregation increased, so did nymphal aggregation. The aggregation response of the small nymphs was especially strong, usually the strongest in the population. First and second instar nymphs are the most gregarious component in a population (Ishii and Kuwahara 1968). As young nymphs mature, they aggregate less (Sommer, 1975b). This was seen in this experiment. The medium nymphs aggregated less than the younger ones.

DISCUSSION

Generally, the cockroaches entered the shelters as expected. One exception to this was the number of small nymphs found outside the shelters. The only instance reported to date in which cockroaches did not collect inside shelters was where only one or two individuals, either adults or large nymphs, were present (Mizuno and Tsuji, 1974). This was explained by a response to low levels of aggregation pheromones associated with very low density. In contrast, the nymphal dispersal in the present study can be best explained by shelter favorability. The 1.00 cm high shelters were larger than the preferred height. Early instars prefer spaces less than 0.50 cm (Berthold and Wilson, 1967) and can even fit in crevices of only 0.05 cm (Wille, 1920; Klunker, 1977). That nymphs sought refuge between the shelters, in the corners of the aquaria, or even escaped, indicates the shelters did not provide the thigmotaxic stimulus required by early instars. However, those nymphs that did remain in the shelters exhibited aggregation responses along with the other components.

Females of at least one cockroach species are capable of influencing the behavior of the population (Ewing 1973). The results of this experiment show that this is also true of the German cockroach. The group formation of the

population varied with the reproductive state and the density of the females in the population. It is also known that the German cockroach produces an array of chemical stimuli that influence behaviors (Ishii and Kuwahara 1967, 1968; Nishida et al. 1975; Suto and Kumada 1981). Thus, it is quite possible that the adult females produce chemical stimuli that influence the behavior of the population, and that these chemicals are mediated by the females' reproductive state and density.

Gravid females apparently produced an aggregation pheromone that caused aggregation of the females and the nymphs. As the density of the females increased, the amount of aggregation pheromone present in the harborage naturally increased. This increased the aggregation response of the females and the nymphal components. Nymphs, especially early instars, showed high degrees of aggregation. The response of medium nymphs to chemical cues was less intense than that of the early instar nymphs. Sommer (1975b), likewise found that the aggregation of nymphs decreases as they age.

The males of these populations did not aggregate. Sommer (1975b) also found adult males to be the least aggregated component in a population. Males may be more responsive to female sex pheromones than to aggregation pheromones. In one study, males that had been isolated from females showed strong aggregation responses to virgin

females (Roth and Willis 1952a). The males in the present experiment were taken from a mixed colony. Therefore, it can be expected that their response to female sex attractant would be somewhat reduced. One must also consider the cyclic nature of the production of female sex attractants. The production of attractants drops sharply after mating (Roth 1967). In this experiment, gravid females apparently did not produce sex pheromones in quantities large enough to induce aggregation among the males. Further, male-female aggregation decreased as the density of females with mature egg cases increased. This may be due to a decrease in the production of sex pheromone with increased female density.

Females without egg cases do produce the sex pheromone. This could, in part, account for the strong aggregation of males at the low density of non-gravid females. Both adult females and adult males aggregated strongly. Males produce an aggregation pheromone and non-gravid females may also, particularly at low densities. A large aggregate of males and females may increase the presence of aggregation pheromones that would in turn reinforce the aggregation behavior of the early and middle instars.

One is tempted to attribute increased dispersal at increased densities of non-gravid females to the physical limitations of the shelters. Limited space would force the cockroaches to disperse. However, this would also have to

apply to gravid females, as they take up almost twice as much space as non-gravid females. Gravid females aggregated more at higher densities than at lower densities so lack of adequate spacing cannot explain the dispersion of non-gravid females. The answer must lie elsewhere.

Three possibilities could account for decreased aggregation associated with increased numbers of non-gravid females. The amount or concentration of aggregation pheromone produced may have decreased, a dispersion inducing substance may have been produced, or a combination of those two events occurred. The effect on the population was greater dispersion.

The production and regulation of chemical cues, and the ensuing behavioral repertoires, have implications for species survival. Reproduction is an energy consuming process. Gravid females need to channel their resources toward the development of the egg case rather than waste energy dispersing. Stationary behavior of gravid females would be enhanced by their close association with themselves and other components. This has been noted in wild populations. In a recent experiment aboard a Naval vessel, gravid females were seen to remain within harborages. Moreover, the harborages were located near food and water (Ross, Bret, and Keil, unpublished). This, also, was an advantageous type of behavior. It ensured that their eggs

would hatch in favorable sites. This increased the chances of survival for the newly hatched nymphs.

The middle and early stage nymphs aggregated in the same manner as the gravid females. The four shelters in this study were identical so the favorability of the site should not be a factor in explaining why the nymphs aggregated with the females. Rather, it appeared that nymphs were particularly responsive to the aggregation pheromone of gravid females. The primary advantage of this behavioral pattern may have been that noted above, increasing nymphal survival. It would be beneficial for nymphs to aggregate with gravid females since gravid females select favorable aggregation sites.

No reproductive benefits would be gained from the aggregation of gravid females and adult males. The presence of an egg case prevents a female from mating. Less obvious is the fact that females generally do not need to be reinseminated after each egg case. Enough sperm from the first mating is stored in the female's spermatheca to fertilize successive egg cases (Cochran 1979). Gravid females can not mate and consequently, do not need to produce sex pheromones in quantities large enough to attract the males. The evolution of cyclic sex pheromone production is probably correlated with the inability of gravid females to mate. The effect of this was seen in the lack of male

aggregation behavior.

Non-gravid females have different biological responsibilities than gravid females. A favorably situated harborage for egg case hatch is not an imminent problem. It is not surprising that these females dispered more readily than gravid females. This was seen in the same shipboard experiment mentioned earlier. The only adult females that moved away from favorable sites were those without egg cases (Ross, Bret, and Keil unpublished). A second aspect of the behavior of non-gravid females is associated with pressures from increased density. As the density of females increases, the reproductive potential of the population increases, and the carrying capacity of the harborage is approached. The effect of non-gravid female behavior on the group could provide a mechanism whereby inhabitants are forced out of an over-crowded harborage at a time most advantageous for survival. Such a time would be when the proportion of gravid females in the population was low. Non-gravid females are better able to invest energy into dispersal. Once a suitable site is found (food, water, shelter, uncrowded conditions), metabolic resources can then be diverted from dispersal into reproduction.

As in the case with gravid females, both middle and early stage nymphs showed aggregation patterns following those of the females. With non-gravid females present,

however, aggregation decreased as female density increased. The aggregation pheromone of non-gravid females apparently decreases or is replaced by a dispersal inducing substance. As noted above, this may encourage dispersal at a time ensuring maximum survival. The increased dispersion of the larger nymphs would possibly insure space for future nymphal production if a harborage was filled to capacity.

The males did aggregate with each other and with the females but only at low densities of non-gravid females. This could be due to the absence of a repellent substance or the presence of an aggregation substance or female sex pheromone. At higher female densities, sex and aggregation pheromone production may be stopped and/or production of the repelling substance increased. The production of the sex pheromone might also play a role in this. The sex pheromone of female German cockroaches is non-volatile (Nishida et al. 1975). Thus, it can only be detected by direct antennal contact. Aggregations of females would increase the number of antennal contacts by males, thereby influencing their aggregation behavior. The sex pheromone has even been shown to rub off on other cockroaches such as the nymphs (Roth and Willis 1952). The aggregation of nymphs with females at low concentrations increases the pool of stimuli which the males are exposed to, serving as an added source of attractant. At higher female densities, the females dispersed and even the

nymphs aggregated less. The focal point of aggregation was thus removed by the increased dispersion of the females. Without an aggregation of females, sex and/or aggregation pheromones are no longer concentrated in one location.

These experiments show that adult females are a motivating force in determining the group formation of the population and its components within a harborage. The cyclic nature of the female sex pheromone is already known (Roth 1967). It now appears that the production of aggregation and dispersal substances may also be cyclic and dependent upon the reproductive state of the females. There may be further relationships between cyclic feeding behavior (Cochran unpublished) and cyclic pheromone production by females of this species. The reproductive state of the majority of females within a group apparently acts to maintain the integrity of the group at times most vital to the viability of the egg cases and subsequently the survival of the newly hatched nymphs. Likewise, the reproductive state of the females also influences the dispersion and possible dispersal of a population at times most advantageous to the success of the species. The importance of females to the understanding of the population behavior and dynamics of the German cockroach is just being realized. It has been said that "...one of the characteristics of Blattella germanica is a large variability of all manners of behavior" (trans.

from Sommer 1975a). The underlying reasons for such variability and the implications of it in the survival strategies of this persistant pest are being unraveled. More work needs to be done on the hormonal and pheromonal control of this insect's behavior in order to find that weak link in its biology which can be best exploited for control purposes.

TABLES FOR GROUP FORMATION

Table 1-Dispersion indices according to female density.(a)

Female Density	Delta Values					Significance Levels				
	♀	♂	M	S		♀	♂	M	S	
	-	-	-	.43	S	-	-	-	<.001	S
	-	-	.48	.45	M	-	-	<.001	<.001	M
4	-	.35	.41	.38	♂	-	<.050	<.050	<.050	♂
	.42	.44	.42	.43	♀	<.001	<.001	<.001	<.001	♀
	Population = .44					Population <.001				
	♀	♂	M	S		♀	♂	M	S	
	-	-	-	.43	S	-	-	-	<.010	S
	-	-	.36	.40	M	-	-	<.010	<.010	M
8	-	.30	.30	.32	♂	-	>.100	<.100	<.100	♂
	.36	.33	.33	.38	♀	>.100	<.050	<.100	<.010	♀
	Population = .36					Population <.001				
	♀	♂	M	S		♀	♂	M	S	
	-	-	-	.60	S	-	-	-	<.001	S
	-	-	.45	.51	M	-	-	<.001	<.001	M
16	-	.29	.31	.32	♂	-	>.100	>.100	>.100	♂
	.41	.32	.43	.48	♀	<.100	>.100	<.010	<.010	♀
	Population = .44					Population <.001				

(a) ♀ = Adult females, ♂ = Adult males, M = Medium-size nymphs, S = Small nymphs.

Table 2 - Dispersion indices according to female reproductive state. (a)

Reproductive State	Delta Values ♀	♂	M	S		Significance Levels ♀	♂	M	S	
A -	-	-	-	.44	S	-	-	-	<.001	S
females	-	-	.41	.41	M	-	-	<.001	<.010	M
without	-	.35	.37	.34	♂	-	<.100	<.100	>.100	♂
oothecae	.25	.31	.32	.31	♀	>.100	<.010	<.010	<.010	♀
	Population = .36					Population <.001				
B -	-	-	-	.53	S	-	-	-	<.001	S
females	-	-	.47	.50	M	-	-	<.001	<.001	M
with	-	.32	.36	.33	♂	-	>.100	<.100	<.010	♂
immature oothecae	.53	.38	.47	.54	♀	<.001	<.010	<.010	<.001	♀
	Population = .47					Population <.001				
C -	-	-	-	.49	S	-	-	-	<.010	S
females	-	-	.40	.44	M	-	-	<.010	<.001	M
with	-	.26	.30	.34	♂	-	>.100	>.100	>.100	♂
mature oothecae	.39	.32	.40	.45	♀	<.050	>.100	<.010	<.010	♀
	Population = .41					Population <.010				

(a) ♀ = Adult females, ♂ = Adult males, M = Medium-size nymphs, S = Small nymphs.

Table 3 - Dispersion indices for populations with non-gravid females (A).

Female Density	Inter- and Intra-Component Delta Values (a)					Population Delta Value
	♀	♂	M	S		
	-	-	-	.51	S	
	-	-	.56	.50	M	
4	-	.50	.55	.51	♂	d = .52
	.44	.51	.50	.51	♀	
	♀	♂	M	S		
	-	-	-	.43	S	
	-	-	.36	.40	M	
8	-	.27	.29	.22	♂	d = .33
	23	.29	.27	.26	♀	
	♀	♂	M	S		
	-	-	-	.38	S	
	-	-	.30	.32	M	
16	-	.30	.28	.28	♂	d = .29
	.24	.28	.29	.28	♀	

(a) ♀ = Adult females, ♂ = Adult males, M = Medium-size nymphs, S = Small nymphs.

Table 4 - Dispersion indices for populations with females bearing immature oothecae (B).

Female Density	Inter- and Intra-Component Delta Values (a)					Population Delta Value
	♀	♂	M	S		
	-	-	-	.38	S	
	-	-	.48	.45	M	
4	-	.31	.38	.30	♂	d = .42
	.45	.40	.44	.39	♀	
	♀	♂	M	S		
	-	-	-	.42	S	
	-	-	.40	.43	M	
8	-	.32	.34	.36	♂	d = .41
	.44	.35	.40	.46	♀	
	♀	♂	M	S		
	-	-	-	.77	S	
	-	-	.52	.62	M	
16	-	.33	.34	.33	♂	d = .55
	.56	.39	.52	.62	♀	

(a) ♀ = Adult females, ♂ = Adult males, M = Medium-size nymphs, S = Small nymphs.

Table 5 - Dispersion indices for populations with females bearing mature oothecae (C).

Female Density	Inter- and Intra-Component Delta Values (a)					Population Delta Value
	♀	♂	M	S		
	-	-	-	.41	S	
	-	-	.39	.39	M	
4	-	.25	.30	.33	♂	d = .36
	.33	.42	.29	.36	♀	
	♀	♂	M	S		
	-	-	-	.44	S	
	-	-	.32	.35	M	
8	-	.30	.28	.37	♂	d = .34
	.37	.34	.31	.40	♀	
	♀	♂	M	S		
	-	-	-	.59	S	
	-	-	.51	.56	M	
16	-	.23	.33	.33	♂	d = .47
	.40	.29	.47	.49	♀	

(a) ♀ = Adult females, ♂ = Adult males, M = Medium-size nymphs, S = Small nymphs.

FIGURES FOR GROUP FORMATION

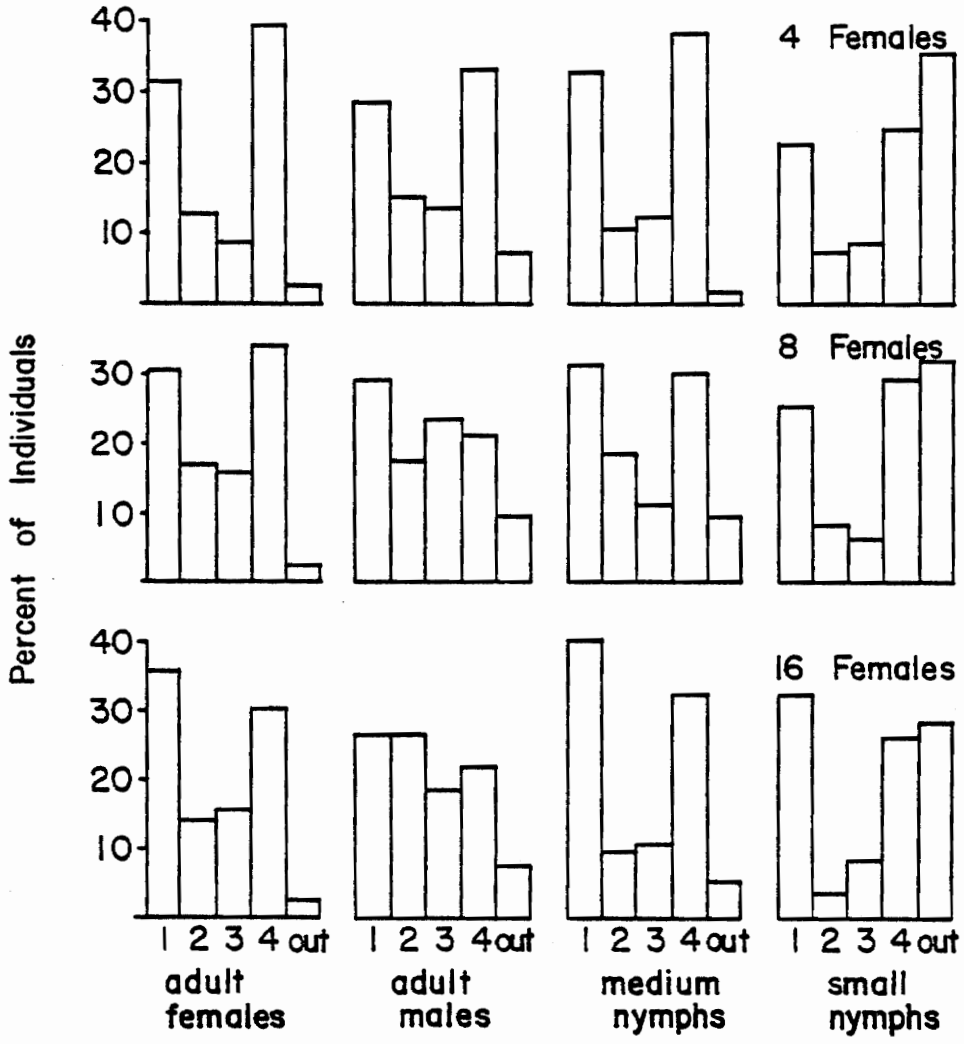

FIGURE 1 - PERCENTAGE OF EACH COMPONENT OF COCKROACH POPULATIONS IN FOUR SHELTERS (1-4) FROM EXPERIMENTS IN WHICH ADULT FEMALE DENSITY WAS VARIED.

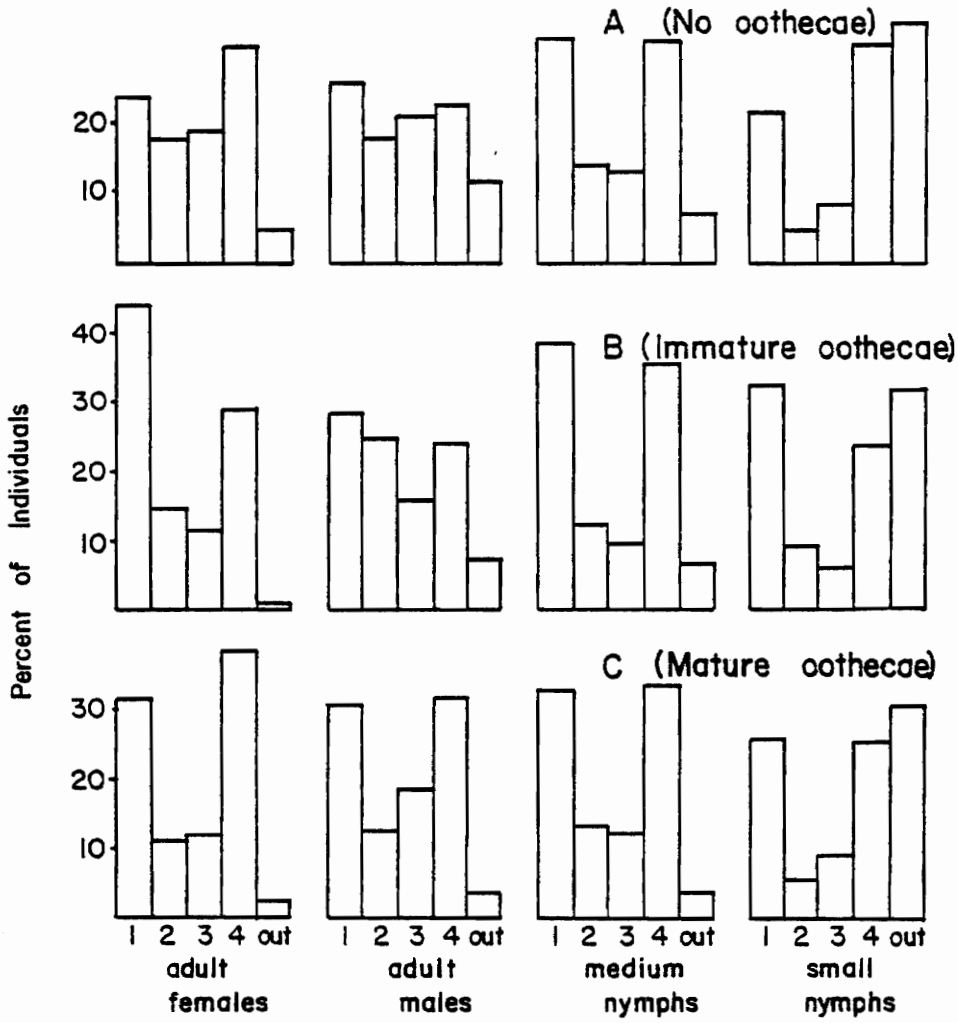

FIGURE 2 - PERCENTAGE OF EACH COMPONENT OF COCKROACH POPULATIONS IN FOUR SHELTERS (1-4) FROM EXPERIMENTS IN WHICH ADULT FEMALE REPRODUCTIVE STATE WAS VARIED.

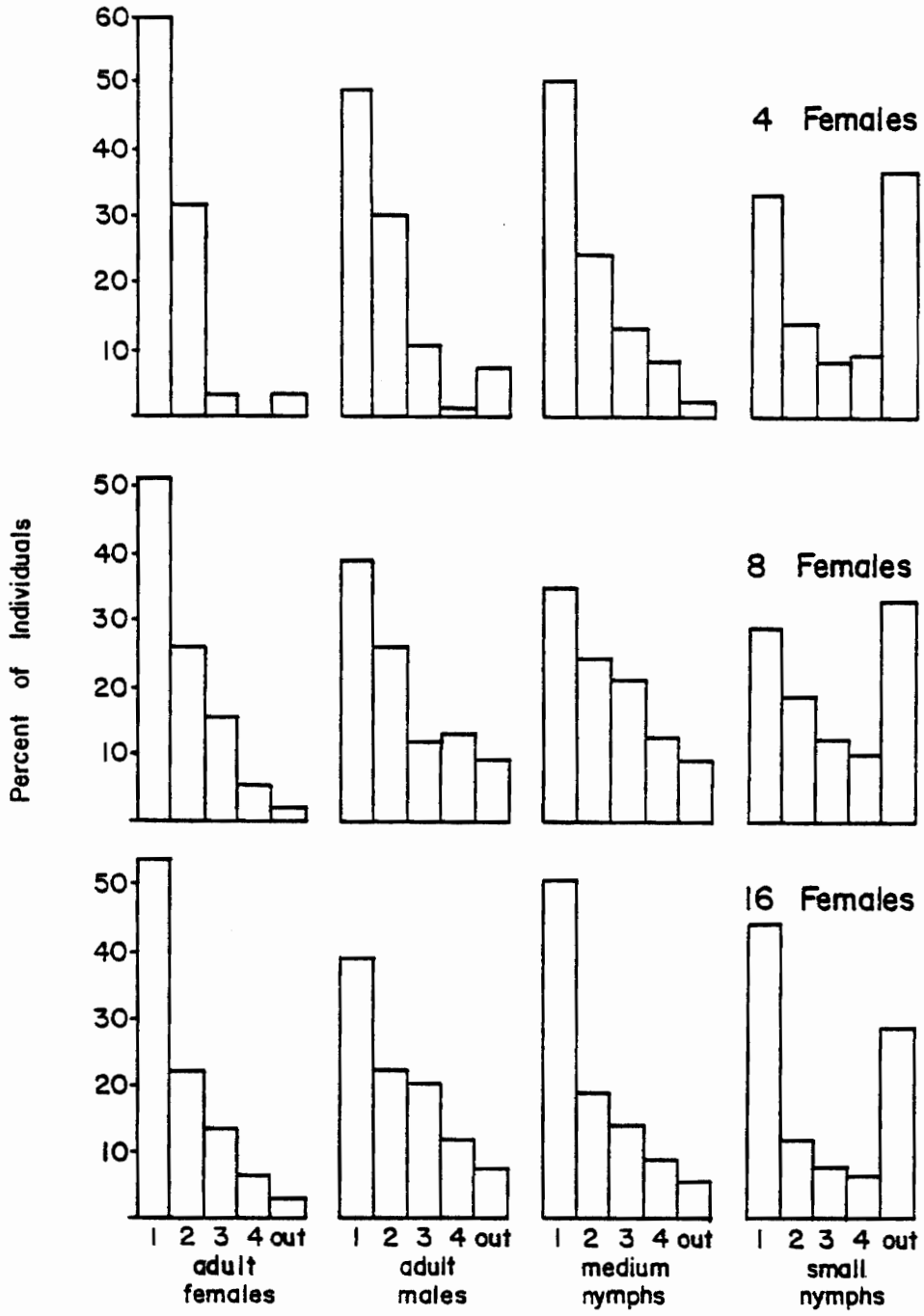

FIGURE 3 - PERCENTAGE OF COMPONENTS OF POPULATIONS IN FOUR "RE-NUMBERED" SHELTERS (1-4) FROM EXPERIMENTS IN WHICH ADULT FEMALE DENSITY WAS VARIED.

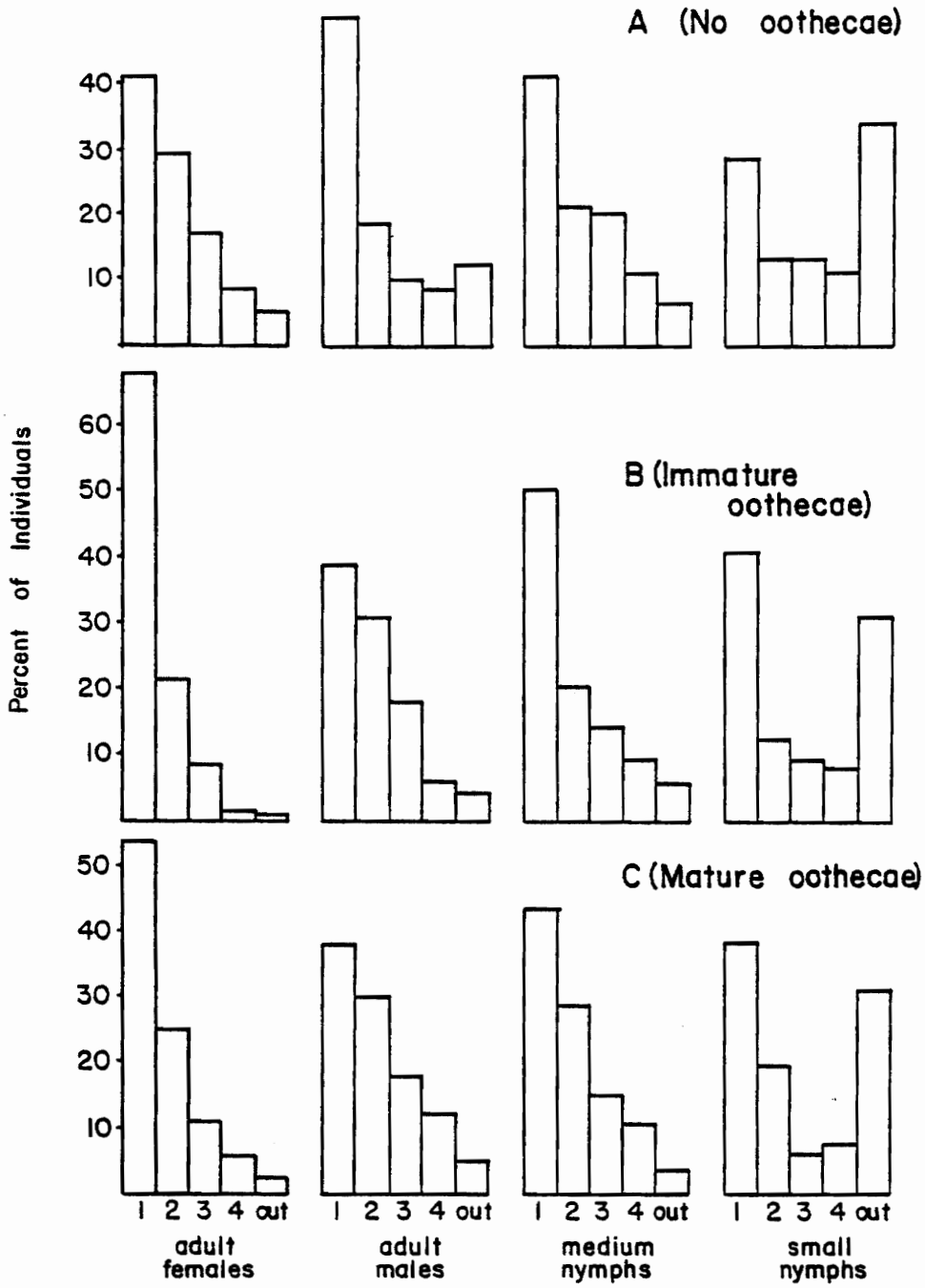

FIGURE 4 - PERCENTAGE OF COMPONENTS OF POPULATIONS IN FOUR "RE-NUMBERED" SHELTERS (1-4) FROM EXPERIMENTS IN WHICH ADULT FEMALE REPRODUCTIVE STATE WAS VARIED.

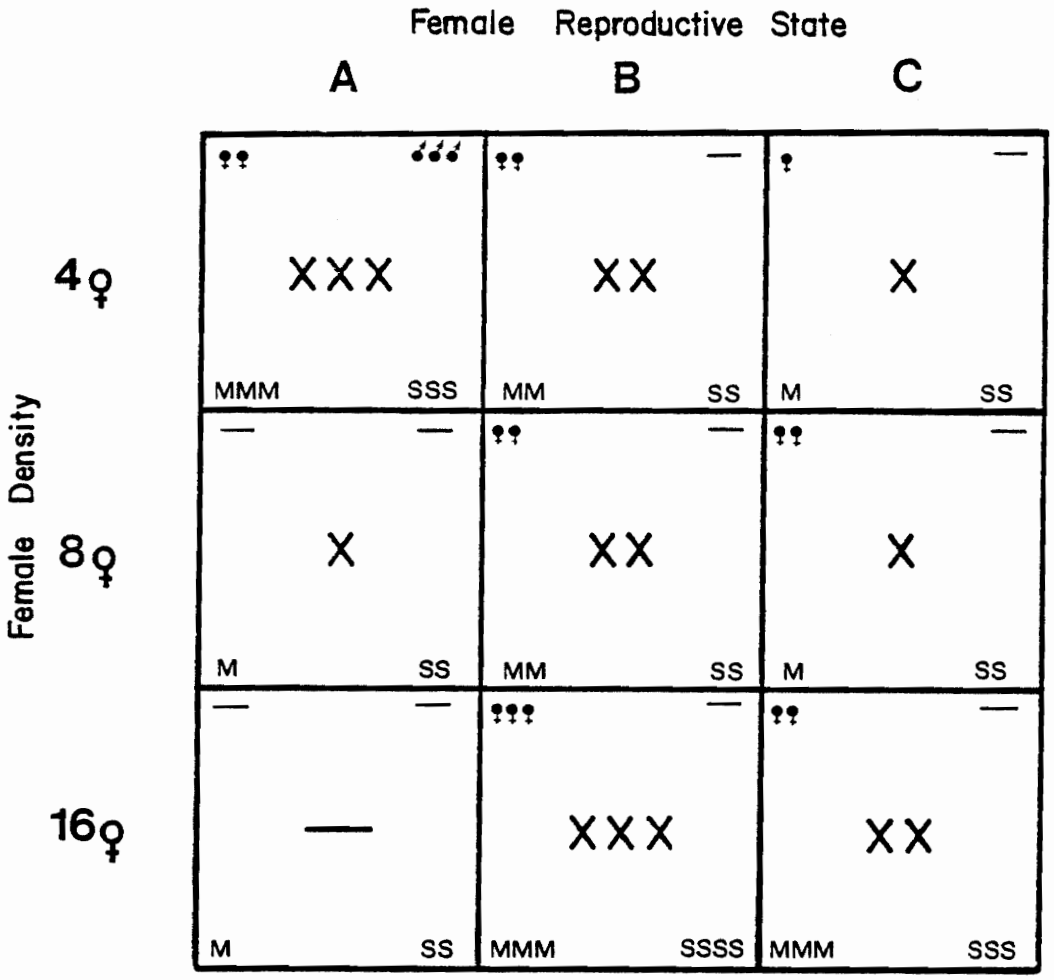

FIGURE 5 - RELATIVE DEGREES OF AGGREGATION DUE TO COMBINED EFFECTS OF FEMALE DENSITY AND REPRODUCTIVE STATE. A = FEMALES LACK OOTHECAE, B = FEMALES BEAR IMMATURE OOTHECAE, C = FEMALES BEAR MATURE OOTHECAE. ABSENCE OF THE FOLLOWING SYMBOLS INDICATES NO AGGREGATION, MANY SYMBOLS INDICATE MUCH AGGREGATION: X = TOTAL POPULATION, = ADULT FEMALES, = ADULT MALES, M = MID INSTARS, S = SMALL NYMPHS.

APPENDIX - STATISTICAL METHODS

The I_δ-index was proposed by Morisita as a measure of the dispersion of individuals in a population (Morisita 1959, 1962). The index is calculated as follows:

$$I_\delta = q \sum_{i=1}^{q} \frac{x_i (x_i - 1)}{T(T-1)}$$

where x_i is the number of individuals in the ith sample unit ($i=1,\ldots,q$), q is the total number of sample units, and T is the total number of individuals or $T=\sum_i^q x_{i.}=x_{..}$

In this application, δ measures the dispersion or distribution pattern, of individuals of different components among four homogenous shelters.

δ is the probability that any pair of individuals from the population will be found together in the same shelter. It is determined by the ratio of R, the number of distinct pairs of individuals in the same shelter, to D, the number of distinct pairs of individuals in the population.

δ_i is the intra-component dispersion index. This gives the probability that any two individuals of the same component i are found in the same shelter by the ratio

R_i to D_i. R_i is the number of distinct pairs of individuals of component i in the same shelter whereas D_i is the number of distinct pairs of individuals of component i in the population.

δ_{ij} is the inter-component dispersion index. This represents the number of pairs of individuals, one of component i and one of component j (i≠j), found in the same shelter divided by the total possible pairs of components i and j.

Mathematically: $\delta = R/D$, $\delta_i = R_i/D_i$, and $\delta_{ij} = R_{ij}/D_{ij}$

where, for only one replicate:

$$R = \sum_k x_{.k}(x_{.k}-1)/2 \qquad D = x_{..}(x_{..}-1)/2$$

$$R_i = \sum_k x_{ik}(x_{ik}-1)/2 \qquad D_i = x_{i.}(x_{i.}-1)/2$$

$$R_{ij} = \sum_k x_{ik}x_{jk}, \ i \neq j \qquad D_{ij} = (x_{i.})(x_{j.})$$

and

x_{ik} = the number of individuals of component i in shelter k where i=1 (adult females), 2 (adult males), 3 (medium nymphs), or 4 (small nymphs) and k=shelter 1,...,t.

$x_{i.} = \sum_k x_{ik}$ = the number of individuals of component i in any shelter where i=1,...,4.

$x_{.k} = \sum_i x_{ik}$ = the number of individuals of any component in shelter k where k=1,...,t.

$T = x_{..} = \sum_i \sum_k x_{ik} = \sum_i x_{i.} = \sum_k x_{.k}$ = the total number of individuals of any component in any of the

shelters.

These relationships can be visualized best in the following table:

component (i)	shelter (k) 1	2	3	4	$x_{i.}$
1	x_{11}	x_{12}	x_{13}	x_{14}	$x_{1\cdot}$
2	-	-	-	-	$x_{2\cdot}$
3	-	- (x_{ik})	-	-	$x_{3\cdot}$
4	x_{41}	x_{42}	x_{43}	x_{44}	$x_{4\cdot}$
population ($x_{.k}$)	$x_{\cdot 1}$	$x_{\cdot 2}$	$x_{\cdot 3}$	$x_{\cdot 4}$	$x_{..}$

The biological null hypothesis is that there is an equal probability of an individual x_i entering any shelter k (k=1,...,t). This takes the form $p_{.k} = 1/t$ for all k. Under the null hypothesis of independence the expected value of δ is 1/t, of δ_i is 1/t, and of δ_{ij} is 1/t. Delta values not significantly different from 1/t indicate random dispersion of the population and its components among the t shelters. Delta values significantly less than 1/t indicate underdispersion or a regular spatial pattern. Delta values significantly greater than 1/t indicate overdispersion or an aggregated/clumped pattern.

Pooled values of each of the replicates were derived by calculating weighted averages of the δ's. The above null hypothesis holds true for the pooled replicates.

In this experiment, four shelters were used so t=4. The null hypothesis becomes $H_0: \delta = 1/4 = 0.25$, $H_1: \delta > 0.25$. A more detailed explanation of the derivation of these statistics and the calculation of significance levels is in preparation (Holtzman *et al.* unpublished).

PART II - DISPERSAL FROM A HARBORAGE

INTRODUCTION

The German cockroach, Blattella germanica (L.) has been an important urban pest throughout the history of man (Cornwell 1968). The reasons for the cockroach's success are numerous. The German cockroach has readily adapted to Man's environment. Food and water sources are invariably available in human establishments. The advent of central heating has proven beneficial to the welfare of blattids as well as humans in providing optimum temperatures year round. Even size is an important asset in the ability of the German cockroach to gain access to suitable harborages. Overlapping generations lead to a pattern of continuous population growth. The presence of genes that impart resistance to most known insecticides has been another major factor in its success. Finally, the German cockroach's role as a stowaway on Man's transports has resulted in a world-wide distribution. This species is believed to have originated in northern Africa where it spread to Europe via Greek and Phoenician trade routes (Rehn 1945). From Europe, it stowed

away on trade ships to the New World. The German cockroach is now found in every state in the continental U.S. Such passive dispersal still occurs today, whether it be from warehouses to grocery stores to homes or from loading docks to ships.

In addition to such passive dispersal, cockroaches are quite capable of active dispersal. As early as the 1890's, "hordes" of German cockroaches were reportedly seen crossing a muddy street in a continuous mass that lasted for two to three hours (Howard 1895). This is certainly an atypical case of cockroach movement. Schoof and Siverly (1954) tried to trace the movement of Periplaneta americana within a sewer system but were unsuccessful. This contrasted with an experiment in Tyler, Texas, that showed widespread dispersal of American cockroaches from manholes into adjacent homes (Anonymous 1953). Jackson and Meier (1955) confirmed the Tyler Project. They found considerable dispersal from the release site did occur, but only when marked cockroaches were added on top of an already existing population.

Some work has been done on short range dispersal and the daily movements of cockroaches from harborages. Bulow and Huggins (1968) found only moderate movement of Supella longipalpa and very little movement of Periplaneta americana between rooms of a building. Several workers have found that German cockroaches will move freely within and between

apartments (Owens 1980; Akers and Robinson 1981; Farmer 1982; Runstrom pers. comm.; Zungoli pers. comm.). In multiple unit dwellings, one particular apartment may provide optimum habitat for cockroaches and become a "focus" site. The movement of cockroaches may be directed towards or away from such foci with free inter-mixing between separate apartments occurring (Akers 1978). Movement of cockroaches is more prevalent between apartments that share plumbing than apartments that lack common plumbing (Owens 1980; Runstom unpubl.). Another study reported less movement between apartments but more movement within the apartments -- e.g. between rooms. Twelve percent of the total marked population moved within the apartment. Of those that moved, 33% were recaptured in different rooms and 15% were recaptured in the same room but at different locations (Zungoli, unpubl.).

Domestic cockroach species aggregate within harborages by day and become active at night. This circadian rhythm has been well studied in many species. Gunn (1940) investigated the daily activity rhythms of Blatta orientalis. Much of the work has been on Periplaneta americana (Harker 1954, 1955, 1956; Cloudsley-Thompson 1953). Roberts (1960) studied Leucophaea maderae and Byrsotria fumigata as well as Periplaneta americana. Blattella germanica has been studied by Darchen (1952) and Hocking (1958). These species are

relatively inactive during the day. A peak activity period in most cockroach species studied occurs just after the onset of night (Cornwell 1968). Activity in the German cockroach is bimodal with one peak just after sunset and another just prior to sunrise (Sommer 1975a). It is during these active phases that movement and dispersal occurs. However, activity rhythms are not as well defined as might be thought. Roberts (1960) only used males in his experiments because females behaved too erratically. Likewise, Lipton and Sutherland (1970) could not find any correlation between the activity rhythms of female Periplaneta americana and the light cycle. They did discover that females with oothecae are more active than females without. Females without oothecae are relatively quiescent. Virgin females, on the other hand, do respond to light cycles with a circadian rhythm similar to males. Wiedenmann and Martin (1980) discovered that virgin Leucophaea madera females also have a circadian activity rhythm, but it is superimposed on their ovarian cycle.

It is apparent that the behavior of female cockroaches differs from that of the rest of the population. Sommer (1975a) identified five different categories of a population with respect to locomotor activity. Males, females without oothecae, females with oothecae, old nymphs (fifth - sixth instar), and young nymphs (second - third instar) display

significant differences in activity rhythms. Differences in behavior extend beyond circadian rhythms. Although not an agonistic species, Blattella germanica females with oothecae are more aggressive than females without oothecae (Breed et al. 1975). The behavior of a female cockroach may even effect the behavior of the other components of a population. Competition for territories by Nauphoeta cinerea males centers around the presence of female groups. The presence of females also increases the incidence of inter-male fighting (Ewing 1973).

The objective of this experiment was to determine if females have any effect on the dispersal characteristics of Blattella germanica populations. Movement studies of the German cockroach have either involved outdoor, uncontrolled experiments on whole populations, or controlled laboratory experiments on individual components of populations. In this experiment a small mixed population was simulated in the laboratory. The effects of the female's reproductive state and female density on the dispersal of a population and its components were examined.

MATERIALS AND METHODS

Three 32 cm X 22 cm X 21 cm aquaria were used for each experiment as shown in Figure 1. Two glass ends were replaced with pieces of plexiglass that had 1 1/4" diameter holes drilled in them. The sides of the aquaria were coated with a film of petroleum jelly to prevent escapes. In addition, lids were placed on each aquarium. Two aquaria were connected linearly to the third one by twelve inch pieces of Tygon tubing. The 1" ID X 1 1/4" OD tubing connected the holes in the sides of the aquaria. Food and water were provided in the end aquaria. The end aquaria were also provided with 1.0 cm X 4.0 cm X 10.0 cm shelters made out of black construction paper. The middle aquarium was left empty.

A mixed population of Blattella germanica was placed in the first aquarium and sealed off from the other aquaria. The cockroaches were allowed to acclimate to their surroundings for two days. At the end of the second day, the first aquarium was opened up to the second and third. One week later, each aquarium was sealed and censused.

Two phenotypes of the German cockroach were used. Half were wild type from the VPI laboratory strain. The other half were VPI strain black-body mutants that had been crossed with cockroaches from a field collection. This was

done to determine if differences occurred between the movement of two different strains as suggested by some workers (Akers 1978).

The base population consisted of 4 adult females, 4 adult males, 16 middle instar nymphs (third-fourth instar), and 16 early instar nymphs (first-second instar). The quantities used were to provide continuity with a previous experiment on group formation (Bret, Ross, and Holtzman, unpubl.). Briefly, multiples of four were used since four shelters were provided in the first and third aquaria. The adult:nymph ratio approximated that found in wild populations (Ono and Tsuji 1972; Ross and Wright 1977).

Two variations of the experiment were done. In one, the density of the females was changed. Female densities of 4, 8, and 16 were used. Secondly, the reproductive state of the females was changed. Females without oothecae and females with oothecae in the first stages of embryonic development (Tanaka 1976) were used at each of the three densities. Thus, a total of six experiments were done. Each experiment had six replicates except for one. The experiment with sixteen gravid females had eight replicates.

Dispersal was measured using the following dispersal index: $DI=(X-Y)/X$, where X= number of cockroaches in the first aquarium at the beginning of the experiment, Y= number of cockroaches remaining in the first aquarium after one

week, and (X-Y)= number of cockroaches dispersed from the first aquarium in one week. The dispersal index ranges for 0 (no dispersal) to 1 (complete dispersal). The higher the index the greater the dispersal. For comparison of the effects of the two female reproductive states a Wilcoxon 2-way non-parametric test was performed on all the experiments combined and on each of the three density experiments. Comparisons of the three densities were tested using the Kruskal-Wallace non-parametric n-way comparisons test on all the experiments combined and on the two different reproductive states. An alpha level less than 0.10 was used to determine significance.

RESULTS

Four aspects of this experiment are looked at. The dispersal of cockroaches from aquarium 1 is first. This includes the effects of female reproductive state and female density. Secondly, the impact of escapees from the system is analyzed. The distribution of cockroaches among all three aquaria comprises third aspect of this experiment. This also entails the effects of female reproductive state and female density. Finally, the differences between the two strains of cockroaches used are presented.

I. Dispersal from Aquarium 1

The percent of cockroaches dispersing from aquarium 1 after one week is provided in Table 1 and is represented graphically in Figures 2 and 3. Figure 2 shows the percent of cockroaches that left the first aquarium for all the experiments combined. Figure 3 shows the percent dispersal of cockroaches from experiments broken down according to each of the three female densities at each of the two female reproductive states.

Figure 2 and Table 1 show that almost half (46.4%) of the population dispersed from aquarium 1. This is primarily due to a large amount of dispersal of small nymphs. Over 60% of the small nymphs dispersed. Dispersal of medium nymphs

was also high with 49.3% leaving. The adult females and males dispersed considerably less (27.2% and 22.4%, respectively).

Effects of Female Reproductive State - Very little difference occurred between populations with non-gravid females and populations with gravid females at each of the three densities (Figure 3). The dispersal indices are presented in Table 2. A Wilcoxon 2-sample test on each of the replicates supported this observation. Table 3 shows the significance levels for the test. The dispersal of components from populations with non-gravid females was not significantly different from populations with gravid females, with one exception. At the lowest density of females, non-gravid females dispersed less than gravid females. This is not significant at a probability level of less than 0.05 but it is significant at a probability level of 0.10.

The reproductive state of the females did not appear to have a significant impact on the rate of dispersal of most of the components of the population. However, this was misleading. The reproductive state of the females did not remain constant throughout the experiment. Many of the non-gravid females developed egg cases by the end of the first week. Comparisons of the experiments with gravid vs "non-gravid" females may not be made with much certainty.

Effects of Female Density - More confidence could be placed on the analysis of density effects. Figure 3 shows the percent of cockroaches dispersing from experiments containing gravid females, while Table 2 shows the respective dispersal indices. A general trend was seen. Dispersal decreased as the density of gravid females increased. The significance levels from a Kruskal-Wallace non-parametric test are in Table 4. Highly significant differences in dispersal occurred with respect to female density when gravid females were present. The populations as a whole dispersed less with increased female density ($p=.015$), as did the females themselves ($p=.001$) and the medium nymphs ($p=.020$). Although Figure 3 shows a trend towards decreased dispersal, the dispersal of males from the harborage was not statistically significant ($p>.200$), possibly because of the low number used in the experiment. The dispersal of small nymphs was very consistant. There was no significant difference in the dispersal of small nymphs ($p>.900$) with respect to female density.

The percent of cockroaches dispersing from populations of "non-gravid" females can also be seen in Figure 3. As previously mentioned, many of these females had developed egg cases after one week. Caution must be exercised in interpreting these results. The significance levels for comparisons of density effects are also in Table 4.

Significant differences in dispersal with respect to female density occurred with the adult females ($p=.003$). No significant differences occurred with the early instar nymphs at significance levels of less than .05, but did occur at significance levels of less than 0.10 ($p=.076$). Confusingly, the differences are neither directly nor inversely related to female density. Females dispersed least at high density but dispersed most at the middle density. Conversely, small nymphs dispersed least at the middle female density and most at the highest female density. No significant differences occurred among the adult males or the middle instar nymphs ($p>.100$).

The "non-gravid" females that remained in the first aquarium are broken down in Figure 4 into those that developed oothecae and those that remained without oothecae. At each density, well over half of the females developed egg cases by the end of one week. One important point to make is that more females with egg cases remained, or did not disperse, than females without. To extrapolate, females with egg cases dispersed the least while females without egg cases dispersed the most. Another interesting characteristic occurred between the females without egg cases and those with egg cases. The greatest percent of the females with egg cases remaining in the first aquarium was found at the highest densities. Conversely, the greatest

percent of females without egg cases that remained in aquarium 1 occurred at the lower densities.

Since most of the females were gravid, the "non-gravid" experiments were combined with the original gravid experiments. As seen in Table 4 and Figure 5, the combined results were closely similar to the experiments begun with gravid females. Female dispersal decreased significantly as female density increased ($p=.001$). Medium-sized nymphs also dispersed less as female density increased ($p<.006$). Neither the males nor the small nymphs displayed significant changes in dispersal ($p>.100$), although again, males tended toward increased dispersal at the higher female densities.

II. Escapees from the Aquaria

Much of the dispersal from aquarium 1 was due to cockroaches that escaped or were unaccounted for in any aquarium or in the tubes connecting the aquaria. Table 5 shows the percent of each component that escaped from all the experiments. Almost a quarter of the populations (23.9%) escaped. This was primarily due to a large percentage of nymphs that escaped. Over half of the small nymphs (54.8%) escaped. Some medium nymphs also escaped (11.8%). Very few adult females or males escaped (2.2% and 2.0% respectively). These patterns remained the same regardless of female reproductive state or female density. The early instars escaped most, the adults escaped least.

III. Distribution of cockroaches among the three aquaria

More insight can be gained by looking at the dispersal of those cockroaches that did not escape from the system. Table 6 provides the percentage of the cockroaches remaining in the system that were collected from each of the three aquaria and from the tubes connecting them. Approximately 70% (70.4%) of the cockroaches from all the experiments remained in the first aquarium. In contrast to Table 1 and Figure 2, Table 6 and Figure 6 show different dispersal patterns of the population components. Very little dispersal of small nymphs occurred from aquarium 1. Of the small nymphs that remained in the system, 86.1% remained in the first aquarium. Most of the adult females and males also remained in the first aquarium (74.0% and 74.7% respectively). The greatest dispersal was by the middle instars, with only 58.6% remaining in the first aquarium.

If the cockroaches did not escape, but did not remain in the first aquarium, where did they disperse to? About 20% (19.1%) of the populations dispersed to aquarium 3. This was the only other aquarium with food, water, and shelter and contained the second largest percentage of each component. More middle instars dispersed to the third aquarium (27.6%) than any other component. Only 10.2% of the small nymphs settled there. The percent of adult females and

males was intermediate to the middle and early instars.

Only 10.4% of those cockroaches that did not escape were found outside the two aquaria provided with food, water, and shelter. Roughly half of these were in the barren, second aquarium and half in the tubes. Again, more of the middle instars were found between aquaria 1 and 3 (13.9%) than any other component. In contrast, only 3.6% of the early instars were between aquaria 1 and 3. The percent of adults ranged between the low of the small nymphs and the high of the medium-sized nymphs.

Effects of Female Reproductive State - Little difference was seen in the patterns described above when the results are broken down according to the initial female reproductive states as in Table 7. Most of the cockroaches of each component remained in the original aquarium regardless of the reproductive state of the females in the population. Of those that dispersed, most were found in the third aquarium. Also, the middle stage nymphs dispersed from aquarium 1 to 3 the most while the small nymphs dispersed the least, without regard to female reproductive state. Only a few discrepencies occurred. Fewer females with egg cases dispersed to aquarium 3 than did females without egg cases. This is not reflected by fewer females dispersing from aquarium 1 as there is virtually no difference between the percent of gravid females remaining (75.0%) and the percent

of "non-gravid" females remaining (72.9%). The reason is instead reflected in the higher proportion of gravid females occurring within the tubes (12.8%) than "non-gravid" females (1.8%). In fact, the percentages of medium nymphs in populations containing gravid females was also much higher than in populations without gravid females. In the experiment with gravid females, 11.2% of the medium nymphs were censused in the tubes as compared to only 3.8% of medium nymphs in the experiment with non-gravid females.

Effects of Female Density - No differences in the pattern of dispersal occurred when the experiments were broken down according to female density as in Table 8. Differences in the degree of dispersal, however, did occur. Movement from aquarium 1 to aquarium 3 was density dependent. The percent of adult females, adult males, and middle stage nymphs that remained in the first aquarium increased with increasing female density. In other words, dispersal of those components decreased as female density increased. The percent of small nymphs remaining changed very little, ranging from 85.6% to 86.5%. The percent of small nymphs dispersed to aquarium 3 at the high and low female densities was very stable (12.5% and 12.2%). A large decrease occurred at the intermediate female density (only 6.7%).

The proportions of components outside the two main

aquaria varied with female density, but in no recognizable pattern. In general, they represent relatively small proportions of the total with two exceptions. First, at a density of four, 18.8% of the females were found within the tubes. This is reflected by the large number of females from the gravid female experiment as described above. Secondly, at a female density of eight, 17.0% of the females were found in the second aquarium. This high figure is due to only two particular replicates in the experiment.

IV. Dispersal Differences Between Strains

Differences in the rates of dispersal between VPI strain wild type and a black body mutant strain were also examined. Since no significant differences occurred between experiments using non-gravid and gravid females, the two were combined. Table 9 shows the number of cockroaches remaining in the first shelter at each of the three female densities and for the total. As explained, half of the populations were wild type VPI strain (wt) and half were black body mutants (*Bl*) crossed to a field strain. There was very little difference between the two strains. The largest difference occurred between the strains of medium nymphs. Figure 7 shows the frequency distribution of middle instar cockroaches remaining in the first shelter. The similarity between the two strains can now be seen more easily, especially with the large degree of variability involved

between the individual replicates. One source of variability may be differences between females in the "non-gravid" experiment that developed egg cases and females that remained non-gravid.

DISCUSSION

That so many small nymphs dispersed away from the food, water, and shelter of the first aquarium is surprising. Other laboratory studies (Bret *et al.* unpubl.) as well as field observations (Ross *et al.* unpubl.) have indicated that early instar nymphs tend to remain stationary near food, water, and suitable refuge. However, the present data do not necessarily contradict this. The large percentage of nymphal dispersal appears to be an artifact due to escape from the system. The first aquarium was sealed off from the others for two days prior to the experiment to allow the cockroaches to acclimate to new surroundings and form an aggregate group. The only means of escape was under the lid. Only the early instars could escape by this route because of their small size. Thus, most of the other members of the population were retained by the first aquarium long enough to settle down and aggregate in the cardboard shelters. In contrast, immediate dispersal by small nymphs was less limited following their introduction to the new environment of the aquarium. This helps explain why so many small nymphs escaped from the system. In a shipboard experiment, disturbance of an infested harborage caused a greater dispersion among small nymphs than any other age class (Ross unpubl.). Another factor that may have played a role in the

escape of large numbers of early instars was the lack of suitable shelters in aquarium 1. Early instar nymphs prefer spaces less than 0.50cm (Berthold and Wilson 1967) and can even fit in cracks and crevices of only 0.05cm (Wille 1920; Klunker 1977). The 1.0cm high shelters did not provide the thigmotaxic stimulus required of early instars. Sommer showed that early instars will search for hiding places suitable to their body size, and later return to the aggregation of the group (Sommer 1975b). Thus, the other components were able to find suitable refuge in the shelters or, being larger than the small nymphs, were unable to crawl under the lids atop the aquaria.

The rest of this discussion centers around the dispersal of those cockroaches remaining in the system of aquaria and connecting tubes. Three aspects of this dispersal are addressed. The first involves the pattern of dispersal from the first aquarium with regard to the components of the population. The second addresses the establishment of additional harborage in the third aquarium. Finally, the dispersal of the two strains of cockroaches is discussed.

I. Dispersal from first aquarium excluding escapees

No concrete conclusions could be drawn from the results of the experiments comparing gravid vs "non-gravid" females due to the development of egg cases by the "non-gravid"

females. This is not because differences did not exist. In fact, there did appear to be a difference in the dispersal of the females. Of the "non-gravid" females, those that developed egg cases dispersed less than those that did not. This ties in with results from another laboratory experiment in which gravid females aggregated more within shelters than females without egg cases (Bret et al. unpubl.).

The percent of non-egg case bearing females remaining in aquarium 1 decreased with increasing density. The presence of a dispersion-inducing substance has been suggested as a response to density pressures (Suto and Kumada 1981). Females without egg cases may be the component of the population responsible, at least in part, for this substance. As the density of non-gravid females increased the amount or concentration of this substance may also have increased. Similarly, a concomitant decrease in production of aggregation pheromone may also have occurred.

The opposite result was seen with those females that developed egg cases in the course of the week. Increasing density resulted in increased aggregation or decreased dispersal. This relationship was similar to that of the females in the gravid female experiment. The presence of aggregation pheromones in males and early instar nymphs has been well recorded (Pettit 1940; Ledoux 1945; Ishii and Kuwahara 1967, 1968). It appears that gravid females may

also produce an aggregation pheromone and that this may be density dependent. As the number of gravid females increased, the amount or concentration of aggregation pheromone presumably increased. This increased pheromone production would also explain the increased numbers of adult males and medium nymphs that remained in aquarium 1 as the female density increased.

The contrasting behaviors of gravid and non-gravid females and their effects on the rest of the population bear a close resemblance to those of another experiment on within-harborage group formation (Bret et al. unpubl.). In that experiment, a direct relationship occurred between the density of gravid females and the degree of aggregation for each component of the population except adult males. An inverse relationship occurred between the density of non-gravid females and the aggregation of the components, again with the exception of adult males. The close similarity between those results and the results of this experiment leave little doubt that the same basic mechanism is involved in both cases. The combined effects of the reproductive state and the density of females in a population influence both the spatial distribution within a harborage as well as the dispersal from a harborage.

The advantages of a regime of pheromone production such as this can be seen in the contexts of resource allocation

and harborage favorability. Gravid females have a large energy budget requirement for the development of egg cases. Gravid females must allocate energy towards this development. They can not afford to expend energy on dispersal when it is needed for reproduction. Females without egg cases lack this energy requirement and thus represent the most favorable state for female dispersion. Metabolic resources are available for dispersal. This behavior may have implications for the other members of the population as well. Females would presumably settle in a habitat most favorable for the growth and development of the egg case and for the growth and survival of newly hatched nymphs. Aggregation pheromones produced by gravid females would ensure that small nymphs remained within the safety of the harborage. This was seen in the large percentage of small nymphs remaining in the first aquarium with the gravid females. This behavior has been noted in other laboratory and "field" experiments by this author. In particular, a recent experiment aboard a Naval vessel showed gravid females and early instar nymphs aggregating together in harborages near food, water, and suitable shelter (Bret _et al._ unpubl.). Other researchers have also noted the strong propensity for aggregation displayed by small nymphs (Pettit 1940; Ledoux 1945; Ishii and Kuwahara 1967).

Sommer (1975b) noted that as young nymphs mature, they

aggregate less. The medium nymphs in this experiment dispersed the most. Larger nymphs are apparently less responsive to aggregation pheromones than small nymphs. It appears that middle and late instar nymphs may be the primary dispersers of a population. Middle and late instar German cockroaches dispersed the most on the shipboard experiment mentioned above (Bret et al. unpubl.). In addition, a recent genetic control experiment indicated that middle to late instars may be readily dispersed by insecticide treatments (Ross et al. 1981). The nymphs of American cockroaches have also been reported to move more than adults (Chadwick and Shaw 1974).

The adult males behaved in a manner similar to the adult females. Males may have responded to their own aggregation pheromone but this alone would not explain their behavior. A response to an aggregation pheromone produced by the females would explain the decreased dispersal of males from the first aquarium as the density of females, and hence pheromone concentration, increased. A response to the females' sex pheromones is unlikely as they are not produced by females with egg cases (Roth 1967).

II. Distribution of cockroaches among the three aquaria

That most of the cockroaches dispersed from aquarium 1 were found in the third aquarium emphasizes the importance of food, water, and shelter in the selection of new

harborages. Aquarium 3 was the farthest removed from aquarium 1, yet contained the most dispersers. This should not be surprising since it was the only other aquarium that provided food, water, and shelter. Mueller (1978) has clearly shown the importance of a regular supply of food and water to cockroach fecundity and survival. Aquarium 2 provided no shelters,food, or water. Cockroaches found there were most likely in transit between aquaria 1 and 3. Likewise, the tubes only provided routes of travel. In the experiment with non-gravid females, the tubes did contain many more cockroaches than would be expected, but it was the last set of experiments. Although the tubes were thoroughly washed after each use, it is possible that they became impregnated with pheromones after repeated use. In fact, the large percentage of females and medium nymphs in the tubes can be traced back to one particular replicate.

III. Comparison of two strains of cockroach

No differences in dispersal occurred between the wild type VPI strain and the black body mutant crossed to a field strain. This does not necessarily mean that no differences occur between wild type and black body strains or between VPI laboratory and field caught strains. Significant differences in the rate of movement between field caught cockroaches and both laboratory reared wild type and laboratory reared black body cockroaches have been shown in

a laboratory experiment (Akers 1978). By crossing black body mutants with field caught cockroaches one should get a behavioral response more representative of natural populations. Black body mutants are particularly useful for mark-recapture studies since the mark, the body pigment, is not lost by the nymphs after each molt. Loss of the mark during molting has been a major obstacle to studies of nymphal movement. The black body mutant, and two other color mutants, have already been used successfully to study cockroach movement on board a Naval ship (Bret et al. unpubl.) and in a multiple dwelling unit (Akers and Robinson 1981).

It is clear that researchers are just beginning to unravel the complexities of cockroach behavior. The knowledge gained by such information can hopefully be applied to improve present methods of controlling cockroach infestations. The reproductive state of the females, as well as the relative numbers caught, may provide important information regarding population dynamics of a group of cockroaches within a harborage. Although Aquaria 1 and 3 were separated by a very short distance, their sex/age class structures were quite different. High numbers of non-gravid females trapped away from harborage sites could well indicate a dispersing population due to diminishing

resources. Conversely, low numbers of non-gravid females might suggest a relatively stable, sedentary population due to favorable harborage conditions.

Middle to late instar nymphs may well be the most important component of the population responsible for the establishment of new harborage sites. Surveys that reveal a high proportion of these nymphs may be indicative of sites that have just been established by dispersal from other, possibly over-crowded, sites. This has also been indicated by the work of others (Sherron, et al. 1982) Conversely, sites with a disproportionatly small amount of medium to late instars may indicate recent dispersal and an additional harborage site might be found upon further scrutiny.

Small nymphs appear to be the least important component in the establishment of new harborages. A preponderance of small nymphs in traps may indicate a stressed environment. A shortage of suitable refuge would force small nymphs to disperse and this should be reflected in trap catches. Unfortunately, most traps are not adequate for the capture of small nymphs (Ross 1981).

Most mark-recapture studies ignore nymphs altogether due to problems involved with loss of the mark. Even more unfortunate are those instances where researchers discuss cockroach populations as whole entities rather than breaking them down by sex and/or age classes. This has been done

successfully in a few instances where differential population structures were related to sanitation, availability of resources, suitability of refuge, and density (Ross and Wright 1977; Keil 1981; and Sherron et al. 1982). These types of critical analyses are imperative if we are to reach a better understanding of the behavior and dynamics of cockroach infestations.

TABLES FOR DISPERSAL

Table 1 - Percent of cockroach populations remaining in or dispersed from first aquarium. (a)

Response	%♀	%♂	%M	%S	%Total
Remained	72.8	77.6	50.7	38.8	53.6
Dispersed	27.2	22.4	49.3	61.2	46.4

(a) ♀ = adult females, ♂ = adult males, M = mid instars (3rd-4th instars), S = small nymphs (1st-2nd instars).

Table 2 - Comparison of dispersal indices of cockroach populations dispersed from the first aquarium. (a)

Female Density	A-Females without oothecae					B-Females with oothecae				
	♀	♂	M	S	Total	♀	♂	M	S	Total
4	.33	.29	.60	.55	.52	.75	.29	.70	.65	.64
8	.52	.42	.60	.40	.50	.27	.17	.46	.68	.48
16	.15	.21	.35	.73	.39	.17	.06	.29	.66	.35

(a) ♀ = adult females, ♂ = adult males, M = mid instars (3rd-4th instars), S = small nymphs (1st-2nd instars).

Table 3 - Comparison of dispersal indices between experiments with gravid females and experiments with non-gravid females.

Female Density	Significance levels of a Wilcoxon 2-way test (a) (b) ♀	♂	M	S	Total
4	.09*	.94	.47	.52	.47
8	.23	.38	.38	.13	.87
16	.33	.27	.65	.61	.44
Total	.66	.14	.49	.20	.85

(a) ♀ = adult females, ♂ = adult males, M = mid instars (3rd-4th instar), S = small nymphs (1st-2nd instar).
(b) * = significant at $p<.10$.

Table 4 - Comparison of dispersal indices between experiments with 4 females, 8 females, and 16 females.

Female State	Significance levels of a Kruskal-Wallace chi-square approximation (a) (b) ♀	♂	M	S	Total
A- no oothecae	.003**	.622	.171	.076	.042**
B- with oothecae	.001**	.233	.021**	.912	.015**
Total	.0001**	.141	.006**	.348	.0004**

(a) ♀ = adult females, ♂ = adult males, M = mid instars (3rd-4th instar), S = small nymphs (1st-2nd instar).
(b) ** = significant at $p<.05$.

Table 5-Distribution of all cockroaches throughout system.

Population Component	% in aquarium #1	% in aquarium #2	% in tubes	% in aquarium #3	% that escaped
Adult Females	72.8	4.6	7.6	13.3	2.2
Adult Males	77.6	2.6	3.9	19.7	2.0
Middle Instars	50.7	5.3	6.7	23.8	11.8
Early Instars	38.8	1.0	0.6	4.6	54.9
Total	53.6	3.4	4.6	14.5	23.9

Table 6 - Distribution of cockroaches throughout the system excluding escapees.

Population Component	% in aquarium #1	% in aquarium #2	% in tubes	% in aquarium #3
Adult Females	74.0	14.7	7.7	13.5
Adult Males	74.7	2.5	3.8	19.0
Middle Instars	58.6	6.1	7.8	27.6
Early Instars	86.1	2.2	1.5	10.2
Total	70.4	4.5	6.0	19.1

Table 7 - Distribution of cockroaches according to female reproductive state excluding escapes.

Female State	Population Component	% in aquarium #1	% in aquarium #2	% in tubes	% in aquarium #3
A (without egg case)	Adult Females	72.9	7.2	1.8	18.1
	Adult Males	70.4	5.6	2.8	21.1
	Middle Instars	57.7	8.8	3.8	29.7
	Early Instars	88.3	3.4	0	8.3
	Total	70.4	6.8	2.2	20.6
B (with egg case)	Adult Females	75.0	2.6	12.8	9.7
	Adult Males	78.2	0	1.2	17.2
	Middle Instars	59.2	3.8	11.2	25.8
	Early Instars	83.7	0.8	3.1	12.4
	Total	70.5	2.4	9.3	17.7

Table 8 - Distribution of cockroaches according to female density, excluding escapees.

Female Density	Population Component	% in aquarium #1	% in aquarium #2	% in tubes	% in aquarium #3
4	Adult Females	45.8	0	18.8	35.4
	Adult Males	64.2	1.9	7.6	26.4
	Middle Instars	41.9	7.5	2.5	35.6
	Early Instars	85.6	1.1	1.1	12.2
	Total	57.0	4.0	10.8	28.2
8	Adult Females	61.7	17.0	5.3	16.0
	Adult Males	69.4	6.1	2.0	22.4
	Middle Instars	53.6	10.7	4.2	31.6
	Early Instars	86.5	4.8	1.9	6.7
	Total	65.5	10.1	3.6	20.7
16	Adult Females	85.4	0.4	6.4	7.7
	Adult Males	89.3	0	1.8	8.9
	Middle Instars	76.3	1.0	5.1	17.7
	Early Instars	86.2	0.5	1.2	12.5
	Total	82.7	0.5	4.7	12.1

Table 9 - Number of wild-type (wt) and black-body (Bl) cockroaches in aquarium 1 over total number at beginning of experiment.

Female Density	Adult Females		Adult Males		Middle Instars		Early Instars		Total Population	
	wt	Bl	wt	Bl	wt	Bl	wt	Bl	wt	Bl
4	12/24	10/24	17/24	17/24	37/96	30/96	38/96	39/96	104/240	96/240
8	31/48	27/48	18/24	16/24	48/96	42/96	43/96	46/96	140/264	131/264
16	93/112	95/112	25/28	25/28	75/112	76/112	36/112	33/112	229/364	229/364
Total	136/184	132/184	60/76	58/76	160/304	148/304	117/304	118/304	473/868	456/868

FIGURES FOR DISPERSAL

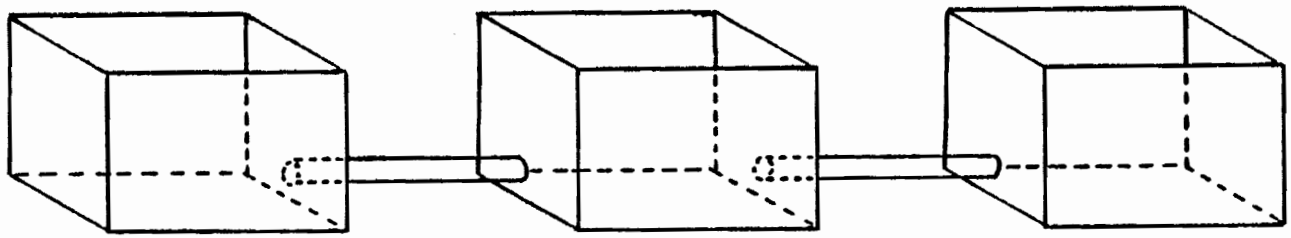

FIGURE 1 - DIAGRAM OF CONNECTED AQUARIA USED IN THE DISPERSAL EXPERIMENTS.

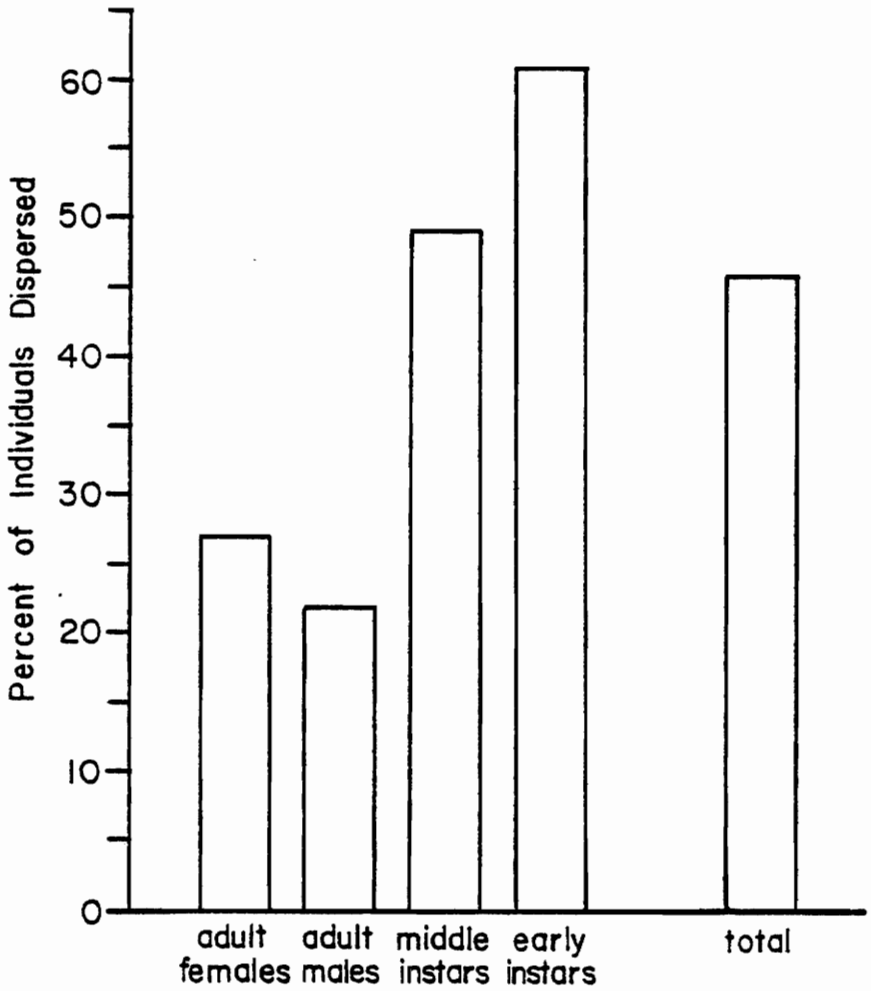

FIGURE 2 - DISPERSAL OF COCKROACHES FROM AQUARIUM 1 AFTER ONE WEEK, USING THE COMBINED RESULTS OF ALL EXPERIMENTS.

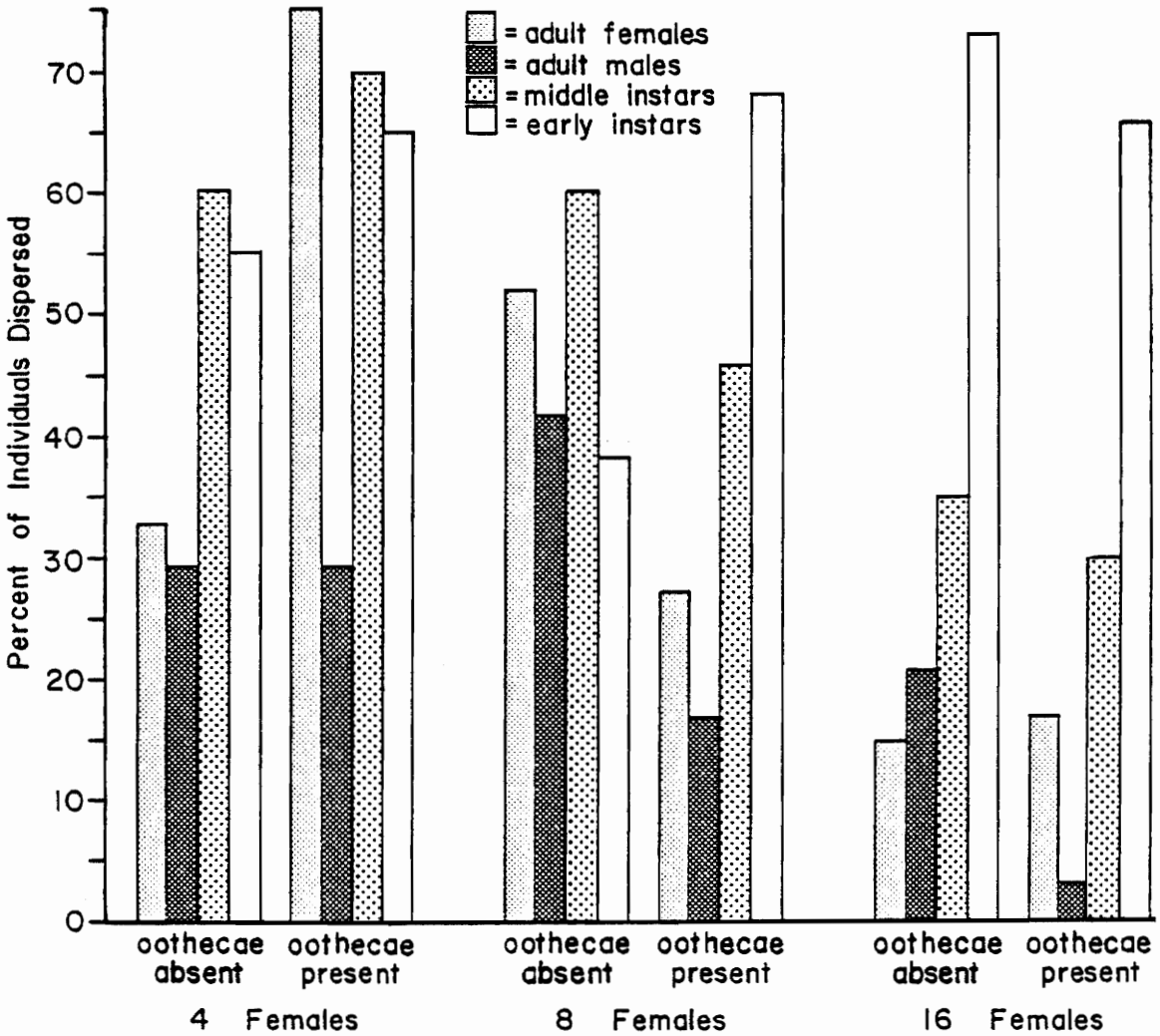

FIGURE 3 - DISPERSAL OF THE INDIVIDUAL COMPONENTS FROM AQUARIAM 1, ACCORDING TO EACH COMBINATION OF FEMALE DENSITY AND REPRODUCTIVE STATE.

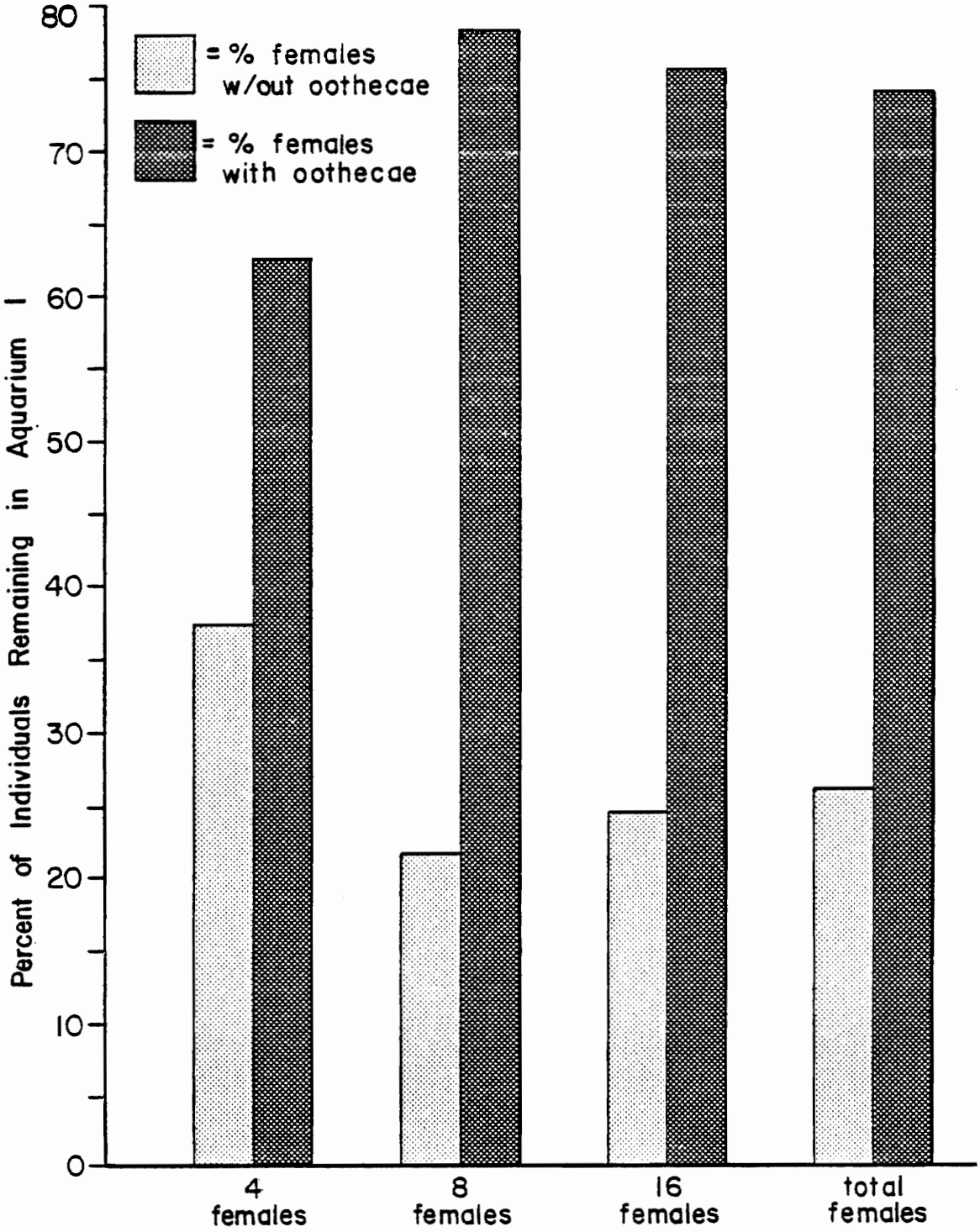

FIGURE 4 - COMPARISON OF EGG CASE AND NON-EGG CASE BEARING FEMALES THAT REMAINED IN AQUARIUM 1 IN EXPERIMENTS THAT STARTED WITH NON-EGG CASE BEARING FEMALES.

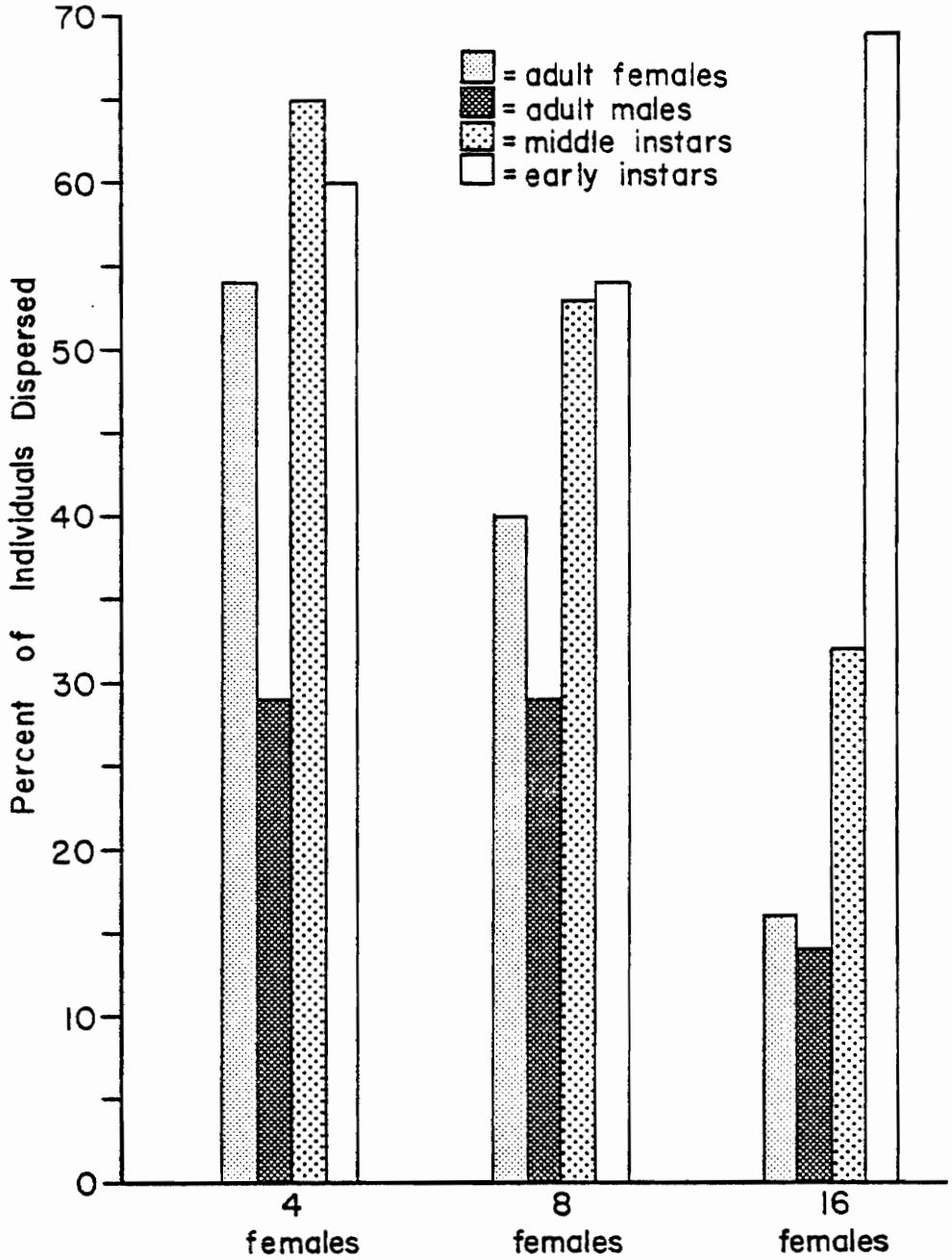

FIGURE 5 - EFFECT OF INCREASED FEMALE DENSITY ON DISPERSION OF EACH COMPONENT FROM AQUARIUM 1.

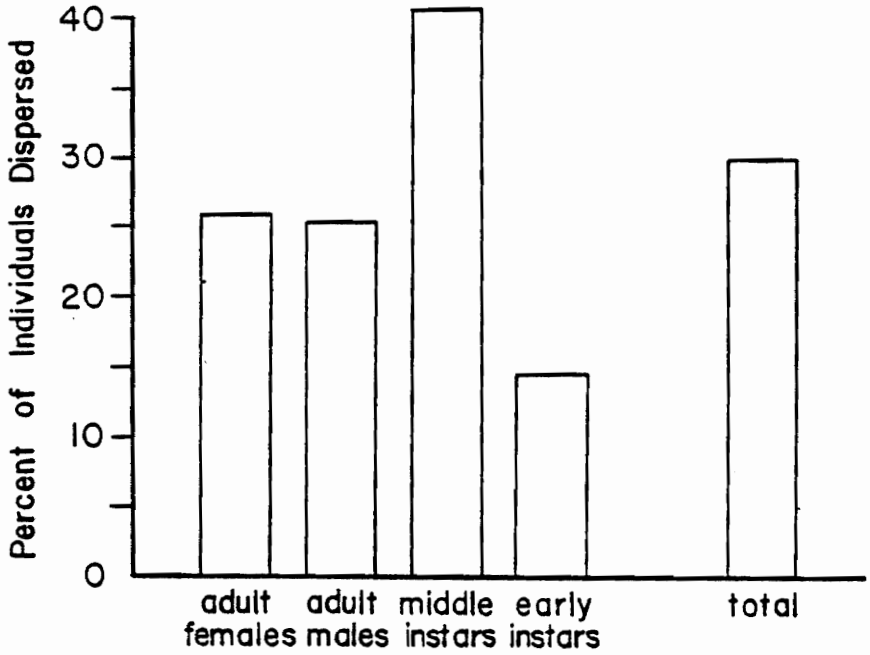

FIGURE 6 - DISPERSAL OF ALL COCKROACHES EXCEPT ESCAPEES, FROM AQUARIUM 1.

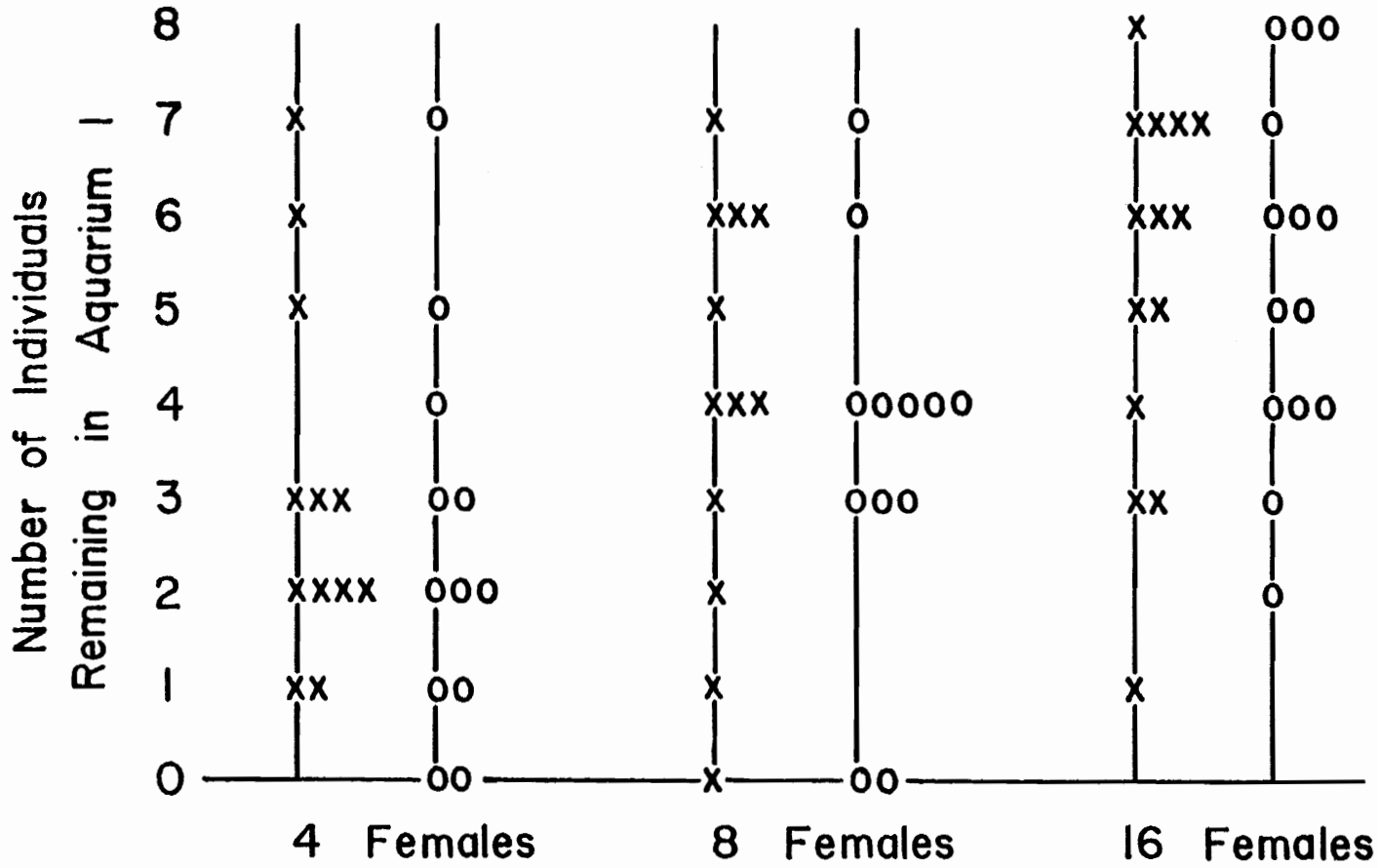

FIGURE 7 - COMPARISON OF MID INSTARS OF TWO STRAINS THAT REMAINED IN AQUARIUM 1. X = WILD TYPE REPLICATES, 0 = BLACK BODY REPLICATES.

SUMMARY

The reproductive state and density of the females in a harborage appears to have a bearing on the behavior of the components of that population. This work indicates the presence of a remarkable system of communication, presumably chemical. The differential production of aggregation and dispersion substances seems to be an effective method of maintaining the integrity of a group under favorable conditions. Under unfavorable conditions this same system can ensure the survival of the species by the selective dispersal of particular components of the population. This work also shows how caution must be exercised in the interpretation of trapping data. Cockroach populations are dynamic, fluctuating due to changes in refuge/resource availability, density, dispersal, and insecticide pressures. Examination of age/sex structures may reveal information about the development of an infestation at that point in time. Proper control decisions regarding the use of insecticides (including where and when to spray), genetic controls, biological controls, or other integrated pest management techniques, may then be made.

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VITA

Brian Louis Bret was born in Schenectady, New York in 1958. From there, the Bret family moved to Lynchburg, Virginia where he spent most of his early childhood. Due to another family move, his late childhood years were spent in Phoenix, Arizona. In Phoenix, Mr. Bret began his educational pursuits by attending Brophy College Preparatory School. The family again moved, this time to Erie, Pennsylvania, where he graduated from Fairview High School in 1976. He attended the University of Notre Dame and received a Bachelor of Science in biology. After graduation in 1980, Mr. Bret returned to Virginia to begin work on a Master of Science in entomology at Virginia Polytechnic Institute and State University. He is presently a member of the Entomological Society of America, the Virginia Academy of Sciences, Gamma Sigma Delta, Phi Sigma, and Sigma Xi.

Brian L. Bret

GROUP FORMATION AND DISPERSAL IN THE GERMAN COCKROACH, *BLATTELLA GERMANICA* (L.) (DICTYOPTERA: BLATTELLIDAE)

by

Brian Louis Bret

(ABSTRACT)

The studies presented here are an effort toward learning about the behavior of small mixed populations of German cockroaches. Of particular interest was the effect of female cockroaches on the behavior of the group, particularly the group formation within a harborage and the dispersal from a harborage. The effect of females was looked at with respect to female density and reproductive state.

Populations aggregated at low female densities. This response increased when densities of gravid females increased but decreased when densities of non-gravid females increased. The effects of female reproductive state on dispersal could not be determined as non-gravid females developed egg cases by the end of the study. Increased female density caused increased dispersal of females and mid-instars. The mid-instars were the primary dispersers in each experiment. Early instars, excluding escapees, dispersed least.

The results of these studies indicate the females of a population can mediate the behavior of that population and its members. It is postulated that this may be achieved by the production and/or regulation of sex, aggregation, and dispersal-inducing pheromones by females.