USE OF A TRANSLOCATION AND A RECESSIVE DELETERIOUS GENE TO RETARD POPULATION GROWTH IN *Blattella germanica* (L.)

by

Timothy Holland Dickens

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APPROVED:

D. G. Cochran, Chairman

E. C. Turner

D. A. West

R. L. Pienkowski

M. H. Ross, Co-Chairman

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Blacksburg, Virginia

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INTRODUCTION

The German cockroach, Blattella germanica (L.) is one of the most important and ubiquitous pests associated with man, requiring expenditures of millions of dollars annually to achieve control (Mallis 1969). It has been implicated in the mechanical transmission of pathogenic organisms causing diarrhea, dysentery, food poisoning, genital and urinary tract infections, gangrene, and human pinworm and whipworm (Roth and Willis 1957; Rueger and Olson 1969). In addition, this species is suspected of transmitting infectious hepatitis (Tarshis 1962). Allergic reaction to contaminants from live cockroaches is of increasing concern (Kang 1976).

Reasonably effective control of the German cockroach has been obtained by conventional insecticides for many years (Mallis 1960). However, the German cockroach has developed resistance to the major groups of modern insecticides (Grayson 1966; Mulrennan and Burden 1974). This factor, coupled with concern over effects of insecticides in man's environment, calls for alternate control methods.

Plausible alternate methods include the use of pheromones (Wharton et al. 1972), ultraviolet radiation (Wharton 1971), carbon dioxide (Cantwell et al. 1973), and genetic control measures (Ross 1975a, 1976, 1977ab, 1980; Ross and Cochran 1973, 1976, 1980; Ross et al. 1982). The most feasible genetic control technique involves genetic load and/or embryonic trapping sterility associated with cockroach translocations (Ross 1976, 1977ab, 1980; Ross and Cochran 1976,

1977, 1981ab). Expanded interest in the use of genetically induced sterility for insect control is an outgrowth of the near eradication of the screw-worm fly by the release of sterile males (Bushland 1971; Bushland *et al*. 1958). The sterility in this case depended on immediate sterility in males induced by irradiation (Bushland 1975) whereas the sterility associated with translocations is inherited and functions as a genetic load.

Translocations were selected over other genetic control techniques because other mechanisms are more difficult to develop and may be less promising. For example, deleterious mutants used alone would be much less effective since mutants known from *B. germanica* have lower lethal effects than translocations. These mutants may, however, be useful in combination with translocations (Ross and Cochran 1973). Sterile males induced by gamma radiation or chemosterilants have the problems of (1) delayed nymphal development making it difficult to time releases, (2) loss of competitiveness in treated males (Burden and Smittle 1963; Vingiello and Ross 1967; Ueda *et al*. 1969) and (3) significant amount of mortality (Ross and Cochran 1963). In addition, there is concern over possible mutagenic effects on humans when chemosterilant baits are used for direct "wild" population exposure.

A reciprocal chromosome translocation is defined by Davidson (1974) as "the breakage of two non-homologous chromosomes, and the re-attachment of the broken parts to the wrong partners". The breakage involved can occur naturally, but in the case of *B. germanica* it was induced by exposure to cobalt radiation (Ross and Cochran 1973). The embryonic lethality resulting from reciprocal translocations is

due to unbalanced gametes which have duplications of genes on one chromosome and deficiencies of genes on the other. Since progeny of the German cockroach are usually non-viable when homozygous for a translocation, the use of males heterozygous for reciprocal translocations was proposed by Ross and Cochran (1973). About twenty different translocation cultures of the German cockroach have been developed and studied, with single translocation heterozygotes showing lethality of approximately 50% (Ross and Cochran 1973) and double translocations heterozygotes showing lethality as high as 80% (Ross 1976, 1977ab; Ross and Cochran 1977, 1979). Promising results have been obtained using a three chromosome reciprocal translocation which provides ancillary sterility in the form of "embryonic trapping" (Ross 1976; Keil and Ross 1977). Double translocation heterozygote males show the best results thus far (Ross 1977, 1980; Ross and Cochran 1979, 1981a; Ross _et al_. 1982).

The release of males heterozygous for a single translocation T(8;9) into laboratory populations markedly retarded population growth (Ross 1975a, 1976). Similar studies reported herein utilize the translocation T(8;9) and a closely linked deleterious mutant, stumpy (_sty_). This deleterious recessive autosomal mutant, was selected because it affects the shape of the body, legs, and wings. Legs are short and thick. Wings of adult males are much shorter than those of the females and both male and female are noticeably shorter than wild type (Ross 1975b). The female homozygote is nearly sterile (Ross 1975b). The sterility of the _sty_ female seemed a logical adjunct to the single translocation T(8;9) due to close linkage. Homozygous

stumpy females would emerge in the F_2 generation, adding an additional sterility factor to that of the translocation (Ross 1975b, 1976; Ross and Cochran 1973).

Laboratory strains of this type were already under development by Dr. M. H. Ross. They consisted of backcrosses of females heterozygous for the translocation T(8;9) and carrying the recessive gene stumpy (*sty*) in repulsion (on the opposite homologous chromosome) to homozygous *sty* males (T+/+*sty* female X *sty*/*sty* male).

To evaluate the impact of the translocation, T(8;9) and *sty* on laboratory populations of *B. germanica*, a study was planned with the following objectives:

1. *Population studies*. Determine the effect on experimental populations of repeated releases of *Blattella germanica* males heterozygous for both the translocation T(8;9) and the recessive deleterious gene (*sty*) compared with the normal development of a wild-type population not subjected to such releases.

2. *Reproductive behavior*. Study the reproductive behavior in relation to three types of males and females present in the experimental populations.

3. *Linkage*. Measure the linkage relationship between the T(8;9) translocation and the deleterious gene (*sty*) in males and, if feasible, in females.

4. *Mass rearing*. Determine the feasibility of and develop improved techniques for mass rearing German cockroaches and selecting semi-sterile males for release.

LITERATURE REVIEW

INTRODUCTION

The concept of using translocations in the control of insects was first proposed by Serebrovskii (1940) and represents one of several proposed approaches to genetic control of insects. Other proposed techniques include the following: sterile insect release method (SIRM) (Knipling 1955); hybrid sterility (Potts 1944; Vanderplank 1944); chemosterilants (LaBrecque 1961); conditional lethal mutations (Klassen *et al*. 1970; Smith 1971); cytoplasmic incompatibility (Laven 1951); and compound chromosomes (Foster *et al*. 1972). Whitten and Foster (1975) reviewed these prospective control strategies.

STERILE MALE RELEASE METHOD

Knipling (1967) described three major uses for sterile insect releases. These are (1) for eradication as in the screw-worm fly; (2) for prevention of incipient infestations such as the Mexican fruit fly; (3) as part of an integrated control program using other methods of control as proposed for the codling moth.

Two primary methods have been used for the sterilization of males for use in sterile insect release method (SIRM) programs. One involves the direct exposure of males to gamma radiation (Knipling 1955) and the other, use of various mutagenic chemicals (chemosterilants) the effects of which were first reported by LaBrecque (1961). Chemosterilants have a second possible use in direct sterilization of a portion of the wild population by the use of baits. Both methods of

sterilization were reviewed by LaChance (1967).

The celebrated screw-worm fly SIRM successes have served as a model for other proposed approaches to genetic or autocidal control of insects. Successful eradication was reported for six locations, and suppression at a seventh. The program in the southwestern U. S. began in 1962 and continues along the entire U. S.-Mexico border area (LaChance 1979) and further south. This continuing program experienced a temporary failure in 1972, postulated to be resistance developed from the selection pressure exerted on the population for some ten years (Smith 1973). Bushland (1975) identified the problems as being primarily due to natural selection and emphasized the need to maintain the compatibility of laboratory strains with field populations into which they were to be released.

Other successful SIRM trials have followed. In a program which began in 1966, the USDA has maintained a continuous release of sterilized Mexican fruit flies *Anastrepha ludens* along the Mexican-California border (Shaw *et al*. 1970). According to LaChance (1979) no infestation has developed north of the border in more than ten years. The melon fly *Dacus cucubitae* and the oriental fruit fly, *Dacus dorsalis*, have been eradicated from the Mariana Islands (Chambers *et al*. 1970).

Populations of the Mediterranean fruit fly, *Ceritisis capitata*, were suppressed in Italy (de Murtas *et al*. 1970), Nicaragua (Rhode 1970), Spain (Mellado 1971), and Hawaii (LaChance 1972). An introduced population of *C. capitata* was eradicated from California (LaChance 1979).

Sustained suppression was obtained using SIRM on the bollweevil (*Anthonomous grandis*) by Carter (1974) and Villavaso *et al*. (1979). Patterson *et al*. (1970) eliminated an island population of *Culex pipiens quinquefasciatus* and had promising results with an indigenous population. *Anopheles albimanus* was controlled up to 99% by SIRM for a five-month period in El Salvador (Lofgren *et al*. 1974).

There have been several unsuccessful attempts at using SIRM for control of pest and vector species. Field studies by Weidhass *et al*. (1962) of sterile male releases used on *Anopheles quadramaculatus* were unsuccessful due to reduced competitiveness in release males. An intensive program on *Culex fatigans* in villages near New Delhi, India, failed to reduce population size (Pal, 1974). Rush and Smith (1975) obtained variable results when evaluating chemosterilized males of *Culex tarsalis*. In field trials, SIRM used on the codling moth *Laspeyresia pomonella*, was technically effective but not cost effective alone (Proverbs 1969, 1974). LaChance (1979) proposed the use of this technique as part of an integrated control strategy.

Several candidate species for SIRM have been proposed for further evaluation based on promising laboratory results. Salama (1976) reported that chemosterilized male gypsy moths were competitive in laboratory tests. Hooper (1975, 1976) described promising results in developing SIRM techniques for *Dacus cucumis* in Australia. Chaudhary and Kapil (1977) reported promising laboratory results from releases of chemosterilized males of *Trogoderma granarium*. Theunnissen (1976) proposed use of the SIRM technique on the onion fly, *Hylemya antiqua*

and Wharton (1976) considered the possibility of SIRM use for tick control

HYBRID STERILITY

Hybrid sterility often results when two closely related species or geographical races are crossed. Overflooding a native population with reared males of a related species theoretically could produce enough sterile matings to provide for significant population reduction (Curtis 1979). Another prospect may include the possibility of population replacement of a pest or vector species with an innocuous form.

Vanderplank (1944) recommended hybrid sterility in *Glossina* species as a new method for control. Whitten and Pal (1974) indicate that certain problems have limited the use of hybrid sterility. These include: (1) sterile hybrids produced by mating sympatric species may exhibit the extensive pre-mating barriers of the parents; (2) sterile hybrids from crosses of allopatric species may have genomes not present in the target area and thus not be as fit as the forms already present. These problems were reported to be present in a field assessment of sterile males produced by crossing two member species of the *Anopheles gambiae* complex (Davidson *et al*. 1970). Hogan (1974) used hybrid sterility as a tool for the control of two species of field cricket in Australia. He reported that hybridization also allowed the introduction of a conditionally lethal trait, non-diapause, from one species to another. This approach was reported to have good potential as a suppression technique to keep the populations below pest thresholds. In hybrid sterility between different strains of

Glossina morsitans (Curtis 1972) and *Anopheles maculipennis* (Fraccaro *et al*. 1977) sterility was shown to segregate as a single pair of Mendelian factors. Curtis (1979) evaluated hybrid sterility in *Anopheles gambiae* and proposed the use of it in genetic control. Curtis (1979) recommended that mate recognition systems in species complexes of medically important species such as *Anopheles gambiae* be thoroughly analyzed in simliar manner to the work by Hogan (1974) on *Teleogryllus* crickets, and by Spieth (1968) on *Drosophila*.

CHEMOSTERILANTS

The success of experiments in 1962 using the chemosterilant aphoxide in baits at a garbage dump in the Florida Keys for fly control (Labrecque *et al*. 1962) generated interest in this concept which continued for ten years (McDonald 1974). Weidhaas *et al*. (1962) conducted the pioneer experiment on mosquitoes when he fed chemosterilants to adult *Anopheles quadrimaculatus* and *Aedes aegypti*. Later Dame and Ford (1964) obtained sterilization by treating larvae in the aquatic habitat. Labrecque and Smith (1968) provided the definitive summary of the principles and use of chemosterilants up to that time.

Klassen *et al*. (1968) suggested chemosterilants as an alternative method of sterilization if gamma and x-ray irradiation proved too damaging. The technique of dipping insects en masse into a chemosterilant would be cheaper and easier than irradiation techniques as found with the Japanese beetle by Ladd *et al*. (1968). The boll weevil, an insect easily injured by irradiation treatments, was successfully sterilized by bisulfan which did not reduce mating ability (Klassen

and Earle 1970).

Another chemosterilant technique in which the females contribute to sterilization was known as the booby trap technique (Smith 1963). Metepa in acetone was soaked into chamois pads and attached to the abdominal tergites of the flies. These were released into cages with normal males which were later mated with virgin females. The results were encouraging. Beattie _et al_. (1974) obtained good results with the "booby" trap technique in field cage experiments with _Lucilia cuprina_. Environmental concerns over the non-selective mutagenic and carcinogenic effects of chemosterilants have limited their use to laboratory sterilization of insects (McDonald 1974). Several important species have been successfully sterilized for SIRM use by exposure to chemosterilants. These include _Anopheles quadrimaculatus_ and _Aedes aegypti_ (Weidhaas _et al_. 1962); _Anastrepha ludens_ (Shaw and Riviello 1965); _Culex pipiens quinquefasciatus_ (Patterson _et al_. 1970); _Anthonomous grandis_ (Klassen and Earle 1970); _Anopheles pharoensis_ (Hafez _et al_. 1971); _Lucilia cuprina_ (Beattie _et al_. 1972); _Culex pipiens fatigans_ (Sharma _et al_. 1973); _Anopheles albimanus_ (Lofgren _et al_. 1974); _Culex tarsalis_ (Rush and Smith 1975); _Porthetria dispar_ (Salama 1976); and _Trogoderma granarium_ (Chaudhary and Kapil 1977).

CONDITIONAL LETHAL MUTATIONS

Conditional lethal mutations are those which predispose the insect to mortality under a limited set of environmental conditions either natural or induced by man. Hogan (1966) proposed conditional lethals as a genetic approach to control based on the physiological

differences between races of _Teleogryllus commodus_. Klassen _et al_. (1970a) advocated the use of dominant conditional lethal traits for insect population suppression. Klassen _et al_. (1970b) provided calculations which indicate that it is theoretically feasible to suppress a population using conditional lethal traits by (1) overflooding with a release strain bearing conditional lethal traits, (2) suppression by conditional lethal traits while a population is held in check by partial sterility, and (3) suppression by conditional lethal traits of a population held static by conventional means. Heat sensitive lethal mutations have been induced by use of ethyl methanesulfonate in _Drosophila melanogoster_ (Suzuki _et al_. 1967; Baille _et al_. 1968; and Suzuki 1970), _Lucilia cuprina_ (Foster and Whitten 1974) and _Culex tritaeniorhynchus_ (Sakai and Baker 1974).

The use of conditional lethal mutations such as temperature sensitive mutations and genes affecting diapausing have been recommended for use with other genetic control concepts (Curtis 1968a; Whitten 1979). McDonald and Overland (1972b) isolated recessive heat-sensitive (hs) lethals in _Musca domestica_. Males are permanently heterozygous for the _hs_ mutation (due to no crossing over) and females are always homozygous for the _hs_ factor, because they inherit it from both parents. This was used as a genetic sexing technique in the production of sterile males by irradiation (Wagoner _et al_. 1974). McDonald (1971) reported conditional lethals in the housefly involving morphological traits. Wagoner _et al_. (1974) reported a variety of pesticide susceptibility factors and dominant heat-sensitive semi-lethal mutations for _M. domestica_.

CYTOPLASMIC INCOMPATIBILITY

Laven (1951, 1972) proposed the concept of using cytoplasmic incompatibility for control of mosquitoes. This phenomenon often occurs when members of the same species of mosquito such as *Culex pipiens* from different geographical areas are mated (Laven 1951). Often as many as one-half of the eggs produced are dead and have haploid embryos. Laven (1967) showed that the factors causing incompatibility were maternally transmitted through the cytoplasm. Mating and insemination appeared to be normal, and an occasional parthenogenetic diploid female was produced from an otherwise incompatible cross.

Yen and Barr (1971, 1973, 1974) showed that the incompatibility was caused by a rickettsia-like organism called *Wolbachia pipientis* Hertig. *Culex fatigans* has been the most thoroughly investigated species and has shown the most potential for use of cytoplasmic incompatibility (Pal 1974). Release of fertile males incompatible with a target population requires that no females be released because population replacement with the released strain may occur with no population reduction achieved (Pal 1974). Laven and Aslamakhan (1970) proposed the production of an integrated strain by combining a male-linked translocation complex with cytoplasmic incompatibility. This has been accomplished for *Culex fatigans* (Pal 1974) in India. Field tests of a strain of *Culex fatigans* with a Delhi genome in Paris cytoplasm showed that released males competed fairly well for wild female *C. fatigans* in the Delhi area (Krishnamurthy and Laven 1976; Krishnamurthy *et al*. 1977). Additional promising uses of cytoplasmic incompatibility include the cherry fly (*Rhagoletis cerasi*) which has

shown unidirectional incompatibility between different stocks (Boller and Bush 1974), and crosses of *Heliothis subflexa* females to *H. virescens* males, in which male sterility was reported to be due to an interaction of *H. subflexa* cytoplasm and *H. virescens* genome (Laster *et al*. 1976). Brower (1979) reported suppression of laboratory populations of *Ephestia cautella* by release of males with cytoplasmic incompatibility.

COMPOUND CHROMOSOMES

Compound chromosomes are yet another potential means for genetic control in insect pests by functioning as a transport mechanism for conditional lethals or as a source of self-perpetuating genetic load (Whitten 1971; Foster *et al*. 1972). A compound chromosome is made up of two homologous arms attached to a single centromere. Theoretically, when a compound strain interbreeds with a normal strain, all intercrosses are sterile. An unstable equilibrium results which causes fixation of one type or the other at a rate dependent upon the release ratio employed (Wagoner *et al*. 1974).

As early as 1960, strains of *Drosophila* were synthesized in which chromosomes II and III are compound (Rasmussen 1960). Foster *et al*. (1972) reported that compound chromosomes of *Drosophila* could be used to fix alleles in populations in three to eight generations. They further postulated that "natural populations of insect pests could be displaced by strains bearing compound chromosomes". Childress (1972) showed that theoretical expectations can be approximated in competition experiments between compound strains and normal strains of

Drosophila melanogaster. Compound chromosomes are readily synthesized in Drosophila melanogaster from pre-existing compound strains and it is relatively simple to generate a compound strain with the desired field genome prior to mass rearing for releases (McKenzie 1976).

Compound chromosomes synthesized in Lucilia cuprina result in a hybrid which is usually inviable (Foster et al. 1976). In L. cuprina, however, this procedure has proven quite difficult. When a compound male mated with the wild-type female some male progeny were produced; however, these were found to be triploid (Whitten 1979). Whitten et al. (1977) reported on an unsuccessful field test with a compound strain of L. cuprina thought to have failed because of the absence of a suitable "field" genetic background.

Wagoner et al. (1974) could not synthesize a compound chromosome in Musca domestica due to nonviability.

TRANSLOCATIONS

GENERAL.

Thorough reviews of chromosomal translocations as a possible genetic control mechanism for use in insect pest management have been presented by several authors (Whitten 1970; Smith and von Borstel 1972; Davidson 1974; Pal and Whitten 1974; LaBrecque 1974; Reid et al. 1976; Curtis 1979). The original hypothesis for use of translocations for insect control was introduced by Serebrovskii (1940). Interest in the idea was rekindled some twenty-five years later (Rai 1967; Curtis 1968a; Laven 1969) and has continued at a sustained high level.

Davidson (1974) defined a chromosome translocation as breakage of two non-homologous chromosomes followed by re-attachment of the broken parts to the wrong partners. During meiosis in a translocation heterozygote a cross-like configuration can be readily seen in cytological preparations made from germinal tissues. When nuclear division occurs in a translocation heterozygote, four directions of segregation can occur (alternate-1, alternate-2, adjacent-1, and adjacent-2) (Cochran 1976, 1977). They may produce a total of eight different types of gametes. Four kinds of gametes are balanced (orthoploid) in that they have a full gene complement. The other four types are unbalanced (aneuploid) with duplications of genes of one chromosome and shortages of the other. The usual result produces 50% balanced and viable and 50% unbalanced and lethal gametes (Davidson 1974).

SYNTHESIS OF TRANSLOCATIONS

Chromosomal translocations in pest insects have been induced by mutagens, primarily ionizing radiation (Davidson 1974; Robinson 1976), but chemical mutagens can also be used (Schalet 1955; Watson 1962). Translocations in pest insects have been isolated by two methods (Robinson 1976). In the first, reduced fertility is used as a marker unless visible markers are present. The F_1 progeny from irradiated parents are usually outcrossed to wild-type insects and the fertility of the matings measured. Where fertility is reduced, F_1 progeny are retained and again mated to wild-type insects. If F_2 progeny again show about one-half normal fertility this is viewed as evidence for

the presence of a translocation. Further evidenee from cytological examination of appropriate tissues is used to verify the existence of a translocation. Once the translocation heterozygote has been isolated the stock is inbred to test for the existence of a viable translocation homozygote. Fertility measurements were used to isolate translocations in the following pest species: Anopheles albimanus (Rabbani and Kitzmiller 1972); Anopheles gambiae (Akiyama 1973); Blattella germanica (Ross and Cochran 1973); Culex pipiens (Laven et al. 1971b); Culex tarsalis (Asman 1976); Culex tritaeniorhynchus (Selinger 1972); Glossina austeni (Curtis et al. 1972); Hylemÿa antigua (Wijnands-Stäb and van Heemert 1974); Tetranychus urticae (van Zon and Overmeer 1972).

The second technique used for isolating translocations is the pseudo-linkage technique developed by Muller and Altenburg (1930). This procedure begins with the mating of irradiated wild-type males to females carrying genes for recessive phenotypic traits on two or more chromosomes. The F_1 males are then crossed individually with parental type females. If the backcross exhibits independent assortment for the recessive mutant phenotypes of the parental females, it is assumed that no translocation occurred between the two marked chromosomes. On the other hand, if the recessive genetic markers segregate together, it is assumed that the F_1 male did have a translocation between the two marked chromosomes. This technique depends on the lack of crossing over (recombination) in the male, as in Drosophila, so that in the back-crosses the markers remain tightly linked to the non-translocated chromosome. The following species have been evaluated by this

technique: *Aedes aegypti* (Rai *et al.* 1970; Rai and McDonald 1971; Bhalla 1973; Seawright *et al.* 1975c); *Culex tritaeniorhychus* (Sakai *et al.* 1971); *Lucilia cuprina* (Foster and Whitten 1974); and *Musca domestica* (Wagoner *et al.* 1969).

USES OF TRANSLOCATIONS.

Robinson (1976) indicated two ways in which translocations can function in pest control. One is the induction of genetic load on a population via inherited partial sterility. The second involves employment of translocations as a possible transport mechanism to introduce desired genes into a pest insect population (Curtis 1968a; Whitten 1970, 1971ab; Foster *et al.* 1972; Smith and von Borstel 1972). These transported genes could include additional factors which add to population reduction such as conditional lethals and deleterious genes or genes for susceptibility to insecticide (Foster *et al.* 1972). The population replacement concept could eventually extend to refractoriness to to pathogenic organisms. The mechanisms of inheritance of the ability to transmit disease have been investigated for: malaria transmission in *Culex pipiens* (Dennhofer 1974), *Aedes aegypti* (Ward 1963; Kilama and Craig 1969), *Anopheles gambiae* (Al-Mashhadani 1974), *Anopheles stephensi* (Frizzi *et al.* 1975), *Anopheles atroparvus* (van der Kaay and Boorsma 1975); filarial transmission in *Aedes aegypti* (Macdonald 1962; Macdonald and Ramachandran 1965; McGreevy *et al.* 1974; Terwedow and Craig 1977), and *Culex pipiens* (Zielke 1973; Zielke and Kuhlow 1977); western equine encephalitis in *Culex tarsalis* (Hardy *et al.* 1978).

ADVANTAGES OF TRANSLOCATIONS

Proponents of the use of translocations in insect control list a number of advantages over the basic sterile male release technique: First, the problem of reduced competitiveness (Wiedhaas *et al*. 1962) in the sterile males is essentially eliminated. Since the translocation males released are several generations removed from the initial exposure to radiation, their vigor may be unaffected and even benefit from heterosis when translocation heterozygotes are used (Laven 1969; Seawright *et al*. 1975ac, 1976ab). Secondly, the number of insects required for release can be substantially less than in the over-flooding required with sterile males (LaBrecque 1974; Wagoner *et al*. 1973). This is particularly true with translocation homozygotes which are released at only a one-to-one ratio to the wild population and can cause a reduction in fertility of the population for several generations (Serebrovskii 1940; Curtis 1968a; Whitten 1971ab).

DISADVANTAGES OF TRANSLOCATIONS

Disadvantages associated with the use of translocations, specifically translocation heterozygotes have been discussed by Whitten (1971ab) and Whitten and Pal (1974). The three main objectives to their use are as follows:

1. Mass rearing of partially sterile translocation heterozygotes would be laborious and time consuming due to culling out the fertile segregants.
2. The problems of a "plateaued" response after releases compared to the "swamping" effect of successive releases of fully sterile insects.
3. Natural selection and genetic equilibrium conditions may lead to rapid removal of translocation heterozygotes.

In addition, Serebrovskii (1940) was concerned about the problem of compensation due to increased likelihood of survival in populations reduced below the carrying capacity of the environment by translocations. This phenomenon was reported in mosquitoes by Lowe _et al._ (1973) and Weidhaas (1974). If the normal survival rate is lower than the fertility rate induced by the translocation then essentially no effect would be obtained in population control.

UNDERLYING HYPOTHESES

The basic premise which governs the use of translocations for genetic control of insects was derived from the fact that during development, approximately 50% of the gametes produced by a single translocation heterozygote are non-viable due to a deficiency in genetic material. This semi-sterility places a genetic load on the population. Serebrovskii (1940) suggested the use of a homozygous translocation breeding stock and the release of individuals from this stock (both sexes) into wild populations at a rate of one translocation homozygote to one wild type. Translocation heterozygotes would then be produced from matings between released and wild-type individuals. These heterozygotes would have a characteristic partial sterility (approximately 50%). Additional mortality would result from matings involving such heterozygotes. By the F_2 generation a 50% reduction in fertility could be expected with even greater reduction occurring in subsequent generations. Additional translocations among chromosomes of single strains released would increase overall mortalities to the following degree: two translocations involving four pairs of

chromosomes, 75.0%; three translocations 89.5%; five translocations 94%; and six, 96.5%. Serebrovskii further postulated that releasing two or more different translocation homozygote stocks in which interchanges had taken place on the same chromosome would also increase mortality. A level of 75% could theoretically be obtained by increasing the number of different stocks released. Using multiple translocations a limit of 93.75% mortality could be attained releasing strains with two translocations each, and those with three translocations, 98.4%. These rather straight forward calculations have been thoroughly discussed by Curtis and Robinson (1971), Curtis and Hill (1971), Whitten (1971), and McDonald and Rai (1971). As seen from Serebrovskii's (1940) relatively simplistic hypothesis, multiple translocations can offer greater potential in limiting reproduction than single translocations. This idea has been supported by others as well (Curtis and Robinson 1971; Robinson 1976; Seawright and Kaiser 1976; Whitten 1971; Ross 1976, 1977ab, 1980; Ross and Cochran 1973, 1975b, 1976, 1979, 1981ab; Seawright et al. 1979). Multiple translocations within a single cell may possibly involve three or four chromosomes.

In general, the more chromosomes involved in a translocation the lower the fertility (Serebrovskii 1940; Curtis and Robinson 1971; Robinson 1976). Multiple translocations may be obtained from multiple break and rejoin events after irradiation, from reirradiation of single translocations and from crosses between different single translocations.

These basic hypotheses concerning translocations are founded by necessity on a set of fundamental assumptions. These assumptions,

often referred to as the Hardy-Weinberg Law, set forth the following basic parameters (Falconer 1960):

1. "A large random-mating population, in the absence of migration, mutation, and selection, is stable with respect to both gene and genotype frequencies; there is no inherent tendency for its genetic properties to change from generation to generation.

2. The genotype frequencies in the progeny produced by random mating among the parents are determined solely by the gene frequency among the parents."

Also referred to as the Hardy-Weinberg equilibrium, this phenomenon functions initially to fix the genetic load introduced by translocations. Natural selection will, however, tend to eliminate translocations from the population due to their lower overall fitness.

Serebrovskii's proposed use of translocation homozygotes is theoretically sound but actual experience points to a problem of low viability, sterility, and lethality in homozygotes (Robinson 1976; Whitten 1979). Translocation homozygotes have been isolated extensively in *Drosophila*. Sobels (1972), Ytterborn (1970), and Patterson *et al*. (1934) showed that approximately 40% of the translocation homozygotes in *Drosophila* were viable. Patterson *et al*. (1934) also reported that 83% of the viable translocation homozygotes isolated were also fertile. This relative abundance of viable translocation homozygotes has not been found in most pest species now under study. Of the insect pest species under study, *Musca domestica* (Wagoner *et al*. 1974) had the largest number of viable homozygotes at 4 out of 18. Two have been reported for *Blattella germanica* (Cochran and Ross 1977b; Ross and Cochran 1975a). Sakai *et al*. (1979) reported a viable homozygous translocation in *Anopheles culicifacies*. In the mite species,

Tetranychus urticae, van Zon and Overmeer (1972), Overmeer and van Zon (1973) and Feldmann (1975) have found 13 of 34 translocations to be viable as homozygotes. The lack of viable translocation homozygotes and poor fitness associated with the ones isolated has greatly hindered the development of translocations as a pest management tool. Two factors are involved--first, translocation stocks should be pure and relatively fertile to facilitate their maintenance in the laboratory. Otherwise, laborious backcross systems with repeated selection are required. Secondly, if different homozygotes are available, the synthesis of various types of heterozygotes to produce higher sterility can be accomplished (Robinson 1976).

Since viable and vigorous translocation homozygotes are difficult to obtain in pest species, the use of translocation heterozygotes has been proposed (McDonald and Rai 1971; Ross and Cochran 1973). Computer simulations by McDonald and Rai (1971), Wiedhaas (1974), and Seawright *et al*. (1979) and Greever and Georghiou (1979) indicate the need for repeated releases of translocation heterozygotes to insure mating between heterozygotes in later generations. Curtis and Robinson (1971) and others have advocated the release of double translocation heterozygotes since the sterility of the double would be considerably higher than either single translocation. They also postulated that heterosis would overcome any weaknesses of the two homozygotes used as breeder stocks.

TRANSLOCATIONS IN PEST SPECIES

Translocations have been investigated as possible genetic control tools in a number of pest species. These include the following: *Aedes aegypti* (Rai 1967; Rai and Asman 1968); *Aedes albopictus* (Laven *et al*. 1971c); *Anopheles albimanus* (Rabbani and Kitzmiller 1972, 1975, 1976; Seawright *et al*. 1979); *Anopheles culicifacies* (Baker *et al*. 1978); *Anopheles gambiae* (Krafsur 1972; Akiyama 1973); *Blattella germanica* (Ross and Cochran 1973); *Culex tarsalis* (Asman 1976); *Culex tritaeniorhynchus* (Selinger 1972; Baker and Sakai 1974); *Drosophila* (Robinson and Curtis 1972); *Glossina austeni* (Curtis 1969); *Hylemya antiqua* (Robinson and van Heemert 1975; Robinson 1977ab); *Laspeyresia pomonella* (Proverbs 1969); *Lucilia cuprina* (Foster and Whitten 1974); *Musca domestica* (McDonald and Overland 1972a); *Rodnius prolixus* (Maudlin 1976); *Tetranychus urticae* (van Zon and Overmeer 1972); *Trichoplusia ni* (North and Holt 1971).

Single Translocations. Radiation and chemically induced single translocations were reported in *Drosophila* as early as 1934 (Patterson *et* al. 1934). Translocations involving a single interchange usually result in fertility levels which approximate 50% in the heterozygotes. For example, the translocations reported by LaChance *et al*. (1964) in *Cochliomya hominivorax* involved a differential fertility level for male and female heterozygote with females averaging 49.2% and males 66.9% and Curtis (1969) isolated five translocations in *Glossina austeni* with average fertility of 42.7 ± 5.5%. Heterozygote fertility levels in *Blattella germanica* averaged 53.9% (Ross and Cochran 1973).

Extensive single translocation studies have been undertaken in several of the more important species some of which include the following: 107 in Musca domestica (Wagoner 1967; Wagoner et al. 1969); 192 in Aedes aegypti (Rai et al. 1970; Rai and McDonald 1972; Bhalla 1973; Rai et al. 1974; Rai and Hartberg 1975; Seawright et al. 1975c); 69 in Culex tritaeniorhynchus (Selinger 1972; Baker and Sakai 1974); 40 plus for the Culex pipiens complex (Laven et al. 1972; Krishnamurthy et al. 1977); about 20 radiation-induced single translocations in Blattella germanica (Cochran and Ross 1969; Ross and Cochran 1973, 1975ab); and 7 in Culex tarsalis (Asman 1976; Asman et al. 1980).

Multiple Translocations. Two chromosome double translocations (where two breaks occur in the same chromosomes) have been demonstrated for Drosophila (Robinson and Curtis 1972). Four translocations of this type have been reported in Aedes aegypti (Rai et al. 1974). The fertilities of these four double translocations were similar to that of a single translocation. This was attributed to a lack of crossing over between breakpoints.

Three chromosome double translocations are reported more frequently in pest insect species than two-chromosome doubles. This type of interchange involves two break and rejoin events involving three chromosomes; thus one of the three chromosomes undergoes two exchanges. Six three-chromosome double translocations have been studied in Culex tritaenioryhnchus by Sakai et al. (1971). However, only three showed less fertility than a single translocation. Sakai et al. (1972) were more successful in obtaining several three-chromosome double

translocations in the same species with fertility significantly lower than single translocations. Additionally, males heterozygous for two independent translocation complexes involving all the chromosomes were synthesized by crossing two different three-chromosome double translocations. These males were 96% sterile when crossed with normal insects (Baker and Sakai 1974). In *Aedes aegypti*, two single translocations with a fertility of 30% were crossed producing a three-chromosome double translocation heterozygote with a fertility of 10% (McDonald and Rai 1970). Rai *et al*. (1974) reported four three-chromosome double translocations with a fertility range of 13-20%. In addition, Bhalla (1973) described a three-chromosome double translocation heterozygote in *A. aegypti* with a significant difference between male (45%) and female (18%) fertility. Seawright and Kaiser (1976) reported seven three-chromosome double translocation heterozygotes in *A. aegypti* with average fertility of 23.6%. Suguna *et al*. (1977a) reported a double translocation heterozygote involved with sex ratio distortion in *A. aegypti*. Double translocations in *Culex tarsalis* were discussed by Terwedow *et al*. (1977). Asman *et al*. (1979, 1980) reported a double sex-linked heterozygous translocation involving three-chromosomes of *Culex tarsalis* with overall fertility of 28%.

A similar fertility level was found for a three-chromosome double translocation by Curtis (1969) in *Glossina austeni*. Sixteen three-chromosome double translocations with an average fertility of 38% have been reported for *Musca domestica* by Wagoner *et al*. (1969). In *Blattella germanica*, Ross and Cochran (1973) reported a three-chromosome single translocation. In crosses between two translocation

heterozygotes (Ross and Cochran 1976), the resulting double translocation heterozygote males displayed lethality of 70-90% when crossed to wild-type females. Ross (1977) reported a double reciprocal translocation in B. germanica with fertility level of 33 to 45%. A three-chromosome double translocation reported by Ross (1980) showed nearly complete sterility as a heterozygote. A newly synthesized double translocation heterozygote of B. germanica has proven to be completely sterile due to embryonic trapping resulting from the very low number of live embryoes in the ootheca (Ross and Cochran 1981a).

POPULATION STUDIES

A limited number of laboratory and caged population studies incorporating translocations have been reported. Cage experiments using Drosophila were studied by Erke (1955) using a 2-3 translocation with a dominant homozygous lethal marker. He began the experiment with an initial translocation frequency of .25 which became fixed at the final frequency of 0.05 possibly due to heterosis of the translocation heterozygote.

Eradication of an artificial field caged population of Culex pipiens by release of a male sex linked translocation was reported by Laven (1969). In later field studies Laven et al. (1971c) were able to inject a male-linked translocation into a wild population so that 95% of the males in the population carried the translocation. In six weeks adult emergence dropped from 20,000 per/day to 100 per/day. First egg-rafts showed 89% semi-sterility; however, the translocation frequency dropped to 1.0% by 1973 (Cousserans and Guille 1974).

Wagoner *et al*. (1971) studied caged populations of houseflies to evaluate the effect of 9:1 (translocation : wild type) release ratio of multiple-translocation heterozygotes on population fertility. Genetic loads of up to 89% were obtained. Males bearing a heterozygous translocation with a fertility of 32.5% when mated to wild type females were released into a wild population by Wagoner *et al*. (1973). The fertility at the test site was 63.5% compared to laboratory results of 27.7%. The test was termed a limited success and migration of released males was given as a possible explanation.

Cage experiments using a translocation homozygote released at the rate of 1:1 homozygote to wild-type *Drosophila* were reported by Robinson and Curtis (1973). Viability of the homozygote was reduced in mixed populations compared to isolated evaluations. Laboratory and field caged populations of *Aedes aegypti* were used to evaluate two single translocation heterozygotes against wild type by Rai and McDonald (1972). Translocation heterozygote males were equal or greater in competitiveness to wild-type males in laboratory experiments. In field experiments males of one of the translocation heterozygote stocks showed reduced competitiveness.

Field competitiveness of *Aedes aegypti* males heterozygous for a translocation was evaluated by Seawright *et al*. (1975a) on a small island. Wild-type males were laboratory stocks as no wild *Aedes aegypti* were thought to be present. Translocation heterozygote (T/+) males were equally competitive with wild type males. Seawright *et al*. (1976b) and Uppal *et al*. (1978) evaluated double translocation heterozygotes of *A*. *aegypti* and found the males to be fully competitive

with wild types.

Curtis *et al*. (1976a) demonstrated eradication of field cage populations of *Aedes aegypti* using three different genetic control systems. Daily releases were made of chemosterilized males, double translocation heterozygote males (T_1T_3), or T_1T_3 with sex ratio distorter (DT_1T_3). The rate of suppression was markedly lower for the double translocation heterozygote than the other two which were similar.

A first field release of a translocation homozygote was reported by Lorimer *et al*. (1976) using both sexes of translocation strains of *Aedes aegypti*. None of the translocation homozygote strains were as fit as wild-type *A. aegypti* and did not become established in the field. The results also illustrate the types of problems which may be encountered in field sampling of wild and released populations. In laboratory experiments, Rabbani and Kitzmiller (1975) studied competitiveness in *Anopheles albimanus* males heterozygous for a translocation. Translocation bearing males and wild-type males were not significantly different in competitiveness. The same authors (1976) obtained encouraging results in the release of translocation heterozygote males for population control of caged populations of *A. albimanus*.

Asman *et al*. (1979) reported a pilot study in which releases of male *Culex tarsalis* carrying sex linked double heterozygous translocations were made into a native population. No impact was observed on the density of the native population and the translocation was not recovered after the release. This failure was thought to have resulted from too few mosquitoes released for the size of the native population.

Six laboratory population studies using semi-sterility from translocations in *Blattella germanica* have been reported by Ross (1975a, 1976, 1977, 1980) and Fox and Huber (1974). The single translocation studies showed population retardation but not suppression. Two studies using double translocation heterozygote males for releases gave more promising results (Ross 1977b, 1980). More detailed discussions of these studies are presented in the section which follows.

GENETIC SEXING SYSTEMS

Genetic methodology has in recent years contributed significantly to improvement of the prospects of SIRM usage for some species. One of the most dramatic cost reducing achievements in this area related to genetic sexing methods for use in rearing programs (LaChance 1979). Genetic sexing systems have been reported for the following pest and/or vector species: *Tetranychus uriticae* (Overmeer 1974); *Musca domestica* (McDonald 1971); *Culex tritaeniorhynhus* (Sakai and Baker 1974); *Lucilia cuprina* (Whitten *et al.* 1977); *Anopheles gambiae* (Curtis *et al.* 1976); *Anopheles arabiensis* (Curtis 1978); *Anopheles albimanus* (Seawright *et al.* 1978).

GENETIC CONTROL OF BLATTELLA GERMANICA

INTRODUCTION

The idea of using genetics as part of a possible control regimen for *B. germanica* was first proposed by Ross and Cochran (1973). Subsequent studies have proceeded toward the ultimate testing of this approach (Cochran and Ross 1974; Ross 1975a, 1976, 1977ab, 1978, 1980;

Ross and Cochran 1973, 1975ab, 1976, 1977, 1979, 1981a; Ross *et al.* 1982). Berndt (1978) reviewed the literature relating to genetic control of *B. germanica*--most of which included studies reported by D. G. Cochran and M. H. Ross.

APPLICATION OF SIRM TO *B. GERMANICA*

The success of the screw-worm SIRM program has stimulated a high degree of interest and has served as a model for research into the genetic control of other species. The conditions and information required for successful SIRM usage have been elaborated by Knipling (1967), Knipling *et al.* (1968), and Waterhouse *et al.* (1973).

Characteristics of the German cockroach which meet these important criteria are outlined as follows (Ross and Cochran 1973):

1. Mating competitiveness is perhaps the most important factor in determining feasibility of using sterile male release. All translocation heterozygotes thus far tested, especially T(8;9), have been shown to be at least equally competitive with the VPI wild-type strain (Ross and Cochran 1973, 1975b; Ross 1975a, 1978). Ross (1978, 1980) showed that double translocation heterozygote males were more competitive than those of a field-derived strain.

2. Mass rearing of German cockroaches is relatively simple and inexpensive. One-gallon glass battery jars, screen harborage, standard dog food or laboratory chow and water are the only supplies required (Grayson 1951). Elaborate environmentally controlled rearing facilities are unnecessary as normal room conditions are adequate. Maintenance procedures are relatively simple and are less exact than for most other pest insects.

3. Limited population densities of 1000-1500 per building (Mallis 1960), 800 (Wright and Hillman unpublished) in eighteen low-income homes and 100-1000 on seven U.S. naval vessels (Ehrhardt and Dickens 1975) have been reported. Populations of 1000-5000 were postulated as feasible for genetic control by Ross and Cochran (1973). In addition, the number of T/+ males required for release will be governed by the number of maturing (5th - 6th instar) nymphs

present in the population. This number can be only a fraction of total laboratory and field populations depending on population size and age structure (Ross 1975). Ross and Wright (1976) reported that "field" populations had a relatively even distribution of nymphal age classes. Shipboard populations analyzed by Kiel (1981) show some degree of variation in age structure.

4. The use of sterile insect release could be augmented by the use of a non-residual insecticide dispersed by ultra low-volume (ULV) equipment (Reierson 1973) or by standard methods. This could lower the number of insects required for release to a minimal number.

5. Female German cockroaches usually mate within 4-6 days after maturation (Ueda et al. 1969). Mating is followed by an immediate loss of receptivity (Barth 1968). A single effective mating occurred in most cases with an occasional remating following deposition of an ootheca (Ross and Cochran 1973; Cochran 1979). This character is important to maintaining a "genetic load" on the population.

6. Adaptability to a "field" environment for B. germanica males should pose no obstacle as laboratory and "field" environments are quite similar. Differences between laboratory and field strains were reported by Wright (1968) but these were concluded to be due to environmental rather than behavioral characteristics. Ross (1980) and Ross et al. (1982) found laboratory males easily adapted to a "field derived" shipboard population in the laboratory and a field population aboard a Navy ship.

7. Limited habitat for German cockroaches has been documented by several workers (Cornwell 1968; Mallis 1969; Sternburg 1947). The species is reported to prefer food preparation areas and other niches (such as city dumps, refuse heaps) near a food and water source and to move about a short distance and then return. This characteristic would limit releases to specific areas on a ship or in a warehouse. The ship environment could provide "the isolation" usually sought on islands for initial field testing of SIRM on other species.

8. While the total costs involved in developing this genetic control technique for B. germanica would be difficult to assess at this time, there may be justification for a larger cost in the use of genetic control due to the potential reduction in insecticide usage in man's environment.

POPULATION DYNAMICS

Wharton et al. (1968, 1976) reported information relating to the effects of population density on survival, growth, and development in the American cockroach. Crowding was reported to be a cause of mortality and retardation of growth in the nymphs of Periplaneta americana.

Information on population structure and growth in B. germanica of wild-type laboratory populations was reported by Mele (1972). Beginning with five pairs of VPI wild-type individuals, populations stabilized at about 1700 after 16 weeks. Population structure after this point was of an hour-glass shape with large number of small 1-3rd instar nymphs, very small numbers of 4-6th instar nymphs, and adults comprising approximately 13% of the population. Crowding was hypothesized as the major factor contributing to this population structure.

Population structure in laboratory populations studied by Ross (1975) showed relatively large numbers among all nymphal instars and the adults. These populations were not allowed to stabilize in size due to space requirements as did Mele's. Further studies by Ross (1976) showed that laboratory rearing by progeny groups versus a freely intrabreeding population gave similar results in population structure (large numbers in all stages) and prevented crowding through the F_2 generation. This technique also simplified censusing and assignment of nymphal origin. Considerable synchrony in the development of nymphal groups was reported. Time required for development (approximately two months) was about the same for isolated progeny groups and intrabreeding

populations. This tendency for synchrony was also reported by Ishii (1970) in isolated nymphal groups.

Nine summer field collections of German cockroaches were evaluated by Ross and Wright (1976). Nymphal numbers were low with a relatively uniform distribution among the six instars. This differed from both Mele's data and Ross's laboratory data. Space was limited for Mele's populations and not for Ross's populations; therefore, other factors such as food, water, and temperature are the probable limiting factors for the wild populations. More importantly, such factors could further limit reproduction in field releases for genetic control.

BASIC GENETICS

Cochran and Ross (1967a) first reviewed the genetics of *B. germanica*. Many new discoveries and developments were added in a more recent review (Ross and Cochran, 1975b). The failure of many of the early field trials of genetic control techniques draws attention to the importance of a sound genetical and cytogenetical research program on the candidate species to back up any genetic control program (Whitten 1979). The basic genetical information gathered for *B. germanica* in recent years has become of great importance in developing methods of genetic control for the species. This information has included over 60 mutants and more than 20 reciprocal translocation stocks.

Mutants. The list of mutant markers for the German cockroach has increased from 30 to more than 60 (Ross and Cochran 1973, 1975b; Ross unpublished). The visible markers which have been formally described

include the following: balloon wing (*ba*) (Cochran and Ross 1961); orange body (*or*) (Ross and Cochran 1962, 1966); prowing (T(9;10)*Pw*) (Ross 1964; Ross and Cochran 1965; Cochran and Ross 1969); broad-banded pronotum (*Bbp*) (Ross and Cochran 1965; Ross 1972, 1973b); fused antennae (*fs*) (Ross and Cochran 1965, 1970; Ross 1971a); ocelliless (*oc*) (Ross and Cochran 1965); pale body (*Pb*) (Ross and Cochran 1965; Ross 1971a); red eye (*r*) (Ross and Cochran 1965, 1966, 1969b); notched sternite (*st*) (Ross and Cochran 1965; Ross 1966ab; Ross and Cochran 1968b, 1971); truncated antenna (*tn*) (Ross and Cochran 1965); black body (*Bl*) (Ross and Cochran 1966, 1968a; Ross 1971b); curly wing (T(2;11)*Cu*) (Ross and Cochran 1966, 1968a; Cochran and Ross 1969; McDonald *et al*. 1969); glassy wing (*gl*) (Ross and Cochran 1966; Ross 1973); rose eye (*ro*) (Ross and Cochran 1966, 1967, 1969b); yellow body (*y*) (Ross and Cochran 1966, 1969a; Ross 1972, 1973b); curved wing (*cv*) (Ross and Cochran 1967, 1969a; Ross 1972, 1973b); fused tarsi (*ft*) (Cochran and Ross 1967a); mottled (*M*) (Cochran and Ross 1967a); pallid eye (*pld*) (Ross and Cochran 1967, 1968a; Ross 1971b; Cochran 1973a); ruby eye (*ru*) (Ross and Cochran 1967, 1968b, 1971); elevated wing (*el*) (Cochran and Ross 1967a); hooded pronotum (*hd*) (Ross and Cochran 1968a); variegated eye (*var*) (Ross and Cochran 1968a); bubbly prowing (T(9;10)Pw^b) (Cochran and Ross 1969); cross-veinless (*crs*) (Ross and Cochran 1970; Ross 1971b); downturned wing (*dtw*) (Ross and Cochran 1970); bulge eye (*bu*) (Ross 1971a, 1972); deficiency prowing (Df(9)*Pw*) (Ross and Cochran 1971); deformed leg (*dfl*) (Ross 1972); elo black body (Bl^e) (Ross 1973c)/ cubitus interruptus (*ci*) (Ross 1973a); narrow abdomen (*na*) (Ross 1973c); notch

pronotum (np) (Ross 1973a); odd body (Ob) (Ross 1974); pale purple eye (pp), pearl eye (ru^{pl}), stumpy (sty) (Ross 1975b); miniature-wing (min) (Ross and Keil 1978). Some 15 additional mutants including one eye color variant, green eye (g) and various structural mutants were briefly described by Ross and Cochran (1975b). These visible markers have been invaluable in conducting linkage group tests for reciprocal translocations (Ross and Cochran 1973), population experiments (Ross 1975a, 1976, 1977b), and determining the number of effective matings (Cochran 1979). Other non-visible physiological mutants which have been measured in B. germanica include DDT resistance (r-DDT) (Cochran and Ross 1962ab); cyclodiene resistance (r-cyclo) (McDonald et al. 1969), pyrethins resistance (r-Pyreth) (Cochran 1973a), and malathion resistance (r-Mal)(Cochran 1973b). Ross and Cochran (1973, 1975b) indicated deleterious mutants might be useful in effecting a degree of population suppression. This usefulness in genetic control would be only as an adjunct to the use of translocations via close linkage with respective break points. Mutants known to affect productivity in B. germanica are as follows: dominant mutants which are lethal as homozygotes include Elo black-body (Bl^{e}), pale-body (Pb), deficiency, 9, prowing Df(9)Pw and odd body (Ob) which also causes death of approximately 50% of the heterozygotes in the last molt; recessive mutants including notched sternite (st) and stumpy (sty) in which the female homozygotes show complete, or nearly complete sterility, respectively; and a recessive mutant, shriveled-wing (sh) which produces a dominant effect in reducing the number of eggs per ootheca.

Linkage. There are 12 pairs of autosomes in *B. germanica* with males having 2n = 23 (Cochran and Ross 1967b; Cohen and Roth 1970; Stevens 1905; Suomalainen 1946; Wassilieff 1907). This XO sex determination may have significance in the reported autosomal sex differences in recombination and sexual dimorphism in the recessive mutant stumpy (*sty*). There are mutant markers known for each of the 12 linkage groups (Ross and Cochran 1973, 1975b). Differences in cross-over frequencies for males and females have not usually been reported as large. However, in linkage groups six and ten recombination was slightly higher in females (Cochran 1977; Ross 1971b, 1973b) and significantly higher in females (7% vs. 3%) for linkage between or and T(7;12) (Ross and Cochran 1975a). In addition, recombination between T(8;9) and Bl was characterized as higher for males than females (4.2 vs. 1.7). The patterns of close and distant linkage with many cases of close linkage between markers provided opportunity for maintaining and identifying translocation heterozygotes in backcross systems (Ross and Cochran 1973, 1975b). For example, T(8;9) was maintained by backcrossing to ruby-eye (*ru*) later with stumpy (*sty*) and notched sternite (*st*). These three backcross systems were also used in mass rearing of semi-sterile T(8;9) heterozygote males for releases into laboratory populations (Ross 1975a, 1976). Ross (1976) reported the translocation T(4;8;10) was maintained in a back-cross system which utilized close linkage with rose eye (RF 0.3 ± 0.5%) and was also mass reared for releases into laboratory populations. Double translocation heterozygote males were synthesized using two markers, ruby eye (*ru*) and hooded pronotum (hd), closely linked with translocation break points T(8;9)

and T(3;12) respectively (Ross 1977b). Stocks of the translocation, T(3;12) and T(7;12) were used to develop T(3;7;12) double heterozygotes by backcrosses to a double mutant stock, or/or,hd/hd (Ross and Cochran 1979).

Cytological examination of the germinal tissues of _B. germanica_ male nymphs enables the distinguishing of the 12 wild-type chromosomes on the basis of length (Cochran and Ross 1969). The centromere location was established in studies of mitotic cells by Cohen and Roth (1970) as metacentric and occasionally submetacentric. These cytological studies proved invaluable as additional verification along with linked markers in identifying the chromosomes involved in reciprocal translocations (Ross and Cochran 1973, 1975b, 1977a, 1979, 1981). Additional data on types of disjunction observed in cytological studies correlated well with the levels of fertility observed in translocation heterozygotes (Cochran 1976, 1977; Ross and Cochran 1973, 1975b, 1977a, 1979, 1981a).

Translocations. The first two translocations, T(9;10) _Pw_ and T(2;11) _Cu_, described by Cochran and Ross (1969) both had dominant phenotypic effects and were lethal as homozygotes. A third related trait, (_Df_(9)_Pw_), was also described by Ross and Cochran (1971). Subsequent translocation stocks were obtained from third-fourth instar male nymphs irradiated with 800r of gamma radiation for a 24-hour period (Ross and Cochran 1973). These were mated to VPI wild-type females. Lethality was determined by presence of dead embryos in oothecae and reduced hatch. Additional verification of the presence of a reciprocal

translocation was obtained by cytologic examination of the testes (Cochran 1976, 1977; Cochran and Ross 1974, 1977ab; Ross and Cochran 1973, 1975ab, 1976, 1977). The presence of a cross-shaped or ring of four chromosome configuration at mid pachytene to early anaphase I of meiosis was readily discernible in cells which had a reciprocal chromosome translocation (Cochran and Ross 1969; Ross and Cochran 1975b). As previously discussed, mutant markers enabled establishment of linkage groups and backcross sytems for the translocations (Ross and Cochran 1973, 1975b). Nine single translocations have been used to correlate linkage groups with specific chromosomes (Cochran and Ross 1969, 1974, 1977ab; Ross and Cochran 1971, 1975a, 1975b, 1976, 1977).

Data for 20 translocation heterozygotes of B. germanica fall into three categories on the basis of ootheca size when mated to VPI individuals (Ross and Cochran 1973, 1975ab). These categories include the following:

1. Translocation heterozygote females with unusually large oothecae with corresponding T/+ males which induced reduction in egg deposition and hence small oothecae in their mates.

2. T/+ stocks which averaged two or three more eggs than the wild type for both T/+ males and T/+ females.

3. T/+ females with average ootheca size almost identical with the wild type.

Category (1) includes five translocation stocks in which the translocation heterozygote males may lack stimulatory capability resulting in smaller oothecae. The act of mating has been reported by Barth (1968) to influence egg maturation in cockroaches. This phenomenon has

been observed with males of pale body (Pb) (Ross 1971a). An additional five translocation stocks showed the characteristics of category (2) which may be due to heterosis (Ross and Cochran 1973). Category (3) included six of 16 stocks. Mortality data from translocation heterozygotes mated to VPI wild-type individuals, reported by Ross and Cochran (1973) showed the expected 50% mortality in seven of 16 stocks. One group of five stocks showed 50% mortality for one sex but 40-45% for the other sex. Higher mortality was associated with T/+ males in two cases and with T/+ females in three cases.

The lowest mortality of 38% and 35% for females and males respectively was obtained in laboratory stock (19a) which was reported to have the smallest chromosome pieces involved in the interchange (Ross and Cochran 1975a). Highest single translocation mortality (68% to 70%) was reported to be associated with the three chromosome single translocation T(4;8;10).

One of the causes of reduced mortality in translocation heterozygote males was thought to be a favoring of alternate versus adjacent disjunction. This phenomenon effectively produces a favoring of the viable type of disjunction (Cochran and Ross 1974). Six translocations including T(9;10)Pw, T(2;11)Cu, T(8;9), T(3;12), T(7;12), T(4;8;10) and T(11;12) were evaluated in this regard (Cochran 1976, 1977; Cochran and Ross 1974, 1977ab; Ross and Cochran 1975ab). Hatch data and counts of disjunction types were closely correlated.

The translocation T(8;9) was the first studied of a group isolated following irradiation (Ross and Cochran 1973). Cochran and Ross (1974) described this translocation initially using techniques

reported earlier (Cochran and Ross 1969) as involving chromosomes 9 and 11. However, subsequent studies revealed this identification to be incorrect (Ross and Cochran 1976). New data (Ross and Cochran 1981a) indicated that chromosomes 8 and 9 were involved in the interchange and the designation was changed to T(8;9) (Ross 1976). This translocation was one of two reported by Ross and Cochran (1973) as showing evidence of directed disjunction favoring the alternate type. This was confirmed cytologically by Cochran and Ross (1974). In the male this explained in part the significant difference in mortality induced when the heterozygotes were mated to VPI wild-type individuals. Average mortality was 42% and 49% for males and females, respectively (Cochran and Ross 1974; Ross and Cochran 1973). When T(8;9) heterozygotes were mated, only one mating was productive with 14 progeny. Therefore, the possibility of obtaining a viable homozygote was considered remote (Cochran and Ross 1974). This intracross sterility was viewed by Ross and Cochran (1973) as similar in intensity to that of double or triple heterozygotes.

This characteristic was one of the justifications for utilizing this translocation in later population studies (Ross 1974, 1976, 1977b). In further studies, Ross and Cochran (1976) synthesized a double translocation heterozygote of T(8;9) and T(2;11)Cu. Lethality when crossed to wild-type females was 90%. When T(8;9) was crossed with T(2;11)Cu, lethality was 82%. Linkage relationships between T(8;9) and other characters will be treated in a later section. Early data from mating double translocation heterozygotes, T(9;10)Pw and T(2;11)Cu averaged 83% mortality with only 6.67 2.4 offspring/

ootheca (Ross and Cochran 1973).

Further increases in mortality from the effect of translocations were obtained in double translocation heterozygotes synthesized by Ross and Cochran (1976). Mortalities of 70% to 90% were reported; however, lethal effects alone could not account for the reduction in hatch. In B. germanica the characteristic hatching of the ootheca usually occurs from the combined efforts of viable progeny in forcing open the keel. This characteristic provided a bonus in further reducing hatch in the translocations with higher lethality because the combined efforts of surviving progeny apparently could not open the ootheca (Ross and Cochran 1975a). Ross and Cochran (1976) termed this phenomenon "embryonic trapping." Ross and Cochran (1977) reported data obtained from a double reciprocal translocation synthesized from T(8;9) and T(3;12). Ruby eye (ru) and hooded-pronotum (hd) mutants closely linked with the respective translocation break points were used in back crosses and intercrosses to enable identification of the translocation heterozygotes. A shift in disjunction tendency from directed to random was reported for T(3;12) males. Disjunction was apparently more stable in females than males during the production procedures used for synthesis of this double (Ross and Cochran 1977). Reduction in hatch approached that reported for T(4;8;10) (Cochran and Ross 1977a). A three chromosome double translocation T(3;7;12) with nearly complete male sterility was reported by Ross and Cochran (1979). Releases into a field-derived population resulted in population suppression (Ross 1980). A new double translocation heterozygote T(8;9);T(4;5;10) was reported to show complete sterility in males from

genetic load and "embryonic trapping" (Ross and Cochran 1981a). These males represent promising candidates for a field experiment in genetic control.

HYPOTHESES

Ross and Cochran (1973) postulated that the best prospect for genetic control of *B. germanica* would include (1) release of different translocations in subsequent steps, or (2) synthesis and release of double and/or triple heterozygotes. Ross and Cochran (1973) reported that the easy production of multiple translocation stocks added support for the use of this technique in *B. germanica*. The 11 pairs of autosomal chromosomes in *B. germanica* increased the possibility of synthesizing many different combinations of interchanges compared to many diptera with only three pairs of autosomes (Ross and Cochran 1973).

POPULATION STUDIES

Early studies were designed to determine the effects of the single translocation T(8;9) which exhibited high sterility in crosses between heterozygotes and semi-sterility with wild-type mating. The directed disjunction characteristic of the heterozygote male of this translocation tended to reduce the level of lethality (Cochran and Ross 1979; Ross and Cochran 1973).

T(8;9) Alone. Ross (1975) studied the impact on population growth of laboratory populations from releases of T(8;9) heterozygote males. A release ratio of 3T+:1 wild-type was used. A single release was made

into the developing F_1 groups of one population which resulted in a 50% reduction in population growth through the F_2 generation compared to the control. In a second population additional releases at the same ratio into the developing F_2 generation resulted in an experimental population only 25% as large as the control. This experiment succeeded in showing that T(8;9) could be successfully incorporated into a population by careful timing of releases.

T(9;10)Pw. A laboratory population study which evaluated the effect of various frequencies of the translocation T(9;10)Pw on population growth of B. germanica was conducted by Fox and Huber (1975). These workers reported that while the single translocation showed measurable impact, suppression was not achieved and recommended the use of more than one translocation released at intervals into the population.

T(8;9,st). The linkage relationship of T(8;9) with the mutant notched sternite (st) was explored by Ross (1976) in a population study using T(8;9) heterozygote males carrying st in repulsion for repeated releases into the developing progeny groups. A release rate of 5-6T:1 wild-type was used. The translocation T(8;9) did not function to successfully drive the mutant gene into the normal segment of the population as only 5-8% of F_2 females were homogous for st compared to an expected 23%. This factor along with reduced male competitiveness prevented the reduction of population growth beyond that expected from the translocation alone. The reduced competitiveness of males was attributed to the difference in genetic background, i.e. ru compared to st. Overcrowding reported in the previous study was eliminated by

changing to the "progeny group" rearing method.

T(4;8;10). A population study reported by Ross (1976) involved the use of a three-chromosome translocation T(4;8;10). Population growth was severely limited by a 6:1 release ratio of males heterozygous for T(4;8;10) and essentially suppressed by 10T(4;8;10)+:1 wild-type release ratio. After seven months, three replicates showed the size of experimental populations to be only 2.1% that of the control. The phenomenon of "embryonic trapping" and high lethality attributed to the T(4;8;10) releases contributed to the reductions of population growth.

T(8;9) T(3;12). In an effort to explore the increased genetic load induced by a double translocation heterozygote Ross (1977) conducted population experiments using T(8;9) T(3;12) males for releases. Ross and Cochran (1977) had demonstrated that the lethality of this double was similar to the T(4;8;10) used by Ross (1976), but additional genetic load would be derived because only 25% of F_1 progeny would be wild-type compared to 50% for releases of the single translocation. In five replicates releases were 1.5 to 2X the number of nymphs in each progeny group. Releases into F_1 and F_2 progeny groups produced genetic load sufficient to cause population decline. The estimated lethality of 78-90% for this double translocation was sufficient to induce total sterility in many oothecae. This total sterility was estimated to occur at 82% lethality by Keil and Ross (1977). It was most evident in the third oothecae produced. Decline in hatch and population numbers occurred in the eighth and ninth month. This study emphasized

the importance of high genetic load associated with sterility due to embryonic trapping for use in field trials of genetic control for *B. germanica*.

T(3;7;12). Ross (1980) moved a step nearer to using translocations in field trials by releasing males heterozygous for T(3;7;12) into a field-derived strain in the laboratory. This population study resulted in near elimination of wild-type matings and a subsequent reduction in population numbers for a single release. The remarkable success of the double translocation heterozygote males in out competing the wild type males was attributed to lower fitness in field-strain males, and released males which were older and unmated with heightened competitiveness first noted by Ross (1978).

FIELD TRIALS

Ross *et al*. (1982) conducted a pilot field experiment using double translocation heterozygote males synthesized from T(4;5;10) and T(8;9). Ross and Cochran (1981a) had determined that males carrying this combination of double translocation would be completely sterile due to embryonic trapping. In this study carried out aboard two Navy ships, insecticide treatments were used to reduce population size and locate cockroach harborage sites. Release ratios were determined by sampling the native population to estimate its size. These data were used to estimate the number of release males needed to provide a ratio of 10 sterile males:1 wildtype. Three releases of 120, 145, and 180 adult males at 4- and 6-week intervals among six harborage sites gave an average of 83% sterility in 37 females mated after the initial release.

Increased wild-type matings which occurred between the second and third releases contributed greatly to population growth. Sterility dropped to 38% in 104 females collected late in the 4-1/2 month study. Considerable variability was reported among the infestation sites where releases were made.

The experiment succeeded in showing that sterile males readily join native populations close to sites of release and that they compete well within these groups. However, a need for refinement of population estimation procedures and a method for detection of new infestation sites was identified.

DELETERIOUS MUTANTS

Deleterious mutants may be found in a number of important pest species including *B. germanica*. Some examples include conditional lethals such as heat-sensitive mutants of *Musca domestica* (McDonald and Overland 1972b), siphonless abdomen of *Culex tritaeniorhynchus* larvae (Baker and Sakai 1974), and sex ratio distorter in *Aedes aegypti* (Hickey and Craig 1966), and a recessive sex-linked mutant (short wing) with reduced fecundity (Uppal *et al*. 1978) in *Aedes aegypti*.

Nine deleterious mutants are currently known for *B. germanica*. These include four lethal factors, two translocations with phenotypic effects, and three autosomal recessives (Ross and Cochran 1975a).

Mutants with lethal effects include: Elo black body (Bl^{e}) (Ross 1973c); odd-body (*Ob*) (Ross, 1974); pale-body (*Pb*); (Ross 1971a); and deficiency prowing (Df(9)*Pw*) (Ross and Cochran 1971). All are lethal as homozygotes and also show some lethality in the hybrids. In

addition, 50% of odd-body heterozygotes die during the terminal molt. Pale-body was originally diagnosed as a semi-dominant lethal by Ross and Cochran (1965) which was later confirmed by new data (Ross 1971a). In addition to being lethal as a homozygote, a significant sex difference in oothecal size and hatchability occurred with the heterozygotes. The egg cases produced by matings with pale-body heterozygote males were significantly smaller and reduced hatch occurred.

Other types of deleterious effects are found in several autosomal recessives. These include: notched sternite (st) (Ross and Cochran 1965; Ross 1966ab); shriveled-wing (sh) (Ross 1972); and stumpy (sty) (Ross 1975). Notched sternite (st) is characterized by complete sterility in the homozygous female. Shriveled wing (sh) was reported as recessive; however, it seemed to have a dominant effect on ootheca size, since homozygous and heterozygous females showed a reduction of 25% in number of eggs per ootheca. Stumpy (sty) was discovered in the F_2 progeny or an irradiated male from the Brazil strain crossed to a wild-type female. It is inherited as an autosomal recessive and the female homozygote has nearly complete sterility. These sterility factors and relatively close linkage (Cochran and Ross 1974) generated interest in using these traits in conjunction with a translocation for population control (Ross 1976).

LINKAGE

The relationship of the translocation T(8;9) to other traits carried on chromosome nine was described by Cochran and Ross (1974). Close linkage was reported between the T(8;9) breakpoint and ruby (ru)

(1.3% recombination). Recombination of T(8;9) with stumpy (sty) and notched sternite (st) was estimated on the basis of other chromosome 9 loci at 1% and 4-4.5% respectively (Ross, 1975). Further linkage measurements (Ross and Cochran 1981a) for the T(8;9) breakpoint with black-body (Bl) indicate a sex difference in crossing over (4.2% for males and 1.7% for females).

The autosomal recessive deleterious gene stumpy (sty) was reported by Ross (1975) to show close linkage with ruby (ru) (> 1.0% recombination), T(9;10)Pw (1.0%), and DF(9)Pw (2.4%). Recombination estimates for other chromosome 9 markers indicated stumpy (sty) was probably within one map unit of the T(8;9) breakpoint (Ross 1975).

REPRODUCTIVE BEHAVIOR

MATING BEHAVIOR

Mating behavior in *Blattella germanica* has been described by several authors (Gould and Deay 1940; Roth and Willis 1952; Ueda *et al*. 1969; Ishii 1970). The mating sequence generally begins with antennal fencing, the male then turns 180°, raises his wings, stretches the abdomen in the direction of the female secreting a substance from his tergal glands which the female obtains by nibbling the tergal glands. The male then stretches his abdomen under the female from the side until contact is made with her genital opening. The characteristic end-to-end position is then assumed and copulation may continue for 15 minutes to more than one hour (Roth and Willis 1952). Roth and Willis (1954) reported that copulation took place when adult males were 2-4 days old and females 4-5 days old. Ueda *et al*. (1969)

report the most active age for mating as 3-6 days after maturation for the male and 4-6 days for the female. Cochran (1979) utilized genetically marked virgin females and males which revealed that females normally receive sperm only once. A remating occasionally occurred following the deposition of an ootheca. Roth and Barth (1964) reported that limited food may affect female receptivity in that German cockroach females which were starving did not mate.

The female averages five oothecae at approximate three-week intervals (Willis _et al_. 1958; Ueda _et al_. 1969). Therefore, a single effective mating will usually assure the continuance of introduced sterility factors throughout the reproductive life of the female. Males may mate up to ten times (Ueda _et al_. 1969).

No volatile sex pheromone is known for _B. germanica_; however, Roth and Willis (1952) postulated that contact chemoreception of the antennae of males with substances found in cuticular wax of sexually matured females played an important role in sex recognition. Nishida _et al_. (1975) reported the isolation of this contact sex pheromone.

Competitiveness. Sammeta and Levine (1970) reviewed the topic of competitive ability, its heritability and relationship to other fitness characters. Competitiveness of released males with wild males for mates may be roughly analogous to the single factor intraspecific competition reported by Gale (1964) for three lines of _Drosophila melanogaster_. The anologous single factor in this case was feeding rate in _Drosophila_ versus competition for mating in sterile male releases. Evaluation of competitiveness of sterile insects for release

has been based largely on variations of a method reported by Fried (1971). In this technique, a point estimate of total competitiveness of sterile insects is obtained from evaluation of egg-hatch data. Expected hatch based on previously determined egg-hatch data for normal matings and matings between treated and normal insects is compared with hatch obtained in various ratios of sterile to wild-type males mated with wild-type females. The ratio most commonly used is 1 sterile male: 1 wild-type male: 1 wild-type female. The basic assumption was made that any factor which affects competitiveness would be reflected in egg hatch when normal and treated males were competing for mates. This technique has been widely employed for competitiveness evaluations on various mosquito species (Seawright _et al_. 1975; Rabbani and Kitzmiller 1975), the house fly (McDonald and Overland 1972), fruit flies (Hooper 1975ab; Anwar _et al_. 1975), and some Lepidopterous pests (Cheng 1972; Young _et al_. 1975; Salama 1976).

Initial evaluations of competitiveness have been accomplished with single pair matings when breeding stocks were limited (Rai and Hartberg 1975; Rai _et al_. 1974; Ross unpublished). Ross (1976) reported competitiveness tests of T(8;9) with _st_ involving ten replicates of five females each with a two semi-sterile males to 1 wild-type male ratio utilized. Most T/+ males tested to date show equal competitiveness with wild-type males. These include T(3;12) T(7;12), T(8;9) with _ru_, T(9;10); and T(4;8;10) (Cochran and Ross 1977; Ross 1975; Ross unpublished). The first evaluation of translocation heterozygote males in releases showed T(2;11)_Cu_ males to be very uncompetitive when released at a 9 _Cu_:1 wild-type ratio but did, however, produce a

significant reduction in population growth (Ross unpublished; Ross and Cochran 1973). The competitiveness of other single and double translocation heterozygote males in B. germanica have been consistently equal to or better than the wild-type in laboratory competition studies (Cochran and Ross 1977b; Ross 1975a, 1976, 1977b, 1978, 1979; Ross and Cochran 1975a, 1976, 1977, 1980). Ross (1978) reported greater competitiveness of T(4;8;10) translocation heterozygote males than wild-type males collected from a Navy ship. Later results show T(3;7;12) heterozygote males considerably more competitive than males from a field-derived strain (Ross 1980). Heterozygote males carrying the double translocation, T(8;9); T(4;5;10) were also more competitive than VPI wild-type males (Ross and Cochran 1981a).

MASS REARING

REQUIREMENTS

Rearing methods for cockroaches were reviewed and described by Smittle (1966). The basic requirements are relatively simple and inexpensive and include the following: rearing room, rearing container, harborage, water, and food. Rearing rooms should be preferably temperature and humidity controlled (Smittle 1966), but this is not a necessity (Grayson 1951). Smittle (1966) reared Blattella germanica successfully at 26.7 ± .5°C and 50% ± 1% RH. Grayson (1951) reared German cockroaches at 24 ± 2°C with humidity uncontrolled.

Rearing Containers. The rearing container may be made of metal, glass, wood, or plastic ranging in size from 80 ml test tube (Noland 1956)

to a large barrel (Piquet and Fales 1952). Grayson (1951) used five-gallon glass aquaria, one-gallon battery jars, and quart jars. Top edges of rearing containers are usually greased with petroleum jelly to prevent escape and are appropriately covered. Dahm (1955) used 15-1/2 gallon galvanized tubs for mass production.

Harborage. Harborage has been constructed from a number of different materials. These include corrugated cardboard (box material) (Smittle 1966), screen wire, and layered masonite panels held apart by nails or staples (Heal 1948; Grayson 1951).

Water. Water has been supplied in a variety of small devices including glass or plastic vials of various sizes for small containers and gravity waterers for large containers (Smittle 1966). These watering devices are usually plugged with cotton or synthetic sponge to prevent spillage (Grayson 1951; Smittle 1966; Ross 1974).

Food. Most types of compressed dog food formulas are satisfactory and have been most commonly used (Gould and Deay 1940; Grayson 1951; Smittle 1966). Commercially prepared food for guinea pigs or rabbits was reported to be unsuitable for rearing cockroaches by Piquett and Fales (1952).

Handling. Collection and sorting of cockroaches used for experiments was done by chloroform or carbon dioxide anesthesia (Grayson 1951; Smittle 1966; Ross and Cochran 1966). Smittle (1966) recommended the separation of adult breeder females from hatching nymphs to facilitate rearing according to generations and age. Regular changing of harborage

and cleaning of containers is required to prevent disease and build up of odor in rearing rooms (Smittle 1966). Smittle (1966) recommended the use of restraining barriers on tables when colonization procedures are carried out to prevent escapes.

Development Times. Under the conditions described by Smittle (1966) 26.7 ± .5° C and 50 ± 10% relative humidity development from hatch to adult required five to seven weeks. Mallis (1969) reported that 50 to 60 days were required for maturation at 26.7 ± .5°C and 40% relative humidity. Smittle (1966) indicated that a period of a year or more may be required to build up a laboratory colony of sufficient size for laboratory experiments. Ross (1976) indicated development times at 53.9 ± 2.1 days (42-65) for completion of nymphal development at room temperature (24 ± 2°C) with uncontrolled humidity. Hatching of successive oothecae occurred at monthly intervals. Grothaus *et al.* (1981bc) reported total development times for nymphs at 43 days (26.7°C). Time required for adult females to develop the first ootheca was 29 days and subsequent oothecae were deposited at 23 day intervals. Similar data with slight variation was reported by Guthrie and Tyndall (1968), Cornwell (1968), and Ishii (1970).

METHODS AND MATERIALS

MASS REARING PROCEDURES

BASIC TECHNIQUES

Rearing techniques initially involved maintaining breeder stocks in quart jars fitted with 258 cm^2 of screen wire harborage. Later one-gallon battery jars with 1290 cm^2 of screen were used. Temperature was maintained at 24 ± 2°C and humidity was uncontrolled. Dog food pellets and four dram water vials stoppered with small sponges were provided as needed. It became clear that in order to handle large numbers of breeder stock a more efficient water delivery system was needed. This objective was met by modifying a 15 dram snap-cap, clear plastic vial by cutting a hole in the center of the cap to accommodate a 12 mm. (O.D.) glass tube four inches in length. The glass tube was firmly packed with absorbent cotton. A small hole was punched in the edge of the lid with a teasing needle to ventilate the system. This type of delivery system was capable of transferring the entire capacity of the vial to the end of the cotton tube. Two 15 dram vials were used to provide water for a 7-10 day period in one-gallon battery jars, and a 3-4 week period in quart rearing containers. The tubes required new cotton after two to three months of use.

Eight to ten breeder females were kept per quart jar at first but later as stocks increased, one-gallon breeder jars were used with 50-100 gravid females per jar. This latter number was arbitrarily

chosen because it kept the number of hatching progeny well below the carrying capacity of the jar as determined by Ross (1975a). Breeder females were removed following hatch of successive oothecae in order to keep nymphs separated according to age and to reduce the incidence of disease. This was accomplished by shaking the contents of the breeder jar onto a U.S. Standard No. 14 sieve and allowing the small numphs to migrate to the receiver pan. Hatch of the first oothecae occurred at 4-5 weeks with offspring from subsequent oothecae hatching in 3-1/2 to 4-1/2 weeks. Breeder females were discarded after hatch of the third oothecae.

To facilitate sexing of the breeder stock, two U.S. standard sieves, Nos. 7 and 8, were employed to sex the 5th - 6th instar nymphs. Late instar females were retained by the No. 7 sieve while late instar male nymphs passed through the No. 7 sieve but were retained by the No. 8 sieve. Nymphs passing through the No. 8 sieve were primarily 3rd - 4th instar but with some 5th instar. These were retained in clean battery jars for later sorting. This sexing technique provided approximately 90% separation which aided in synchronizing development and in phenotyping the breeder stock.

BACKCROSS SYSTEM

The backcross system used for mass rearing semi-sterile males for release utilized the linkage relationship of the T(8;9) translocation and the recessive deleterious gene sty (Ross 1975a). Males homozygous for sty were mated with females which were heterozygous for both the translocation and sty. Offspring gave 50% normal and 50% sty

phenotypes. Male offspring showing a normal phenotype were identified and selected for release under a dissecting microscope during CO_2 anesthesia. Newly-emerged (1 to 3 days) males with stumpy phenotype and females with normal phenotype were placed into new breeder jars for continued backcrossing. Females with stumpy phenotype were discarded.

Even though the cross-over rate was quite low, breeder-stock oothecae were still screened to assure that the translocation stocks remained pure. This was accomplished during the third week after mating. The breeder females were anesthesized and the egg cases examined under a microscope for evidence of the translocation. If 25% to 50% of embryo compartments were filled with whitish material (embryos which died in early development) the female was considered to be heterozygous for the T(8;9) translocation. Females bearing normal appearing oothecae were discarded.

Mass Rearing Production Rate. Breeder stocks were gradually increased over a 14-month period due to the larger releases required for F_2 groups maturing in the experimental populations during the months of August, September, October, and November 1976. About 10,000 semi-sterile males per month were required for release. This demand necessitated the maturing of 40,000 plus nymphs per month reared in approximately thirty one-gallon battery jars.

POPULATION STUDIES

PRELIMINARY EXPERIMENTAL POPULATIONS

Experimental populations were established from five VPI wild-type German cockroach females mated with males heterozygous for both the T(8;9) translocation and the autosomal recessive deleterious gene, stumpy (sty). Parental females (P_1) were held in quart jars fitted with approximately 258 cm^2 of screen harborage with water and standard dog food pellets provided as needed. Upon hatching of the first F_1 groups the populations were transferred to one-gallon battery jars with approximately 1290 cm^2 of screen harborage.

Population censuses were made at approximately monthly intervals. Groups were separated according to size, sex, and phenotype where appropriate. Criteria used for grouping nymphal instars were numbers of cercal segments (Murray 1967) in instars 4, 5, and 6 and size as well as date of hatch for smaller instars (1, 2, 3). Three size classifications were used--small, (1st and 2nd instars), medium (3rd and 4th instars), and large (5th and 6th instars). The census was accomplished in a similar manner to that described by Ross (1975a). A few cockroaches were placed in individual quart jars allowing adults and small nymphs to be sight counted without use of anesthetization. Medium and large nymphs were anesthetized briefly with CO_2 to facilitate sexing and phenotyping of F_2 groups. Egg cases of each group of females were examined microscopically (20X) as described above or just following hatch. Females with immature egg cases were retained until classification was complete before returning them to

the populations. The classification followed was that used by Ross (1975a) to indicate the types of matings which occurred. The criteria were as follows:

Normal - normal embryos in most or all compartments

Semisterile - about half of the compartments with dead embryos

Sterile - less than ten viable embryos or compartments filled with whitish material accompanied by irregular air spaces at one end.

The latter is characteristic of matings between T(8;9) heterozygotes (Cochran and Ross 1974).

Releases of male nymphs heterozygous for T(8;9) and sty were made to match oncoming nymphal groups in the population. A 6:1 effective ratio of release males to non-translocation bearing males in the experimental populations was maintained until the numbers became too large to be supported by the available translocation stocks.

Control Population. A control population was established with five VPI wild-type females mated to VPI males. This was followed by censuses which approximated those of the experimental populations in regularity and detail.

PRIMARY EXPERIMENTAL POPULATIONS

Subdivision of Experimental Populations. During the course of preliminary studies, it was discovered that maintenance of entire populations in single containers was too cumbersome. The overlapping progeny groups, which are inherent in this species, and eventual crowding which occurred, in addition to the time-consuming nature of the

censusing procedure, precluded following more than one or two populations at a time. This problem was resolved by resorting to the progeny group method reported by Ross (1976). In this technique, individual groups were maintained in separate containers. F_1 groups were separated from P_1 females immediately upon hatching. They were counted and placed in one-gallon battery jars. Individual F_2 groups were separated from the F_1 groups in a similar manner and held in one-gallon battery jars. Since the first three oothecae were known to be the most productive of the average of five viable oothecae (Willis *et al*. 1958; Ueda *et al*. 1969), the population sampling employed in this study included only the progeny groups from the first three oothecae of P_1 and F_1 groups, respectively. In F_2 groups the progeny of the first oothecae were counted and the progeny group then terminated. This approach was elected in order to conduct additional population replicates.

A total of five experimental population replicates were begun as previously described with five females mated to T+/+*sty* males at approximately 4-6 week intervals. Releases of semi-sterile males into the F_1 and F_2 groups were accomplished for the progeny from the first three oothecae. Two control populations were also begun and followed in a similar manner to the experimental populations using the progeny group method.

Population censusing was greatly simplified by following separate progeny groups. The censusing interval was very close to that employed in preliminary studies. The techniques for data collection, however, were greatly improved by employing two mechanical devices. The

newly-hatched nymphs were separated from adults by gently depositing all the individuals from a given jar onto a U.S. Standard (No. 14) sieve. Within 3-5 minutes, the newly-hatched nymphs migrated through the sieve to the receiver pan. Adults were then transferred to a clean battery jar, anesthetized (CO_2) and counted using a stereo microscope. Secondly, newly-hatched nymphs were counted individually by use of a vacuum-powered aspiration equipped with a small nozzle tip constructed from flexible Tygon^R tubing.

F_1 data included types of oothecae, number of nymphs hatching, numbers and sexes of late instars, and mortality. These data were used to determine the number of semi-sterile males needed for release into experimental populations.

Data collected on F_2 progeny groups included initial hatch, counts of nymphs according to phenotype, and sex at 5th and 6th instar, types of oothecae and mortality data estimated from number of live individuals in subsequent counts. When hatching of the first oothecae was complete, F_2 groups were discarded.

F_2 females were anesthetized with CO_2 and oothecae were examined for mating type. The same classification scheme for oothecae was used as previously described for the preliminary study except for the addition of the stumpy oothecae as found in the F_2 on sty sty females which are recognized by the noticeably narrower shape and usually unhatched condition after deposition. Oothecae already deposited were collected by mouth aspirator after being sifted from debris. This was necessary to avoid possible damage from the power aspirator.

The ratio of release was approximately eight semi-sterile males to one non-translocation bearing male (8T/+:1+/+) for releases into F_1 groups and five semi-sterile males: 1 non-translocation male (5T/+:1+/+) in the releases into F_2 groups. In addition, the F_2 males and males released into the F_2 progeny groups were reduced to a low number one month after the release data by separating the males and females using a U.S. Standard No. 7 and 8 sieve as described previously. This tended to reduce density and the possible effects of crowding and the disease problem associated with it. To produce a similar final density in control groups, F_2 males were removed as described above.

LINKAGE STUDIES

Close linkage of the recessive deleterious trait *sty* with T(8;9) was suggested by Ross (1975b). Procedures followed in linkage studies of T(8;9) and *sty* are similar to those described by Ross and Cochran (1966), Cochran and Ross (1969), and Ross (1975b).

T+/+STY FEMALES

German cockroach females heterozygous for both T(8;9) and *sty* were backcrossed to homozygous *sty* males. Oothecae were examined for the characteristic 25% to 50% lethality of embryos to determine the presence of the translocation. Females carrying oothecae suspected of being normal were held singly in quart jars for hatching of the oothecae. Hatch data were recorded and the nymphs retained until 20-40 days of age. The males were then scored according to phenotype and examined cytologically for the presence or absence of the translocation.

To obtain chromosome preparations, testicular tissues were squashed in accordance with procedures described by Cochran and Ross (1969). A dorsal incision was made. The testes were removed one at a time and placed on separate slides in a drop of 15% acetic acid. Fat body adhering to the testes was removed. Acetolacticorcein stain (15% acetic acid, 15% lactic acid, and 2% orcein) was applied to the tissue for 5 to 10 minutes. The tissue was then rinsed with 15% acetic acid and suspended in a drop of 15% acetic acid. A cover glass was placed over the tissue and any excess acetic acid removed. The slide was then carefully wrapped in paper toweling and steady, firm pressure was applied to the back of the slide using the thumb in a back and forth motion. Slides were examined with a Zeiss phase-contrast microscope. The presence of the translocation was confirmed by a ring configuration or V-shaped (zig-zag) configuration in metaphase I and early anaphase I cells (Cochran and Ross 1969, 1974). At least ten cells of appropriate stages of development were examined per slide.

T+/+STY MALES

The reciprocal cross of males heterozygous for T(8;9) and *sty* to homozygous *sty* females was conducted. Data were difficult to obtain due to the nearly complete sterility of *sty*/*sty* females. However, a few progeny were obtained in mass matings. Oothecae were also examined but data were limited by low viability. Male offspring 20 to 40 days of age were scored to phenotype and examined cytologically as described above.

LINKAGE MEASUREMENT

Linkage was measured as percent recombination by cytologically confirming crossovers in cells prepared from the developing testes of immature males. In addition, crossing over was also estimated by observing the number of normal appearing oothecae from backcrosses involving sty/sty males with T+/+sty females and T+/++sty males with sty/sty females.

REPRODUCTIVE BEHAVIOR STUDIES

MATING COMPETITIVENESS

Mating competitiveness was evaluated by four methods. The first method involved 5 to 10 replicates each in which five VPI wild-type males and 10 (2:1), 15 (3:1) and 30 (6:1) heterozygote males respectively were placed in one-quart breeder jars with five VPI wild-type females. Only males 3-6 days postemergence and females 4-6 days postemergence were used because according to Ueda *et al*. (1969), this age is the most active for mating. Oothecae were observed three weeks following mating. Data were collected by oothecal type in accordance with the classification described by Ross (1974). Hatch data were also recorded in these studies.

The second method involved conducting one-to-one competition studies using two males (each a different type) with one female in a quart-jar. Three types of males and three types of females included in the population studies were evaluated in this manner. Fifty or more replicates of the following combinations were set up in individual quart-jar breeders:

T+/+*sty* ♂ vs VPI ♂ X VPI ♀
T+/+*sty* ♂ vs *sty*/*sty* ♂ X VPI ♀
T+/+*sty* ♂ vs VPI ♂ X T+/+*sty* ♀
T+/+*sty* ♂ vs *sty*/*sty* ♂ X T+/+*sty* ♀
T+/+*sty* ♂ vs VPI ♂ X *sty*/*sty* ♀
T+/+*sty* ♂ vs *sty*/*sty* ♂ X *sty*/*sty* ♀
sty/*sty* ♂ vs VPI ♂ X T+/+*sty* ♀

Special care was taken to use males and females of the same age--3-6 days postemergence. In addition, the test insects had been reared under similar conditions of density and in the same type of breeder. In individual test replicates competing males of the same type originated from the same breeder jar. Data were evaluated on the basis of oothecal classifications except for the last one listed in which the phenotype of progeny was used to determine the type of mating which occurred.

The third method used the results of oothecae data and F_2 phenotypes in the experimental population studies to evaluate the competitiveness of males under population conditions.

The fourth method evaluated male competitiveness on a similar basis as laboratory tests reported for the *Diptera* (Fried, 1971; Seawright *et al*. 1975b, 1976). In these tests, 100 T+/+*sty* males, 100 VPI males and 100 VPI females of approximately similar age (3-6 days postemergence) were placed in a one-gallon battery jar breeder with screen, water, and dog food as previously described. The type of oothecae were again used as the criteria for determining mating type, and progeny were counted. The number of replicates was limited to three due to poor availability of breeder stock of similar age.

REPRODUCTIVE POTENTIAL OF INDIVIDUAL GENOTYPES

Individual females heterozygous for T(8;9) and sty were held in individual quart-size jars after mating to sty males. Data collected included total hatch, number of embryo compartments per oothecae, number of non-viable embryos, total number of oothecae, and longevity. Progeny were removed and classified by phenotype for use in the back-cross system and for release.

Individual females homozygous for sty were also held in separate containers. Three groups of 24 females were mated to VPI wild-type males, semi-sterile heterozygote males, and homozygous sty males. Data included hatch, number of embryo compartments, and number of non-viable embryos. These females were followed through the deposition of the third oothecae and then discarded.

During selection of egg cases for breeder stock an occasional sty female was found which had what appeared to be a fully viable egg case. These females were held in individual quart breeder jars. Hatch and oothecal data were collected. Females with nearly 100% hatch were kept for evaluation of subsequent oothecae. F_1 and F_2 progeny produced from these females were allowed to inbreed to select for sty females with higher than normal hatch characteristics.

Reproductive potential of males was evaluated by placing semi-sterile males and VPI males individually into quart-sized breeder jars containing ten VPI females. The number of effective and partially effective matings was recorded by observing the oothecae for viable embryos approximately three weeks after mating and again after hatch to check for emergence. An effective mating was defined as one which

resulted in hatching of the ootheca. A partially effective mating was one which produced viable embryos too few in number to result in hatching of the ootheca, but still enough to prove that a mating had indeed occurred.

Individual semi-sterile males, VPI males and sty males were placed in separate jars that included five females each of the three types of females known to be present in the populations under study. The purpose of this study was to measure male mating capacity and possible tendencies toward assortative mating. All individual adults used in the above tests were 3-6 days postemergence in age (Ueda *et al.* 1969).

MUTANT STUDIES

During the sorting and selection of breeder stock two suspected wing mutants were seen in both males and females. These involved the right or left forewing being shorter by about 25% than normal wing length. Males showing this aberration were crossed with VPI females. F_1 progeny were scored and then discarded. Two teneral females (probably unmated) with right wing shorter were mated with males of the same phenotype. Off-spring of this cross were scored and discarded.

STATISTICAL METHODS

Population data and mating preference data were subjected to chi-square cross connected contingency table analysis (Fienberg 1977) conducted by Dr. S. K. Lee and Miss Jill Stewart of the Statistics Department, VPI & SU. Other data were analyzed by standard error or

simple chi-square analyses as appropriate.

RESULTS

PRELIMINARY EXPERIMENTS

Preliminary experiments in which T(8;9)+/+sty males were repeatedly released into populations of the German cockroach were conducted from December 1974 to August 1975. The progeny groups originating from the P_1 females were all kept together in one container, thus giving a freely interbreeding population. Table 1 gives a theoretical picture of population growth and structure for the first eight months of this type of experiment. Results of counts from preliminary experimental populations A and B are shown in Table 2.

As seen in Figures 1 and 2, experimental population size was approximately 50% that of the later control population (data presented in Table 5) until month four when the F_2 generation began to appear. Similar results were reported by Ross (1975a, 1976). From month four to month seven, experimental populations were approximately 25% of the control in size indicating that most matings in the population were by translocation bearing males. F_3 generation progeny groups which were estimated to appear in month seven, heralded a substantial increase in population numbers. At this time, experimental populations were about 15% as large as the control. Control data used for comparison are from later data obtained by the "progeny group method" (Table 5).

PRELIMINARY EXPERIMENTAL POPULATIONS

The different progeny groups arising in experimental populations were easily traced as to ancestry until F_2 groups began to appear.

Table 1. Hatch and origin of progeny groups in a laboratory population of the German cockroach.

Month of Hatch	Progeny Group[a]				
1	F_1-1[b]				
2		F_1-2			
3			F_1-3		
4	F_2(1-1)[c]			F_1-4	
5	F_2(1-2)	F_2(2-1)			F_1-5
6	F_2(1-3)	F_2(2-2)	F_2(3-1)		
7	F_3(1-1-1)[d]	F_2(2-3)	F_2(3-2)	F_2(4-1)	
	F_2(1-4)				
8	F_3(1-1-2)	F_3(2-1-1)	F_2(3-3)		
	F_2(1-5)	F_2(2-4)			

[a]Groups are classified according to the F_1 progeny group from which each arose.

[b]F_1-1 through F_1-5 represent the progeny from the successive oothecae of the parental groups.

[c]F_2(1-1) through F_2(1-5) are the progeny groups from successive oothecae of the F_1-1.

[d]F_3(1-1-1) and F_3(1-1-2) are progeny from the first and second oothecae of the F_2(1-1).

Table 2. Population[a] growth and structure in preliminary experiments using T(8;9)+/+sty males to reduce population growth in *B. germanica*.

Age[b]	Population	Month of Growth					
		1	2	3	4	5	6
Adult	A	10	8	82	126	164	776
	B	10	10	72	140	194	502
Large	A				43	634	327
	B				0	22	441
Medium	A		89	44	0	117	410
	B		76	17	22	300	437
Small	A	91	54	47	639	959	951
	B	77	53	53	323	928	1407
Total	A	101	149	173	808	1444	2342
	B	87	139	172	528	1874	2787

[a]All progeny groups were kept together in the same containers.

[b]Age is indicated by large for instars 5-6, medium for instars 3-4, and small (instars 1-2) nymphs.

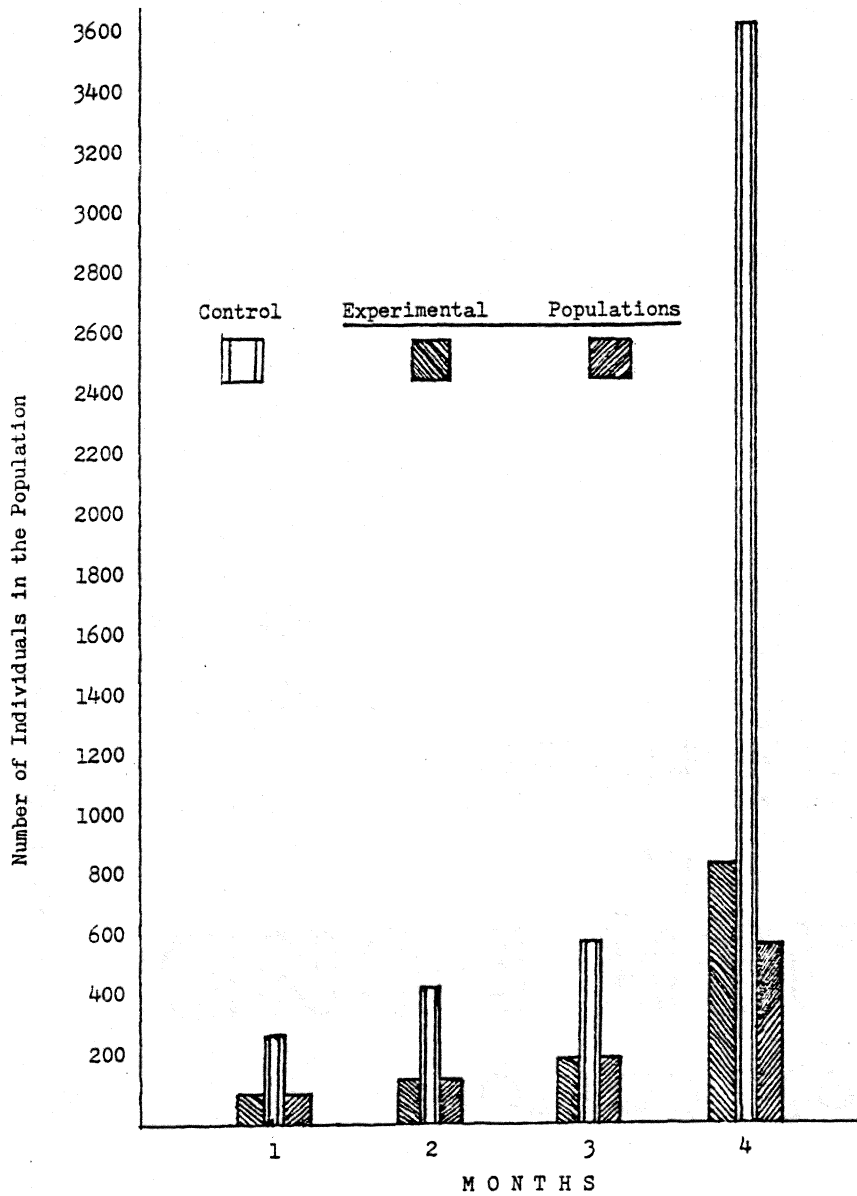

Figure 1. Comparison of population growth between T(8;9)+/+*sty* preliminary experimental populations and the wild-type control during the first four months in experiments with *B. germanica*.

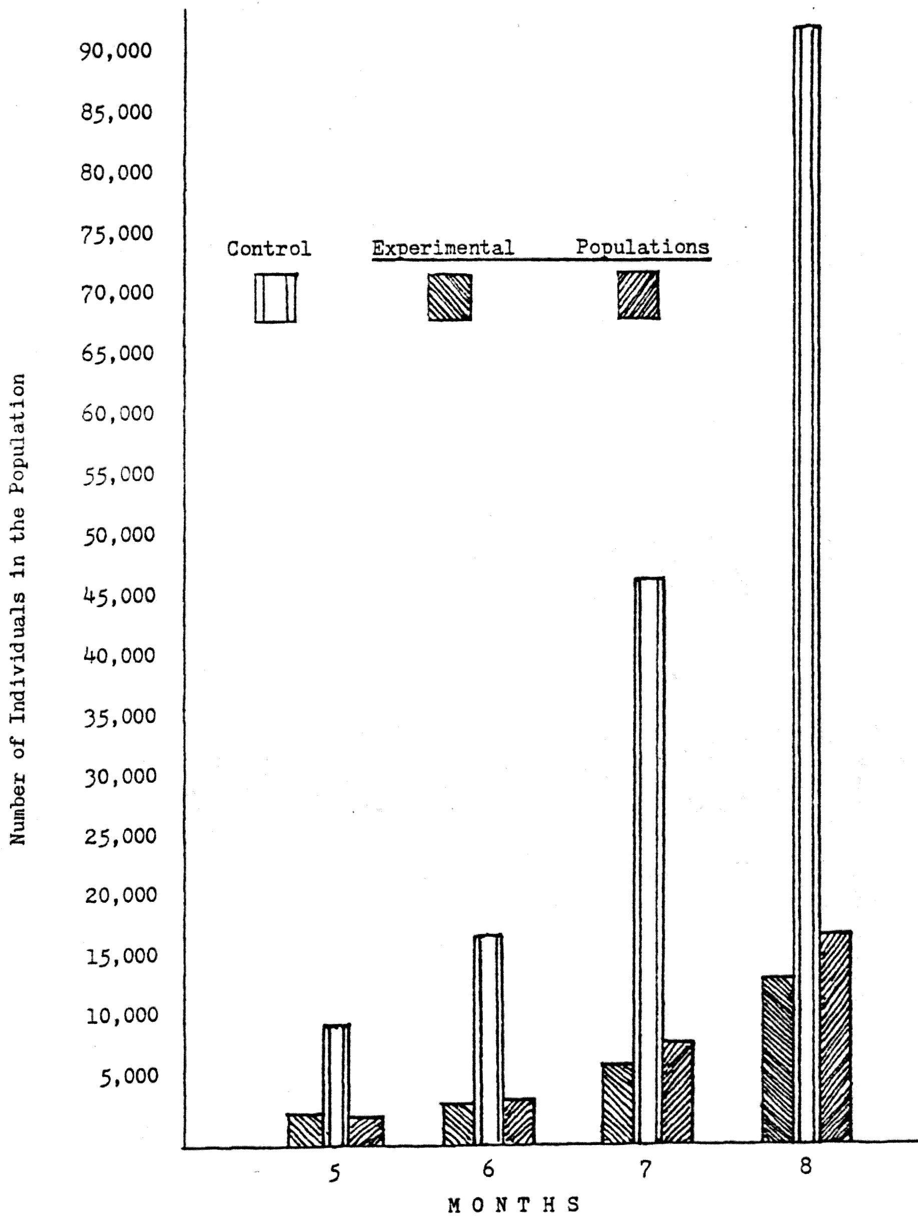

Figure 2. Comparison of population growth between T+/+sty preliminary experimental populations and the wild-type control from month five to eight in experiments with B. germanica. (Data for months 7 and 8 projected from earlier hatch.)

As F_2 groups began to hatch, it became infeasible to determine ancestry. For example (Table 1), the small nymph counts during the fifth month census include the following progeny groups: F_2(2-1), F_2(1-2), and F_1-5.

Population structure through time was essentially as predicted by Ross (1975a) with all stages being present by the third month (Table 2). Exponential increase in population size occurred at month four when the F_2 generation hatched and as would be predicted to occur in month seven when the F_3 generation would be expected to hatch (Figures 1 and 2).

Results of the releases of T+/+sty males into populations A and B are given in Table 3. The number of wild-type matings point toward good competitiveness of released males. The types of crosses and matings which occurred in these studies are described in Table 4 and Figures 3 and 4.

VPI WILD-TYPE (+/+) EXPERIMENT

Progeny groups from one wild-type experiment are presented in Table 5. All groups hatching from the first 3 oothecae of parental (P_1) and F_1 groups and the first ootheca only of F_2 groups are included. The first two oothecae of F_1 females were similar in productivity with mean progeny per female of 31.07 ± .33 while the third egg case was somewhat less at 29.3 ± 1.2 progeny/female. F_1 female mortality estimated at 10% contributed to the reduction. The first oothecae of the 5 parental females showed a higher number of progeny (42.0 ± 1) per female than the expected 40.1 ± 1 for VPI wild-type matings reported by Ross (1971a). This occurrence was aided by the fact

Table 3. Preliminary results of releasing T(8;9)+/+sty males into two populations of *Blattella germanica* (L.).

Progeny Group[a]	Population	No. Released	Approx. Ratio[b] T/+ : +/+	Mating Types[c]					
				I	(I+II)	II	III	IV	V
F_1-1	A	135	7:1	2	35	33	4	-	-
	B	72	6:1	0	27	27	0	-	-
F_1-2	A	39	6:1	12	19	7	1	-	-
	B	114	6:1	8	24	16	0	-	-
F_1-3	A	84	6:1	11	23	12	0	-	-
	B	99	6:1	11	42	31	4	-	-
F_2(1-1)	A	450	2:1	7	116	109	28	73	66
	B	199	2:1	26	72	46	10	34	29

[a]Progeny groups classified as to origin relating to successive parental oothecae.

[b]The ratio is the estimated total translocation-bearing males to non-translocation bearing males in the population.

[c]Mating types described in Table 4.

Table 4. Classification of mating types by examining oothecal characteristics in developing *Blattella germanica* populations after releases of T(8;9)sty males.

Mating types/Class	I		II		III		IV		V	
Phenotypes/ Ootheca class	wildtype sterile[a]		wildtype semi-sterile[b]		wildtype non-translocation[c]		sty-translocation[d]		sty non-translocation[e]	
	females	males	females	males	females	males	females	males	females	males
Genotypes Mating in F_1	T+/++	T+/++	T+/++	++/+sty	++/+sty	++/+sty				
		T+/+sty	++/+sty	T+/++						
				T+/+sty						
Genotypes Mating in F_2	T+/++	T+/++	T+/++	++/+sty	++/+sty	++/+sty	++/sty sty	T+/++	++/sty sty	++/+sty
		T+/+sty		++/sty sty		++/sty sty		T+/+sty		++/sty sty
	T+/+sty	T+/++		++/++		++/++				++/++
		T+/+sty	T+/+sty	++/+sty	++/++	++/+sty				
				++/sty sty		++/sty sty				
				++/++		++/++				
			++/+sty	T+/++						
				T+/+sty						
			++/++	T+/++						
				T+/+sty						

[a]Mating between translocation heterozygotes (T/+ X T/+) with wildtype phenotype: Normal sized ootheca with less than 10 developed embryos typical of T(8;9) intercrosses.

[b]Mating between females with wildtype phenotype which resulted in approximately one-half of the embryos dead (T/+ X +/+).

[c]Mating between non-translocation bearing females with wildtype phenotype and a non-translocation bearing male. Normal size ootheca with the usual number of developed embryos is produced.

[d]Mating of females with stumpy (sty) phenotype with a translocation bearing male. Ootheca noticeably more slender than wildtype with striped appearance is produced.

[e]Mating of females with stumpy (sty) phenotype with a non-translocation bearing male. Ootheca produced is noticeably more slender without striped appearance.

P ++/++ X T+/+sty

Gametes formed (++) (++) (T+) (+sty)

F_1

♂ / ♀	(T+)	(+sty)
(++)	T+/++	++/+sty
(++)	T+/++	++/+sty

F_2 T+/+sty ♂, T+/++ ♂, ++/+sty ♂ X T+/++ ♀, ++/+sty ♀

♂ / ♀	(T+)	(+sty)	(++)
(T+)	T+/T+	T+/+sty	T+/++
(+sty)	T+/+sty	+sty/+sty	++/+sty
(++)	T+/++	++/+sty	++/++

Figure 3. Diagram of the crosses involved in B. germanica in T(8;9)+/+sty experiments.

$$F_1 \quad \hat{f}\,\text{♂}_a C \times \hat{f}\,\text{♀}_a + \hat{f}\,\text{♂}_a C \times \hat{f}\,\text{♀}_b + \hat{f}\,\text{♂}_b C \times \hat{f}\,\text{♀}_a +$$
$$\hat{f}\,\text{♂}_b C \times \hat{f}\,\text{♀}_b = 1$$

$$F_2 \quad \hat{f}\,\text{♂}_a C \times \hat{f}\,\text{♀}_a + \hat{f}\,\text{♂}_a C \times \hat{f}\,\text{♀}_b + \hat{f}\,\text{♂}_a C \times \hat{f}\,\text{♀}_c +$$
$$\hat{f}\,\text{♂}_a C \times \hat{f}\,\text{♀}_d + \hat{f}\,\text{♂}_a C \times \hat{f}\,\text{♀}_e + \hat{f}\,\text{♂}_b C \times \hat{f}\,\text{♀}_a +$$
$$\hat{f}\,\text{♂}_b C \times \hat{f}\,\text{♀}_b + \hat{f}\,\text{♂}_b C \times \hat{f}\,\text{♀}_c + \hat{f}\,\text{♂}_b C \times \hat{f}\,\text{♀}_d +$$
$$\hat{f}\,\text{♂}_b C \times \hat{f}\,\text{♀}_e + \hat{f}\,\text{♂}_c C \times \hat{f}\,\text{♀}_a + \hat{f}\,\text{♂}_c C \times \hat{f}\,\text{♀}_b +$$
$$\hat{f}\,\text{♂}_c C \times \hat{f}\,\text{♀}_c + \hat{f}\,\text{♂}_c C \times \hat{f}\,\text{♀}_d + \hat{f}\,\text{♂}_c C \times \hat{f}\,\text{♀}_e +$$
$$\hat{f}\,\text{♂}_d C \times \hat{f}\,\text{♀}_a + \hat{f}\,\text{♂}_d C \times \hat{f}\,\text{♀}_b + \hat{f}\,\text{♂}_d C \times \hat{f}\,\text{♀}_c +$$
$$\hat{f}\,\text{♂}_d C \times \hat{f}\,\text{♀}_d + \hat{f}\,\text{♂}_d C \times \hat{f}\,\text{♀}_e + \hat{f}\,\text{♂}_e C \times \hat{f}\,\text{♀}_a +$$
$$\hat{f}\,\text{♂}_e C \times \hat{f}\,\text{♀}_b + \hat{f}\,\text{♂}_e C \times \hat{f}\,\text{♀}_c + \hat{f}\,\text{♂}_e C \times \hat{f}\,\text{♀}_d +$$
$$\hat{f}\,\text{♂}_e C \times \hat{f}\,\text{♀}_e = 1$$

where

$\hat{f}$ = genotypic frequency

$_a$ = T+/+sty

$_b$ = T+/++

$_c$ = ++/+sty

$_d$ = ++/++

$_e$ = +sty/+sty

C = mating competitiveness = 1

Figure 4. The algebraic expressions illustrating the interaction of genotypic frequencies and mating competitiveness

Table 5. Progeny groups and their numbers from experiments with VPI wild-type (+/+) *B. germanica*.

F_1 Progeny (Group and No.)	No. Progeny/F_1 Female	F_2 Progeny (Group and No.)	No. Progeny/F_2 Female	F_3 Progeny (Group[a] and No.)
		F_2(1-1): 3078	19.59	F_3(1-1-1): 26466
F_1-1: 210	30.3 ± .87	F_2(1-2): 2894	14.52	F_3(1-2-1): 17860
		F_2(1-3): 2642	15.04	F_3(1-3-1): 16890
		F_2(2-1): 2880	17.903	F_3(2-1-1): 21913
F_1-2: 201	31.28± .52	F_2(2-2): 2874	19.904	F_3(2-2-1): 24323
		F_2(2-3): 2572	18.161	F_3(2-3-1): 19850
		F_2(3-1): 2632	17.696	F_3(3-1-1): 21837
F_1-3: 187	29.3 ±1.2	F_2(3-2): 2556	15.539	F_3(3-2-1): 16891
		F_2(3-3): 2042	17.99	F_3(3-3-1): 15615

[a]Groups from 1st egg cases only and estimated from counts of ca. 15% of each group.

that the parentals were selected for higher numbers of F_1 offspring from a group of 10 jars set up with 5 VPI females each. The first three F_2 progeny groups averaged 14X, 14X, and 12X the respective parental F_1 groups while the F_3 groups were approximately 8X the respective F_2 parental group. F_3 groups were reared at densities of 500-600 per jar to simulate densities of F_2 progeny groups of the experimental populations. Productivity of F_2 females averaged 17.37 ± .64 progeny/female under these conditions.

Since the first three egg cases were known to be significantly more productive than later egg cases, only the first three were followed for parental and F_1 groups. The F_2 groups were limited to 9 first egg case counts of F_3 progeny as these would be compared with 9 F_3 groups from experimental populations.

Isolated groups developed synchronously, as reported previously (Ross 1976) with successive hatch occurring at approximate monthly intervals during a period of 4-6 days. Population growth and structure, reconstructed with data from appropriate progeny groups, are presented in Table 6. As reported in previous studies (Ross 1974, 1976) population structure remains simple for the first 6 weeks with about equal numbers of the various stages achieved at 3 months. The onset of F_2 hatch in month 4 and F_3 hatch in month 7 greatly increased growth rate and shifted population structure toward the smaller stages. F_3 data are based on partial counts (15%) of the respective F_3 groups. Data for the first F_3 group F_3(1-1-1) were used to estimate hatch from the F_3(1-1-2) which was not measured.

Table 6. Population[a] growth and structure from an experiment with VPI wild-type (+/+) *B. germanica*.

Age[b]	Month of Growth							
	1	2	3	4	5	6	7	8
Ad	10	10	204	386	558	3260	8100	15260
Lg Md		194	183	171	2702	4840	6819	26855[c]
Sm	210	201	187	3078	5774	8148	31594[c]	50421[c]
Total	220	405	574	3635	9034	16248	46513	92536

[a]Population reconstructed from isolated progeny groups.

[b]Age is indicated by "Ad" for adult, "Lg" for large (instars 5-6), "Md" for medium (instars 3-4), and "Sm" for small (instars 1-2) nymphs. Numbers of adults are estimated as 2X the number of adult females.

[c]Includes F_3 groups which were estimated using counts of hatch from approx. 15% of the respective F_2 groups.

PRIMARY EXPERIMENTAL POPULATIONS

The primary experiments were conducted from December 1975 to March 1977. Basic biological parameters (longevity, fecundity, life cycle, etc.) previously described for preliminary results and by Ross (1976) also apply for these experiments. Four or five experimental populations gave F_3 results from nine F_2 groups while lack of time prevented the completion of three F_3 progeny groups in the fifth experiment. Overall mortality ranged from 10 to 20% with some variation being caused by sporadic bacterial infection. Introduction of 800-1000 T(8;9)+/+*sty* males into F_2 progeny groups tended to promote bacterial infections and retarded development of the maturing F_2 nymphs. The bacterial disease affected few females before they deposited the first ootheca. Experimental populations were similar in results with minor variation. Populations A and C are presented in detail to provide examples of individual variation, followed by the overall summary data.

EXPERIMENT A

Experiment A ran from December 1975 until October 1976. The F_1 and F_2 progeny counts and the results of releasing T+/+*sty* males into the respective F_1-1 groups are presented in Table 7. The F_2 groups associated with F_1-1 females are appreciably larger due in part to the lower release ratio of 6:1 which resulted in a greater percentage of normal matings than for the other F_1 groups. The larger number of F_1-1 females also contributed to higher F_2 progeny counts for the F_1-1 group. Since the parental (P_1) females were all mated to T(8;9)+/+*sty* males it was assumed that the F_1 offspring were equally divided

Table 7. Summary of T(8;9)+/+*sty* male releases into experiment A, and their effects on progeny groups.

F_1 Progeny Group and No.	No. T+/+*sty* Released	Approx. Ratio of T/+♂:+/+ [a]	No. Matings (= No. Adult ♀♀)	% +/+ Matings	F_2 Progeny (Group and No.)
F_1-1:101	125	6:1	52	7.6%	F_2(1-1):834 F_2(1-2):826 F_2(1-3):814
F_1-2: 85	175	8:1	46	4.3%	F_2(2-1):607 F_2(2-2):629 F_2(2-3):689
F_1-3: 96	175	8:1	47	6.3%	F_2(3-1):693 F_2(3-2):642 F_2(3-3):699

[a]It was assumed that 1/4 of each progeny group was T/+ males.

between T/+ and +/+ genotypes. If either introduced or sibling T/+ males mated with F_1 females, about equal numbers of the matings would involve T/+ X +/+ and sterile T/+ X T/+. The frequency of the reciprocal cross of T/+ X +/+ VPI males would be indicative of the competitiveness as would the frequency of matings between wild-type. Both of these types of matings are classified as "translocation-type" matings. Expected progeny per translocation-type mating were estimated as 12.3 or one-half the average hatch of the T/+ X +/+ reported by Cochran and Ross (1974). The following formula was used to calculate the number of progeny per "translocation-type" mating (Ross, 1976):

$$\text{No. of progeny/translocation-type mating} = \frac{F_2 \text{ progeny group} - (\text{no. +/+ matings X } 31.3)}{\text{No. of translocation-type matings}}$$

The progeny per translocation-type mating for the F_1 groups of population A averaged 14.57 ± .22, 13.6 ± .70, and 12.42 ± .43 for the F_1-1, F_1-2, and F_1-3, respectively. Only the F_1-1 was significantly different from the previous estimate of 12.3 (Cochran and Ross 1974). Table 8 presents the data for observed egg case classifications and F_2 progeny analyzed by use of chi-square. The total number of translocation matings was very close to the number expected for all three F_1 groups. The number of non-translocation matings was also very close to the predicted number. A consistent feature of these F_1 data and others to be presented is a higher than expected number of oothecae classified as the T/+ X +/+ mating type.

The deleterious recessive gene (<u>sty</u>) was assumed to be at a frequency of 0.25 in the F_1 progeny because all F_1 females were mated

Table 8. Analysis of oothecae and F_2 progeny numbers from T(8;9)+/+*sty* experiment A with the German cockroach.

Progeny Group		Mating Types[a] I	(I + II)	II	III	χ^2 [b]	No. F_2 Progeny	χ^2 [c]
F_1-1	E_i [d]	23	50	27	4	5.34	789.4	4.22
	O_i [e]	14	48	34	4		830	
F_1-2	E_i	21	44	23	2	3.28	628.4	.729
	O_i	15	44	29	2		618	
F_1-3	E_i	21	45	24	3	5.42	684.3	2.73
	O_i	13	42	29	5		667.5	

[a] Mating types described in Table 4.

[b] Chi square for differences in ootheca classes (2 degrees of freedom).

[c] Chi square for differences in F_2 progeny numbers (1 degree of freedom).

[d] Expected numbers based on normal probability and equal competitiveness of males. (see appendix for explanation.)

[e] Observed numbers: F_2 progeny average of first 2 oothecae.

to males which were supposed to be heterozygous for sty with close linkage to the T(8;9) locus on chromosome 9 (Ross 1973). On this basis it was assumed that one-half of the F_1 progeny would be heterozygous for sty while the other half would be heterozygous for T(8;9) (see Figure 3). Males heterozygous for T(8;9) and sty were released into the maturing F_1 groups at an approximate ratio of 8T+:1++. The F_2 progeny produced were classified to phenotype in the 5th-6th instar. Phenotypic data are presented in Table 9.

The frequencies of progeny reported as homozygous for sty are consistently higher than would be predicted from a 3 wt:1 sty segregation which is expected in this mating scheme. Difficulty in classifying nymphs to phenotype probably produced the greater part of this error. The calculated expected frequency of sty in the F_2 progeny based on normal probability would be .200, .217, and .204 for F_1-1, F_1-2, and F_1-3 parental groups, respectively. (See appendix for method of calculation.)

Data from releases into the F_2 progeny groups accomplished at an approximate 5T+:1++ non-translocation are presented in Table 10. Males were removed at the beginning of the first hatch of F_3 progeny which was approximately four weeks after the releases were made. This reduced crowding somewhat; however, the late instar F_2 nymphs tended to show a slower rate of development while the released males were present in the population. This caused the hatch of the first F_3 oothecae to be spread over 4-5 weeks versus approximately 4-6 days for F_2 groups to hatch.

Table 9. Experiment A: Analysis of phenotypes following release of T(8;9)+/+sty males into a laboratory population of B. germanica.

F_2 Progeny Group	Segregation at F_2[a]		sty/sty Frequency
	Normal Phenotype	Mutant Phenotype (sty)	
F_2(1-1)	492	300	.379
F_2(1-2)	500	276	.356
F_2(1-3)	489	298	.379
F_2(2-1)	343	218	.389
F_2(2-2)	323	237	.423
F_2(2-3)	357	297	.454
F_2(3-1)	403	214	.347
F_2(3-2)	336	197	.370
F_2(3-3)	394	271	.407

[a]Phenotypes obtained following at 8 T+/+sty♂ :1 wildtype ♂ release into the F_1 progeny groups.

Table 10. Summary of T+/+*sty* male releases and their effects on F_3 progeny groups in T(8;9)+/+*sty* experiment A with the German cockroach.

F_2 Group and No.	No. Released	Approx. Ratio T/+ :+/+ [a]	No. Matings (= No. 1st Oothecae)	% +/+ Matings	F_3 Progeny [b]
F_2(1-1): 792	989	5:1	334	15	2879
F_2(1-2): 776	800	4:1	282	16	3235
F_2(1-3): 787	1048	5:1	346	15	2844
F_2(2-1): 561	800	5:1	258	19	3283
F_2(2-2): 560	855	5:1	270	15	3788
F_2(2-3): 654	960	5:1	307	10	2868
F_2(3-1): 617	1050	5:1	288	17	2911
F_2(3-2): 533	965	5:1	272	15	2565
F_2(3-3): 665	873	5:1	302	16	3114

[a] Estimate based on assumption that the number of T+/+*sty* males present before releases was equal to the number of *sty*/*sty* males observed.

[b] Groups from 1st ootheca only.

Female mortality in F_2 groups arising from F_1-1 parentals was highest at 14% compared to an average of7.8% for other F_2 groups. This may have been partially due to the higher initial numbers contributing to crowding. Differences in parental mortality among F_2 parental groups in large part prevented the expected differences in F_3 progeny which should have resulted from normal matings in F_1 parentals and higher numbers of F_2 offspring. The number of normal matings was determined on the basis of hatched egg cases and tended to be approximately 3X the number expected if equal competitiveness of males is assumed. The classification of F_2 egg cases as to mating types, presented in Table 11, differs from the frequencies expected for equal competitiveness among males and random mating (X^2 = 41 for F_2(1-1), for example, in Table 12). Mating types are similar to results expected if no T+/+<u>sty</u> releases had been accomplished for the F_2 progeny groups as shown in Tables 12 and 13. The projected progeny numbers in Tables 13, 17, and 22 were calculated by determining expected frequencies as described in the appendix and multiplying these by the average number of offspring for each mating type. Since the Type II (T/+ X +/+) mating types were capable of 20 plus nymphs/ootheca, the average number for Type III (+/+ X +/+) matings for containers with similar densities, was arbitrarily used when projecting expected progeny numbers for both Type II and III matings.

The number of progeny per translocation type mating for F_2 females in the population with a wild-type phenotype was determined by the following formula:

Table 11. Analysis of F_2 oothecae from T(8;9)+/+*sty* experiment A with the German cockroach.

Progeny Group	Mating Types[a]							
	I	(I + II)	II	III	IV	V	Other[b]	Total
F_2(1-1)	85	204	119	52	27	36	13	334
F_2(1-2)	46	184	138	43	29	21	2	282
F_2(1-3)	74	197	123	51	48	45	5	346
F_2(2-1)	31	141	110	48	32	30	7	258
F_2(2-2)	38	176	138	41	26	25	2	270
F_2(2-3)	56	220	164	31	37	16	3	307
F_2(3-1)	37	188	151	49	27	18	6	288
F_2(3-2)	34	188	154	41	19	23	1	272
F_2(3-3)	23	178	155	49	41	35	2	302

[a]For mating type descriptions refer to Table 4.

[b]Unidentifiable, because of damage or other factors.

Table 12. Expected numbers[a] of different mating types occurring in *Blattella germanica* experimental population A with or without releases of T(8;9)+/+*sty* males.

Generation		Mating Types[b]					
		I	(I + II)	II	III	IV	V
P_1	All females mated to T(8;9)+/+*sty* males			5			
	Expected Number Without Releases	13	39	26	13		
F_1-1	Expected Number with Releases	23	50	27	4		
	Observed Number with Releases	14	48	34	4		
	Expected Number Without Releases	51	185	134	83	26	41
F_2(1-1)	Expected Number with Releases	108	237	129	9	56	12
	Observed Number with Releases	85	204	119	52	27	36

[a]Determined by calculations described in the Appendix.

[b]Mating types described in Table 3.

Table 13. Expected and observed mating types and progeny numbers for experiment A of *B. germanica* populations involved in releases of males heterozygous for T(8;9) and *sty*.

Progeny Group		Mating Types									
		I	(I+II)	II	III	IV	V	X^2	Expected # Progeny[a]	X^2	Observed Number of Progeny[b]
	E_i	51	185	134	83	26	41[c]	37.35	4353[c]	489	
F_2(1-1)	E_{ii}	108	245	137	24	56	12[d]		3253[d]	42.99	2879
	O_i	85	204	119	52	27	36[e]	102.95	3492	107.6	
	E_i	48	148	100	52	24	31	10.03	3100	10.80	
F_2(2-1)	E_{ii}	94	187	93	15	47	8		2238	487.9	3283
	O_i	31	141	110	48	32	30	183.22	3237	.65	
	E_i	48	162	114	67	24	35	27.99	3638	141.3	
F_2(3-1)	E_{ii}	104	219	115	17	51	8		2679	20.09	2911
	O_i	37	188	151	49	27	18	138.46	3816	214.6	

[a]Progeny numbers projected by multiplying the number of type II and III matings by 17.37, type IV by 6.3 and type V by 10. See text for explanation.

[b]Actual population counts.

[c]Expected numbers of the respective mating types if no releases of T(8;9)+/+*sty* males were made into the developing F_2 group.

[d]Expected numbers of the respective mating types with releases of T(8;9)+/+*sty* males at the rate of 5 translocation bearing males to 1 non-translocation bearing male.

[e]Observed numbers of the respective mating types and progeny after releases of T(8;9)+/+*sty* males were made.

$$\frac{F_3 \text{ progeny group} - (\text{No. } +/+ \text{ matings X } 17.4 + \text{no. of } \underline{sty}/\underline{sty} \text{ matings X } 8.11)}{\text{No. of translocation type matings}}$$

The mean number of progeny for wild-type matings was obtained under conditions and densities similar to that of the F_3 of experimental populations. The average number of progeny for females with the sty phenotype was obtained under similar mass mating conditions. The number of progeny per translocation mating for females with wild-type phenotype in Experiment A ranged from 7.1 to 13.7 with a mean of 9.75 ± .9. These lower numbers reported here may have resulted in part from crowding.

EXPERIMENT C

Experiment C was begun in January 1976 and was concluded December 1976. General characteristics of this population study are similar to Experiment A in terms of growth rates and population size, with a few exceptions. The number of F_2 progeny was significantly less than in Experiment A. This was the result of fewer wild-type matings after T+/+sty male releases into the F_1 groups, and fewer F_1 parental females. Table 14 presents an analysis of mating types resulting after T+/+sty releases into the F_1 progeny groups of Experiment C. These data fit an hypothesis for equal competitiveness of released males with F_1 males already present in the population ($p < .80 > .50$). As in Experiment A, there is a consistent trend toward more oothecae classed as T/+ X +/+ than for equality between the two translocation mating classes. At the release rates of 8 T+/+sty to one non-translocation bearing F_1 male the two translocation matings should occur in approximately equal numbers with T/+ X +/+ slightly greater. It is noteworthy that the

Table 14. Analysis of oothecae and F_2 progeny numbers from T(8;9)+/+sty experiment C with the German cockroach.

Progeny Group		Mating Types[a] I	II	III	χ^2 [b]	No. F_2 Progeny	χ^2 [c]
F_1-1	E_i [d]	22	25	3	.887	708.9	27.76
	O_i [e]	18	27	3		611	
F_1-2	E_i	21	24	3	5.23	684.3	10.57
	O_i	12	29	4		739	
F_1-3	E_i	19	21	2	1.27	579.2	92.64
	O_i	15	24	2		742	

[a]Mating types described in Table 4.

[b]Chi square for differences in ootheca classes (2 degrees of freedom).

[c]Chi square for differences in F_2 progeny numbers (1 degree of freedom).

[d]Expected numbers based on normal probability and equal competitiveness of males. See text for explanation.

[e]Observed numbers: F_2 progeny average of first two oothecae.

number of matings between non-translocation bearing individuals was almost identical to the number expected when the genotypic frequencies were calculated using the known number of each type present and assuming that all males in the population are equally competitive. (Refer to appendix for calculations.)

The progeny per translocation mating value was calculated using the formula presented in the results of Experiment A. Results ranged from 11.85 to 16.96 with a mean of 14.39. These results (except for the F_1-3) compare favorably with the expected average of 12.3/mating.

Releases into the maturing F_2 progeny groups of Experiment C are summarized in Table 15. The percent normal matings are somewhat less than for Experiment A at approximately 2X the expected values. Progeny group F_2(1-2) showed unexpectedly high mortality and thus gave a greatly reduced F_3 hatch. Progeny group F_2(1-3) was reduced by an unaccountable occurrence when some 249 nymphs disappeared after the initial counts. Aside from these two exceptions, F_3 progeny groups were similar in size to Experiment A.

Results of analyses of F_2 oothecae are presented in Tables 16 and 17. Mating type results show trends similar to Experiment A. The results appear to approach the expected numbers projected if no releases of T(8;9)<u>sty</u> males were made into the F_2. The data for <u>sty</u> egg cases show a greater tendency toward the expected frequency of .25 than do the nymphal phenotypic data. Adult phenotypes checked during analyses of oothecae tend to confirm these results. Phenotypic data obtained during phenotyping of 5-6 instar nymphs are presented in Table 18.

Table 15. Summary of T+/+sty male releases and their effects on F_3 progeny groups in T(8;9)+/+sty experiment C with the German cockroach.

F_2 Group and No.	No. Released	Approx. Ratio T/+♂:+/+♂[a]	No. Matings (= No. 1st Oothecae)	% +/+ Matings	F_3 Progeny[b]
F_2(1-1): 615	975	5:1	268	11	2917
F_2(1-2): 505	749	5:1	177	9	1628
F_2(1-3): 315	490	5:1	166	11	1787
F_2(2-1): 609	761	5:1	281	11	2966
F_2(2-2): 692	904	5:1	254	11	2738
F_2(2-3): 639	702	4:1	302	11	3384
F_2(3-1): 602	862	5:1	263	9	2425
F_2(3-2): 720	867	5:1	261	13	3425
F_2(3-3): 646	978	5:1	239	10	2363

[a]Estimate based on assumption that the number of T+/+sty males present before releases was equal to the number of sty/sty males observed.

[b]Groups from 1st ootheca only.

Table 16. Analysis of F_2 oothecae from T(8;9)+/+sty Experiment C with the German cockroach.

Progeny Group	Mating Types[a]							
	I	(I + II)	II	III	IV	V	Other[b]	Total
F_2(1-1)	40	171	131	30	41	23	3	268
F_2(1-2)	23	123	100	17	13	21	3	177
F_2(1-3)	23	114	91	15	13	22	2	166
F_2(2-1)	37	172	135	40	34	33	2	281
F_2(2-2)	29	157	128	29	37	22	9	254
F_2(2-3)	39	188	149	32	34	39	9	302
F_2(3-1)	38	161	123	30	35	33	4	263
F_2(3-2)	28	154	126	32	37	30	8	261
F_2(3-3)	36	104	68	14	41	13	5	177[c]

[a]Mating types as previously described in Table 4.

[b]Unidentifiable, because of damage or other factors.

[c]Count was incomplete.

Table 17. Expected and observed mating types and progeny numbers for experiment C of *B. germanica* populations involved in releases of males heterozygous for T(8;9) and *sty*.

Progeny Group		Mating Types I	(I+II)	II	III	IV	V	X^2	Expected # Progeny[a]	X^2	Observed Number of Progeny[b]
	E_i	45	152	107	62	23	34[c]	40.88	3413[c]	72.08	
F_2(1-1)	E_{ii}	93	195	102	17	47	8[d]		2429[d]	98.04	2917
	O_i	40	171	131	30	41	23[e]	67.34	3273	38.72	
	E_i	47	159	112	65	24	35	20.74	3568	101.57	
F_2(2-1)	E_{ii}	95	205	110	19	49	10		2635	41.58	2966
	O_i	37	172	135	40	34	33	121.79	3574	103.43	
	E_i	48	154	106	55	24	33	21.22	3271	218.8	
F_2(3-1)	E_{ii}	94	193	99	15	47	9		2352	2.27	2425
	O_i	38	161	123	30	35	33	111.02	3198	186.84	

[a]Progeny numbers projected by multiplying the number of type II and III matings by 17.37, type IV by 6.3, and type V by 10. See text for explanation.

[b]Actual population counts.

[c]Expected numbers of the respective mating types if no releases of T(8;9)+/+*sty* males were made into the developeing F_2 group.

[d]Expected numbers of the respective mating types with releases of T(8;9)+/+*sty* males at the rate of 5 translocation bearing males to 1 non-translocation bearing male.

[e]Observed numbers of the respective mating types and progeny after releases of T(8;9)+/+*sty* males were made.

Table 18. Experiment C: Analysis of phenotypes following release of T+/+*sty* males into a population of *Blattella germanica* (L.).

F_2 Progeny Group	Segregation at F_2[a] Normal Phenotype	Mutant Phenotype (*sty*)	*sty* Frequency
F_2(1-1)	355	260	.423
F_2(1-2)	291	214	.424
F_2(1-3)	198	117	.371
F_2(2-1)	256	256	.420
F_2(2-2)	417	275	.397
F_2(2-3)	419	220	.344
F_2(3-1)	381	221	.367
F_2(3-2)	447	273	.379
F_2(3-3)	355	291	.450

[a]Phenotypes obtained following at 8 T+/*sty* : 1 wildtype release into the F_1 progeny groups.

SUMMARY DATA

Summary data with means and standard errors were prepared for F_1, F_2, and F_3 population counts as well as F_2 oothecae analyses. Average progeny counts are presented in Table 19. Progeny counts for the first two oothecae of F_1 females were approximately equal in productivity; however, the progeny counts for the third ootheca were significantly different at 87% of the counts for the first two oothecae.

Results of the 5:1 releases of T+/+sty males into the first three F_2 groups of the five experimental populations are presented in Table 20. Large differences in the F_2(1-3) are related to an unexpected loss of F_2 progeny in population C. Data for the third F_2 progeny group F_2(3-3) in population E were affected by high mortality. The analysis of cross-connected contingency tables indicated there was no interaction between variables which were F_1, F_2, and F_3 population counts. This can be explained in part by variable mortality among the groups. Population growth of the experimental populations compared to the control population (Table 5) was significantly different at the .01 level.

Summary data for the classification of F_2 oothecae as to mating types are presented in Table 21. The percent of matings between non-translocation bearing cockroaches in the five populations ranged from 8.8% to 14.8% with a mean of 11.8%. The basic model (see appendix) would predict the following mating types for females with wild-type phenotype: Type I (T+ X T+) 33.3%; Type II (T+ X ++) 38.3%; Type III (++ X ++) 7.07%. Observed numbers estimate average percentages of

Table 19. Five replicate summary of T+/+sty male releases and their effects on F_2 progeny groups in experiments with the German cockroach.

F_1 Progeny Group and No.	No. T+/+sty Released	Approx. Ratio of T+♂:++♂[a]	No. Matings (= No. Adult ♀♀)	% +/+ Matings	F_2 Progeny (Group and No.)
					F_2(1-1): 789± 63.9
F_1-1: 105.6±4.2	185±18.3	7:1	53.4±2.5	5.8± .7	F_2(1-2): 753± 70.0
					F_2(1-3): 677± 47.7
					F_2(2-1): 685± 48.6
F_1-2: 102.8±5.5	203±12.4	8:1	49.0±1.1	6.3±1.3	F_2(2-2): 707± 39.4
					F_2(2-3): 611± 44.2
					F_2(3-1): 641± 52.8
F_1-3: 96.6±3.8	185±11.5	8:1	46.2±1.8	5.6±1.4	F_2(3-2): 630± 61.1
					F_2(3-3): 567±117.9

[a]It was assumed that 1/4 of each progeny group was T/+ males.

Table 20. Five replicate summary of T+/+*sty* male releases and their effects on F_3 progeny groups in experiments with the German cockroach.

F_2 Group and No.	No. T+/+*sty* Released	Approx. Ratio[a] of T+ :+/+	No. Matings (=No. 1st Oothecae)	% +/+ Matings	F_3 Progeny[c]
F_2(1-1):706.3±17.4	920±49.7	5:1	307.3±17.4	13±1.3	2780±236
F_2(1-2):643±61	789±58.7	5:1	273.3±23	14±1.8	2757±391
F_2(1-3):563±98	881±131.8	5:1	261±37	10±1.2	2625±302
F_2(2-1):603.3±36	742±17.2	5:1	270±16.4	15±1.7	2941±132
F_2(2-2):638.5±19.8	936±53.9	5:1	272±7.07	11±3.6	2708±389
F_2(2-3):610.8±21.6	830±62.6[b]	5:1	280±14.51[b]	9±1.3[b]	2815±208[b]
F_2(3-1):615.3±21.7	920±69.4	5:1	267±38.4[b]	11±2.1	2464±163[b]
F_2(3-2):615.8±50.0	938±72.0[b]	5:1	265±2.72[b]	11±1.7[b]	2858±211[b]
F_2(3-3):641.5±19.5	914±58.4[b]	5:1	242±25.9[b]	11±1.8[b]	2660±265[b]

[a]Estimate based on assumption that the number of T+/+*sty* males present before releases was equal to the number of *sty*/*sty* males observed.

[b]Four replicates.

[c]Groups from 1st ootheca only.

Table 21. Five replicate summary analysis of F_2 oothecae from T(8;9)+/+*sty* experiments with the German cockroach.

Progeny Group	Mating Types[a]						
	I	(I + II)	II	III	IV	V	Total
F_2(1-1)	54.6±14.6	196.2	141.6± 7.7	41.0± 4.8	40 ±4.3	30.6±4.2	321±19.3
F_2(1-2)	43.4± 7.9	176.6	133.2±11.3	44.4±10.9	22.4±5.9	25.6±4.7	299±38.2
F_2(1-3)	52.2±10.2	161.1	109.4± 8.7	27.4± 6.5	32.0±6.2	28.8±4.6	264±30.1
F_2(2-1)	42.0± 6.4	171.2	129.2± 8.3	41.8± 3.0	42.0±5.6	24.4±3.1	283±17.3
F_2(2-2)	39.8± 2.9	180	140.2± 5.6	29.2± 4.3	34.0±2.7	24.4±2.3	285±13.7
F_2(2-3)[b]	40.3± 5.5	183.3	143.0± 3.9	24.5± 4.7	33.7±2.5	27.5±5.0	280±14.5
F_2(3-1)	40.6± 5.8	145	104.4±20.6	28.2± 7.6	29.3±4.4	20.2±3.6	267±12.4[b]
F_2(3-2)[b]	31.7± 2.3	174	142.3± 7.1	30.3± 4.7	26.8±6.8	25.3±1.9	265± 2.8
F_2(3-3)[c]	29.3± 4.5	154.6	125.3±15.6	31.7± 8.2	34.8±6.0	35.0±1.8	242±27.6

[a]Mating types previously described in Table 4.

[b]4 replicates.

[c]3 replicates.

mating types for females with the wild-type phenotype to be as follows: 16.5% Type I; 46.6% Type II; 11.9T Type III. Due to apparent error in identifying the two types, a more accurate measure of translocation type matings is obtained by adding mating Types I and II.

Mating types for the sty females were much more difficult to accurately classify than females with wild-type phenotypes. A rough measurement of mating types was accomplished and the results were very different than calculated expected numbers (see appendix for method of calculation). Expected percentages were 17.6% Type IV and 3.8% Type V while observed percentages were estimated at 11.8% and 9.7%, respectively. The projected and observed impact of stumpy (sty) on population numbers can be seen in Table 22. Data in Table 22 illustrate the impact of the sty gene on F_2 progeny production. Reductions ranged from 11.0% to 22.2% when estimated from mating type data. These data also tend to clarify the error involved with previously reported phenotypic data derived from late instar nymphs. Adult phenotyping seemed to approach expected numbers more closely. Eight of 15 F_3 progeny counts are closely similar to expected numbers of sty homozygotes. Others are significantly smaller than expected numbers.

Population Growth. A summary of overall population numbers derived from the progeny group method is depicted in Table 23. The experiments showed minor differences between the "progeny group method" and the freely interbreeding populations when the populations were reconstructed. Total numbers at the end of eight months are somewhat less than in a freely interbreeding population because the F_1-4, F_1-5,

Table 22. Frequencies and expected numbers of progeny with and without the presence of the deleterious gene *sty* compared to actual counts in experiments with T(8;9) +/+*sty* in *B. germanica*.

Pop.	Progeny group	Calculated[a] expected # F_2[a] *sty* frequencies	Observed #[b] F_2[b] *sty* frequencies	Expected #[c] F_3[c] without *sty*	Expected #[d] F_3[d] with *sty*	Observed # progeny F_3 with *sty*	Expected[e] % reduction
	F_2(1-1)	.200	.210	4343	3492	2879	19.6
A	F_2(2-1)	.217	.240	3822	3273	3283	15.3
	F_2(3-1)	.204	.160	4360	3816	2911	12.5
	F_2(1-1)	.209	.251	5211	4358	3214	16.4
B	F_2(2-1)	.208	.266	4412	3432	2861	22.2
	F_2(3-1)	.208	.269	2762	2144	2132	22.1
	F_2(1-1)	.208	.246	3960	3273	2917	17.3
C	F_2(2-1)	.207	.242	4238	3574	2966	15.7
	F_2(3-1)	.214	.259	3908	3198	2425	18.2
	F_2(1-1)	.214	.222	4638	3828	2108	17.5
D	F_2(2-1)	.216	.180	3509	3034	2652	15.7
	F_2(3-1)	.211	.173	4429	3663	2386	11.0
	F_2(1-1)	.214	.246	5003	4152	2953	17.0
E	F_2(2-1)	.213	.216	4725	3938	3578	16.7
	F_2(3-1)	.210	.376	1268	1005	872	20.7

[a]Frequencies calculated as described in the appendix.

[b]Frequencies of *sty* observed during analysis of mating types in the F_2 groups.

[c]This number was obtained by multiplying by 17.37 the number of females left after subtracting the type I mating class females. See text for explanation.

[d]Calculated by multiplying the number of type II and III matings by 17.37, the type IV matings by 6, and the type V matings by 10.

[e]Calculated by methods described in the appendix.

Table 23. Five replicate summary of population growth and structure for experiments using T(8;9)+/+*sty* in *B. germanica*.

Age[b]	Month of Growth							
	1	2	3	4	5	6	7	8
Ad	10		106	209	315	1046	2372	4201
Lg Md		106	103	97	731	1326	1829	3561
Sm	106	103	97	789	1438	2025	4055	6506
Total	116	209	306	1095	2484	4397	8256	14268

[a]Refer to Table 5 for comparison.

F_2(4-1), F_2(1-4), F_2(4-2), F_2(1-5), F_2(1-5), F_2(2-4), and F_2(5-1) were not included in the total counts. The total counts would have been approximately 5-10% higher if these groups had been accounted for. However, the general mortality of the adult males which occurred at approximately three months was not deducted from the data presented. When this is taken into account actual numbers would be reduced by approximately 150-200. In month nine the number of males dying approached 500. Population structure was described previously and was not notably different through time for the summary data.

Growth rates of the wild-type compared to the experimental populations are presented in Table 24. As expected, growth rate increased noticeably with the appearance of F_2 groups in month four and F_3 groups in month seven. It is noteworthy that the growth rate for the experimental populations was similar to the VPI wild-type groups except for months four and seven.

LINKAGE STUDIES

Previous work (Cochran and Ross 1974; Ross 1975b) had shown the *sty* gene as a group VIII marker located on chromosome 9, but the crossover frequency had not been determined between *sty* and T(8;9). Oothecae examined in 900 backcross matings indicated a recombination frequency of 0.79 ± .02 in double heterozygote females. Over 400 oothecae from backcross matings involving males heterozygous for T(8;9) and *sty* were examined; however, only 141 had enough viable embryos to identify easily whether crossing over had taken place. Ootheca results indicated a recombination frequency of 0.71 ± .4 for hybrid males.

Table 24. Growth rates[a] of wild-type (+/+) and experimental populations[b] of *B. germanica*.

Experiment	Group	Month 2	3	4	5	6	7	8
+/+	sm nymphs	1.0X	1.0X	16.4X	1.9X	1.4X	3.9X	1.6X
	Total	1.84X	1.4X	6.3X	2.5X	1.8X	2.9X	2.0X
T(8;9), + *sty*	sm nymphs	1.0X	1.0X	8.1X	1.8X	1.4X	2.0X	1.6X
	Total	1.8X	1.5X	3.6X	2.3X	1.8X	1.9X	1.7X

[a]Reconstructed from isolated progeny groups. See text for explanation.

[b]Experimental populations consisted of the following genotypes: T+/+*sty*, T+/++, +*sty*/+*sty*, and ++/++.

Linkage data for sty and T(8;9) based on individual offspring are presented in Table 25. Crossing over in females was somewhat higher than for males although not significantly different. The number of males evaluated for crossing over was less than the number of females due to near sterility associated with the sty females. Sty females selected for increased fertility over a period of two years were utilized to obtain additional male data toward the end of the studies reported herein. Several sty females were also selected from backcross breeding stock when they were observed to have viable oothecae.

REPRODUCTIVE BEHAVIOR STUDIES

MATING COMPETITIVENESS

Preliminary mating competitiveness studies involved ratios of 10T+:5+/+ (2:1), 15T/+:5+/+ (3:1), and 30T/+:5+/+ (6:1) of T+/+sty males versus VPI males. Five VPI wild-type females were used in each test. None of the three ratios gave consistently 100% translocation heterozygote matings.

One to one mating competition experiments were conducted in 1975 involving one VPI ♂ and one T+/+sty ♂ competing for one VPI ♀ replicated 41 times. Results indicated that 30 translocation type matings and 11 normal matings occurred. The probability of equal competition was less than .005 ($P < .005$). Data for three types of B. germanica males evaluated for competitiveness in mating with three types of female B. germanica are presented in Table 26. As can be seen, three out of seven trials were significantly different than the hypothesis

Table 25. Linkage data for stumpy (sty) with T(8;9).

Back Cross Parents			Segregation				%
Male		Female	Normal Phenotype		Mutant (sty) Phenotype		Recombination
+sty/+sty	X	T+/+sty	7++/+sty	548 T+/+sty	521+sty/+sty	2 Tsty/+sty	0.83±0.45
T+/+sty	X	+sty/+sty	2++/+sty	246 T+/+sty	218+sty/+sty	1 Tsty/+sty	0.64±0.18

Table 26. Mating competitiveness of males involved in population studies of T:(8;9)+/+sty.

Males			Female Genotype	Mating Success	
Genotype 1	vs	Genotype 2		Genotype 1	Genotype 2
T+/+sty		++/++	++/++	37	22
T+/+sty		+sty/+sty	++/++	52	23***
T+/+sty		++/++	T+/+sty	23	18
T+/+sty		+sty/+sty	T+/+sty	29	16*
T+/+sty		++/++	+sty/+sty	19	22
T+/+sty		+sty/+sty	+sty/+sty	39	28
+sty/+sty		++/++	T+/+sty	11	28**

* $P < .1 > .05$ for chi-square test when expected ratio of 1:1 is assumed.

** $P < .01$

*** $P < .005$

of equal competition. Stumpy (sty) males were less competitive than T+/+sty for both VPI and T+/+sty females. Stumpy (sty) males were also less competitive than VPI males for T+/+sty females. VPI and T+/+sty males were equally competitive for T+/+sty and +sty/+sty females. These evaluations seem to point toward the sty/sty males being less fit than the larger males.

Additional mating competitiveness evaluations conducted in 1977 involved mass matings of equal numbers of T+/+sty males and VPI males with VPI females (2 males per female) in one-gallon battery jars in single replicates. A mass mating test involving 50 of each type (150 total) resulted in 22 T+/+sty matings and 23 VPI matings ($0.9 > P > 0.5$). In a second mass mating test, a group of 100 each (300 total) gave 57 T+/+sty matings and 43 VPI matings ($0.5 > P > 0.1$). These results illustrate equal competitiveness between the T+/+sty males and VPI males. A third mass mating test of 38 each resulted in 15 T+/+sty matings and 16 VPI matings ($0.9 > P > 0.5$). Thus, in mass mating the T+/+sty males were equally, but not significantly more competitive than the VPI males for VPI females.

MATING PREFERENCES

Mating preference studies (Table 27) conducted using one each of the three types of males with five each of the three genotypes of females (VPI, T+/+sty and +sty/+sty) per container gave somewhat surprising results. Statistical analysis revealed significant deviation from random mating in one case. The cross connected contingency table analyses of the data show that the VPI males demonstrated a

Table 27. Evaluation of mating preference of three male genotypes for three different female genotypes in experiments with *B. germanica*.

# Males/ Genotype	Females Mated: T+/+*sty* Partial[a]	Complete[b]	Total	+*sty*/+*sty* Partial	Complete	Total	++/++ Partial	Complete	Total	Avg. # matings per male
27 VPI(++/++)	30	42	72	39	21	60	27	39	66	8.19±0.3
30 T+/+*sty*	37	32	69	45	27	72	37	50	87	7.73±0.22
12 +*sty*/+*sty*	6	15	21	5	22	27	10	12	22	5.83±.38

[a]Partial matings resulted in a small number of fully developed embryos but no hatch.

[b]Complete mating resulted in the usual number of fully developed embryos for each type of cross.

preference for the T+/+sty female over the VPI female and for either of these two over the homozygous sty female ($X^2 = 17.13$). The T+/+sty male demonstrated a preference for the VPI female over either of the other two genotypes. Homozygous sty males showed no preference among the three types of females.

REPRODUCTIVE POTENTIAL OF INDIVIDUAL GENOTYPES

The results of individual mating studies of three genotypes included in T(8;9)+/+sty population studies are presented in Table 28. VPI wild-type females exhibited the highest reproductive potential of the three genotypes when mated to the VPI male, and sty homozygote males. VPI males mated to heterozygote (T+/+sty) females were significantly less productive than the heterozygote male (T+/+sty) mated to VPI females. This relates well to the differences in disjunction between males and females reported by Ross and Cochran (1973) which indicated directed disjunction occurs in T+/+sty males. This favors alternate disjunction. Heterozygote females (T+/+sty) were the least productive of the three genotypes when mated with heterozygote (T+/+sty) males.

Homozygote stumpy (+sty/+sty) females showed significantly lower overall productivity when mated with the +sty/+sty males than with the two other genotypes. The stumpy female was, however, more productive than the heterozygote female (T+/+sty) when both were mated to the heterozygote (T+/+sty) male. The heterozygote (T+/+sty) males were the least productive of the three genotypes when mated with the VPI and heterozygote females. The VPI male showed greater reproductive

Table 28. Initial productivity of genotypes used in population experiments with T(8;9) and *sty* in *Blattella germanica*.

Genotypes						
Female	Male	No Matings	Egg compartments/ oothecae[a]	Range	Average # offspring	Range
++/++	++/++	71	44.84±.52	32-53	41.8±.87	19-50
++/++	T+/+*sty*	72	42.13±0.9	34-50	26.2±0.9	8-31
++/++	+*sty*/+*sty*	25	41.84±.68	36-49	40.3±.94	27-49
T+/+*sty*	++/++	63	45.3±.35	39-51	22.07±3.4	8-39
T+/+*sty*	T+/+*sty*	32	43.45±0.72	38-48	0.516±.32	0-9
T+/+*sty*	+*sty*/+*sty*	43	45.8±.4	39-52	24.3±1.6	0-38
+*sty*/+*sty*	++/++	89	41.7±.5	33-47	14±1.8	4-47
+*sty*/+*sty*	T+/+*sty*	69	43±.04	36-49	13.2±1	0-36
+*sty*/+*sty*[b]	+*sty*/+*sty*	32	37.91±.8	25-46	9.94±1.5	0-36[b]
+*sty*/+*sty*[c]	+*sty*/+*sty*	52	44.8±.5	32-51	35.5±.72	17-47[c]

[a]Data from the first oothecae only.

[b]Stumpy selected by routine sorting of progeny from the backcross system used for mass rearing.

[c]Stumpy selected for increased hatch for a period of two years significantly different for number of offspring ($P < .01$) and number of egg compartments per ootheca ($P < .1$).

potential than the *sty* male when mated to two of the three types of females. The homozygote (+*sty*/+*sty*) male was least productive when mated to the homozygote (+*sty*/+*sty*) female. Homozygote *sty* females selected for increased hatch over several generations were significantly more productive than females derived from the backcross system employed for mass rearing.

MUTANT STUDIES

Wing abnormalities observed while using the *sty* backcross system for mass rearing were evaluated by test crosses but none of the traits proved to be heritable changes.

DISCUSSION

EXPERIMENTAL POPULATIONS

INTRODUCTION

The theoretical basis (Cochran and Ross 1973) for the release of translocation bearing males into oncoming groups of late instar nymphs in a cockroach population was born out by the results of four different experiments (Ross 1975a, 1976, 1977b, 1980). The results reported here reinforce those findings. Releases of males heterozygous for T(8;9) and sty were successful in forcing both T(8;9) and sty into the normal segment of the experimental laboratory populations.

POPULATION DEVELOPMENT

Mortality data and other characteristics of T(8;9) (Cochran and Ross 1974) provided a basis for predicting results obtained by Ross (1975a) of approximately 50% reduction in the experimental population compared to the control after one release. Repeated releases resulted in the experimental population reaching only one-fourth the size of the control after four months (Ross 1975a, 1976). F_1 and F_2 offspring were reduced 50% by the introduction of the translocation T(8;9).

The results of five replicates reported here are similar using males heterozygous for T(8;9) and the deleterious gene sty. In months 7 and 8 these populations were 17.6% and 15.4%, respectively, as large as the control population. As recommended by Ross (1975a), hatch data were collected for the first three oothecae as they are the most

productive. As previously reported (Ross 1975a, 1976, 1977), the first two oothecae were slightly more productive than the third. The few exceptions were due primarily to reduced hatching of early oothecae because of lowered humidity. Ross (1976) using T(8;9)+/+*st* heterozygote males for release, obtained a ten-fold reduction from the control by month 7 compared to a six-fold reduction obtained here with T(8;9)+/+*sty* males. The release ratios (T+/+*sty* : ++/++) of 6:1 in the *st* studies (Ross 1976) were similar to the *sty* studies which were conducted at 8 to 1. The development of the progeny groups was not measurably affected by crowding until the F_2 groups matured and releases were made into the experimental populations. The 500-600 F_2 large nymphs exhibited symptoms of crowding when 700-900 semi-sterile males were added to the container. Several of the containers showed retarded development when the released males were present. The retardation effect appeared to affect male nymphs to a greater extent than females with several male nymphs failing to mature 2-3 weeks after the releases had been made. The magnitude of difference in the F_3 population counts between experimental populations and the control might have been larger if the effect of crowding had not been present.

Population growth in the control population compares favorably with that reported by Ross (1976). The overall growth rate of 42 X per generation for the 8 month study was identical to that reported for laboratory populations studied by Grothaus *et al*. (1981abc).

MALE COMPETITIVENESS

Released males were shown to be at least equally competitive with non-translocation males already in the population during releases into the F_1 generation. One to one competition studies conducted earlier pointed toward a heterotic effect in favor of the T(8;9)+/+sty males. This was not verified by later mass matings or experimental population data. The overall results of T(8;9)+/+sty male releases into the F_2 generation were somewhat less satisfactory than those expected on the basis of competitiveness studies. The reduced impact could have been caused by a number of factors including the following:

(1) the lower release ratio (T+:++) of 5 T+:1++ versus 8 T+:1++ for F_1 releases;

(2) reduced male vigor from prolonged backcrossing with sty versus the ru eye backcross sytem used by Ross (1975a);

(3) errors in phenotyping large releases of up to 1000 individuals could have contributed more non-translocation bearing sty and fewer T+ males than expected;

(4) differential mortality in large F_2 progeny groups, i.e., translocation females may have died off; and

(5) inaccurate timing of male releases along with retarded development of male nymphs caused by crowding in F_2 containers.

MATING TYPES

Data for mating types included some unexpected inconsistences: higher than expected semi-sterile matings in the F_1 and higher than expected semi-sterile and non-translocation matings in the F_2. The reasons for these inconsistencies include: (1) less competitive released males; (2) human errors in which fewer translocation males were released due to errors in determination of phenotypes with a

resulting increase in sty males released; (3) differential mortality resulting in a shift toward more non-translocation bearing wild-type females in the population; and (4) the directed disjunction of T(8;9) (Cochran and Ross 1974) shifting toward alternate disjunction giving less lethality with higher hatch (Ross and Cochran 1977). The latter could cause error in identification of the translocation mating types as well. Assortative mating was another possible contributing factor as shown by other test results. For example, the non-translocation males may have mated with the T(8;9)+/+sty females significantly more often than with the other genotypes. The possible error in mating type classification is evident when types I and II data for the F_1 generation are added together giving close to the expected total number of translocation matings. Further evidence is provided by the fact that non-translocation matings were also close to the number expected. Ross (1975a) reported a shift toward more semi-sterile matings in a population study using T(8;9).

IMPACT OF STY

The incorporation of a recessive deleterious gene carried in repulsion with a reciprocal translocation into a population for control was first proposed by Ross and Cochran (1973) and again by Ross (1975ab). The near sterility of the sty homozygote females was thought to lend additional impact in reducing the F_3 generation. Ross (1976) conducted similar experiments to the ones reported here using T(8;9) heterozygote males with homozygous st females being completely sterile. While the overall results of population counts were somewhat

better than those presented for T(8;9) _sty_, Ross (1976) postulated that little benefit was gained from _st/st_ female sterility compared to the results expected for the use of the translocation alone. The _st_ experiments failed possibly because of reduced competitiveness in released males. Also, the number of sterile _st_ females was significantly less than expected (Ross 1976). In the T(8;9) _sty_ experiments reported here, the released T+/+_sty_ males were competitive and the _sty_ gene undoubtedly helped retard the growth of the population at the onset of the F_3 generation. The F_2 _sty_ females exhibited reduced fecundity of no more than 25% of normal. This reduction in average hatch had a projected impact of 11% to 22% in total F_3 generation numbers as seen in Tables 20 and 23.

T(8;9) did successfully force _sty_ into the normal segment of the population; however, a shift in hatch rate tended to cause the impact on the F_3 generation to be less than that initially predicted.

A significant problem which occurred during the T(8;9) _sty_ experiments should be noted. The magnitude of error involved in sorting late instar nymphs of the _sty_ phenotype quickly and in large numbers was apparently much greater than anticipated. This was seen in the phenotypic data for F_2 groups in which the _sty_ frequency was consistently higher than expected. There is little doubt that the _sty_ phenotype was present because adults classified by phenotype during observation of oothecal development gave frequencies which approached the number expected. This error in determining the phenotype of nymphs probably caused release of fewer T+/+_sty_ males than planned especially in the large (up to 1000) F_2 releases which were accomplished

on several populations simultaneously. This was reflected in the larger than expected number of non-translocation matings reported for the F_2 releases.

LINKAGE STUDIES

Earlier work (Cochran and Ross 1968, 1974, 1975; Ross 1975b) established linkage groups, linkage with other markers, and linkage with two translocations for the recessive deleterious mutant stumpy (sty). Ross and Cochran (1975) and Ross (1975b) placed sty between the break point for T(8;9) and ruby (ru) on the linkage map of chromosome 9, but closer to (ru). Ross (1975b) reported linkage measurements for sty with Ru, T(9;10)Pw, and Df(9)Pw. These data establish sty at less than 1.4 crossover units from ru, 1.0 from T(9;10)Pw and 2.4 units from Df(9)Pw.

The linkage data reported herein differ somewhat for males and females although not significantly. This compares with previous results reported by Ross (1975b) where no clear cut sex difference in crossing over could be established (precisely) for other group VIII markers. The linkage data for males are less accurate than for females due to incomplete sterility in the sty females rendering the data difficult to obtain and evaluate. The linkage data reported here confirm previous estimates that crossing over between sty and T(8;9) was less than 1% (Ross 1975a). The data for females were much easier to evaluate and the estimate of 0.83 ± .04 would position sty on the linkage map of Group VIII markers within the area previously postulated (Ross 1975b) on the basis of linkage measurements of sty with ru (0.4) and ru with

the T(8;9) break point (1.3).

Ruby (ru), st, and sty were reported to show close linkage in the absence of translocations (Ross and Cochran 1968; Cochran and Ross 1974; Ross 1975b). As postulated by Cochran and Ross (1974), this close linkage may be affected by proximity to the centromere and central portion of the chromosome except for st.

REPRODUCTIVE BEHAVIOR STUDIES

MATING COMPETITIVENESS

Inherited semi-sterility is a feasible method for solving the problem of reduced competitiveness associated with chemosterilized or radiation sterilized males used for population control because males are not exposed directly to the mutagen and may also benefit from heterosis (Curtis 1968a; Ross and Cochran 1973). Early competition studies reported herein for T(8;9)sty heterozygote males versus VPI males tended to favor the heterozygote males. The dynamics of two males and one female per container may be very different from mass mating trials and population studies. For example, any tendency toward assortative mating would be very different in the actual population. Other authors have used the method described by Fried (1971) and have usually conducted laboratory analyses that included at least a 100:100:100 count of competing males and wild-type females, respectively (Anwar *et al*. 1975; Ashrafi *et al*. 1975; Cheng 1975; Hooper 1975; Kitzmiller 1972; Lowe *et al*. 1974).

Ross (1975a) indicated good competitiveness for T(8;9) males heterozygous for st, but they were less competitive than those

previously used which were heterozygous for ru. The T(8;9) males used in the experiments reported herein were heterozygous for sty and were better competitors in individual tests than in mass matings. Ross (1976) reported a slight shift in competitiveness data during population studies of T(4;8;10) compared to data obtained in laboratory competition trials. Ross (1978) also reported that laboratory translocation stocks T(4;8;10), released at a 9-10:1 ratio of T+/++ outcompeted non-translocation bearing wild-type cockroaches collected from a Navy ship and resulted in a frequency of ++ mating of only 0.7%. T(8;9), T(4;5;10) double translocation heterozygote males were more competitive than VPI wild-types in later studies (Ross and Cochran 1981a).

COMPETITION AMONG THREE GENOTYPES

Three genotypes of males (T+/+sty, ++/++, +sty/+sty known to occur in the populations under study were tested to determine any differences between their mating performance competing for females of a given genotype. The results indicate that the males with wild-type phenotypes (T+/+sty and ++/++) outcompeted the homozygous sty males in every mating test. This may have been due to the smaller size of the sty males or less stimulatory ability for the females involved. This was postulated for curly T(2;11) (Cu) males by Ross and Cochran (1968a).

REPRODUCTIVE POTENTIAL OF INDIVIDUAL GENOTYPES

The lethality and hatch associated with crosses of the translocation heterozygote of T(8;9) was previously reported (Ross and Cochran

1973; Cochran and Ross 1974). The results reported herein compare well with previous data. The T+/+sty females evaluated here tended to have larger oothecae than the wild-type although not significantly larger. This may be a heterotic effect present only in the females (Ross and Cochran 1973). Robinson and Curtis (1972) postulated an heterotic effect for Drosophila T/+ females which exhibited increased egg productivity. The T(8;9) translocation is similar to the Brc translocation in the screw-worm fly in that no apparent preferential alternate disjunction occurs in females (LaChance et al. 1966).

VPI females produced significantly smaller ootheca when mated to T+/+sty males versus VPI males. Ross (1971a) reported productivity reductions from +/+ males were similar to the results obtained with Pb/+males. This may represent a loss in stimulatory capability in the T/+ males as observed in B. germanica and Drosophila (Ross and Cochran 1973; Robinson and Curtis 1972), respectively. The data for T+/+sty females mated with homozygous stumpy males parallels previous results (Ross and Cochran 1973).

The average number of offspring for T+/+sty males mating with VPI females was somewhat higher than reported previously (Ross and Cochran 1973; Cochran and Ross 1974). These results reflect the tendency toward directed disjunction in T(8;9) males reported by Cochran and Ross (1974). The number of offspring per ootheca is higher than previous results indicate, which may reflect a shift toward even stronger directed disjunction. This type of shift was reported for T(4;5;10) which had been selected in the laboratory (Ross and Cochran 1973). Laven et al. (1971) reported preferential alternate

disjunction in Culex pipiens L. As indicated by McDonald and Rai (1970) matings between different translocation heterozygotes may be highly sterile. Ross and Cochran (1973) reported matings between T(8;9) heterozygotes were usually unproductive. This was certainly true of the data reported herein.

Data for homozygous stumpy females reported by Ross and Cochran (1973) and Ross (1975ab) indicated near sterility. The sty/sty females in these studies however showed surprising productivity. The number of offspring from sty females mated to VPI or T+/+sty males was significantly greater than when mated to sty males. The sty male may lack the ability to stimulate the female as hypothesized for T(2;11) Cu males by Ross and Cochran (1969a).

The data reported in this section were collected late in the population studies after many generations of mass rearing had occurred. This may reflect the impact of selection for higher reproductive potential in the T+/+sty males and the homozygous stumpy females.

MATING PREFERENCE

The data obtained for mating preference indicated a significant preference by the male combined with levels of receptivity in the female for mating between the T+/+sty female and VPI male. This could be a measure of female preference in part as the T+/+sty female may have had a greater tendency to mate with the VPI male and hence was more receptive than with the other two genotypes. Another view of these tests could be to call it three-way competition between three lines of B. germanica females for one male. Gale (1964) studied

three-way competition between three lines of *Drosophila*, but used two-way tests to evaluate total competition.

MUTANT STUDIES

The variability in wing length of T+/+*sty* males observed during mass rearing did not prove to be heritable traits. The clear sexual dimorphism which occurs in stumpy wing length (Ross 1975b) may have been related to the reduced right or left wing length observed only in three instances in T+/+*sty* heterozygote males and females. These observed aberrations were similar to what would be expected from a partial expression of minature wing *min* described by Ross and Kiel (1978).

SUMMARY AND CONCLUSIONS

Growth of six laboratory populations of *Blattella germanica* was followed by monthly censuses for a period of eight months. Five populations, A through E, were begun from five VPI females mated with T+/+*sty* males. The sixth was a control population started with five pairs of VPI females.

Heterozygote T(8;9) male nymphs carrying the deleterious gene, stumpy (*sty*) in repulsion were released into developing F_1 and F_2 progeny groups of populations A through E. Releases into the F_1 were conducted at the rate of 8 T+/+*sty* males:1 non-translocation bearing male. F_2 releases were timed to match developing groups of females in age. Hatch, development, and other data were recorded for each progeny group and were used to reconstruct total populations for the first eight months of growth. Cross connected contingency table analyses of results showed a highly significant retardation of growth in experimental populations compared to the control. Experimental populations were only one-fourth the size of the control after four months and only 15.4% as large after eight months. The deleterious gene *sty* caused a projected reduction in hatch of the F_3 generation of 11 to 22%.

Linkage tests of T(8;9) with *sty* showed cross-over frequencies of less than 1% for both males and females. The frequency of *sty*/*sty* homozygote females in the F_2 groups was predicted at 0.20. Observed frequencies approached the expected frequency for data obtained during

analysis of mating types in adult females. T(8;9) provided a successful mechanism for driving the deleterious gene, sty, into the normal segment of the populations. These results were less than optimum because of the following: (1) a possible reduction in competitiveness of released males; (2) higher than expected fecundity in the sty homozogote female; (3) possible shift in the frequency of alternate disjunction in T(8;9) sty heterozygote males; (4) possible assortative mating between non-translocation bearing wild-type males and T+/+sty females in the population as well as with T+/+sty females and non-translocation bearing wild-type females; (5) fewer T+/+sty males and more sty males released than planned due to phenotyping errors in larger releases.

Studies of the reproductive behavior of three genotypes (T+/+sty, ++/++, +sty/+sty) from the experimental populations evaluated mating competitiveness among males, initial productivity, maximum number of matings per male, and assortative mating among the genotypes. T+/+sty males consistently outcompeted wild-type males at mating in small number tests, but in later assessments by mass mating and population studies, there was no difference. A statistically significant tendency toward assortative mating bewteen VPI males and T+/+sty females was observed. The feasibility of mass rearing of semi-sterile males for releases of up to 10,000 males per month was demonstrated.

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APPENDIX

CALCULATION OF EXPECTED FREQUENCIES OF GENOTYPES AND MATING TYPES*

1. Genotypic frequencies (F_1 generation)

   a. Male frequencies

   $$T+/+\underline{sty} = \frac{\text{no males released}}{\text{Total males}}$$

   $$T+/++ = \frac{\text{\# males present before releases}}{\text{Total males}}$$

   or $$++/+\underline{sty} = \frac{\text{frequency of naturally occurring males}}{2}$$

   b. Female frequencies: because of the linkage relationships, the genotypes were assumed to be equally divided between T+/++ and ++/+sty therefore female genotypic frequencies were considered to be equal to 0.5 in both cases.

2. F_1 mating frequencies produced were calculated as $\hat{f}\,♂_{(a-c)}$ X $\hat{f}\,♀_{(a-b)}$ = mating frequency or

   a.

♀ \ ♂	T+/+sty .778	T+/++ .111	++/+sty .111
T+/++ 0.50	.389	.0555	.0555
++/+sty 0.50	.389	.0555	.0555

*Note: Actual data from Population C F_1-1 and F_2(2-1) progeny groups is used throughout this discussion as an example.

b. F_1 productive mating frequencies. Since crosses between T(8;9) heterozygotes were known to be non-productive, the "effective mating frequency within the F_1 generations was corrected as follows:

Productive mating frequencies were totaled and then each frequency corrected by dividing it by the new total.

$$\text{Prod. Mating } \hat{f} = \frac{\hat{f}}{\Sigma\ \hat{f} \text{ productive matings}}$$

i.e. $.0555 + .055 + .055 + .389 = .554$

then $\frac{.055}{.554} = .0999$

$\frac{.389}{.554} = .700$

Then the frequencies of productive matings were as follows:

♀ \ ♂	T+/+<u>sty</u>	T+/++	++/+<u>sty</u>
T+/++	//////	//////	.0999
++/+<u>sty</u>	.700	.0999	.0999

c. Effective frequency of F_1 productive matings. Previous laboratory evaluation had shown the matings between translocation heterozygotes and non-translocation bearing individuals to be one-half as productive as normal or wild-type matings. Differences in disjunction between males and females had also been

measured. Therefore, the productive mating frequencies needed an additional correction as follows:

(1) frequencies for matings between T+/+*sty* females and T+/+*sty* or T+/++ males were multiplied by 0.59.

(2) frequencies for matings between T+/++ females and ++/+*sty* males were multiplied by 0.51.

(3) these new frequencies were totaled and then corrected by dividing each by the new total.

(4) the final corrected "effective frequency" for productive matings were as follows:

♀ \ ♂	T+/+*sty*	T+/++	++/+*sty*
T+/++			.082
++/*sty*	.663	.160	.160

3. F_1 gametic frequencies involved in productive matings.

a. Genotypic frequencies of productive females. The genotypic frequencies of productive females were determined by adding the mating frequencies for each productive genotype in No. 2c(4) with the sum representing the frequency of F_1 productive females in the population. In other words from 2c(4) the genotypic frequency for ++/+*sty* females was = .663 + .160 + .160 = .918.

(1) female gametic frequencies. The gametic frequencies for (T+), (+sty), and (++) from the females in the population were calculated by:

$\hat{f}$ (T+) = $\frac{.082}{2}$ = .041

$\hat{f}$ (+sty) = $\frac{.918}{2}$ = .459

$\hat{f}$ (++) = $\frac{.918}{2} + \frac{.082}{2}$ = .459 + .041 = 0.5

b. Frequencies of productive males. Secondly, genotypic frequencies of the productive males (males actually mating) were calculated by multiplying the mating frequencies for each productive mating type times the number of females available in the population. For example:

$\hat{f}$++/+sty ♀ (.50) X $\hat{f}$T+/+sty ♂ = (.788) = .389 $\hat{f}$ mating type

.389 X # ♀♀ in population (48) = 19 matings involving T+/+sty ♂♂ and ++/+sty ♀♀

(1) similarly, three matings between T+/++ ♂♂ and ++/+sty ♀♀
three matings between ++/+sty ♂♂ and ++/+sty ♀♀
and three matings between ++/+sty ♂♂ and T+/++ ♀♀
giving 28 total productive matings for the F_1.
Therefore, the frequency of productive males mating was obtained by dividing the total number of each productive mating type by the number of productive matings as follows:

$\frac{19}{28}$ = .679 = $\hat{f}$ productive T+/+sty ♂♂

$\frac{3}{28} = .107 = \hat{f}$ productive T/++ ♂♂

$\frac{3}{28} + \frac{3}{28} = \hat{f}$ productive ++/+sty ♂♂

(2) Male frequencies. Gametic frequencies of (T+), (+sty), and (++) contributed by F_1 males in the population was calculated in the following manner:

$\hat{f}$ (T+) $= \frac{.679}{2} = .393$

$\hat{f}$ (+sty) $= \frac{.214}{2} + \frac{.697}{2} = .4465$

$\hat{f}$ (++) $= \frac{.214}{2} = \frac{.107}{2} = .1605$

4. F_2 genotypic frequencies. These were calculated by using the gametic frequencies from 3a(1) and 3b(2) as follows:

		T+	+sty	++
	$\hat{f}$	.393	.4465	.1605[a]
T+/	.041[b]	.016 T+/T+	.0185 T+/+sty .019	.007[c] T+/++ .007[d]
+sty	.459	.180 T+/+sty .183	.205 +sty/+sty .208	.074 ++/+sty .075
++	.50	.197 T+/++ .200	.223 +sty/++ .227	.080 ++/++ .081

[a] frequencies of F_1 gametes from ♂♂

[b] frequencies of F_1 gametes from ♀♀

[c] uncorrected genotypic frequencies of F_2 progeny

[d] corrected genotypic frequencies of F_2 progeny after elimination of the non-viable T+/T+.

5. F_2 mating ratios. Expected mating ratios were calculated using the expected frequencies from No. 4 and numbers obtained from population counts.

a. Male genotypic frequencies were determined as follows:

Number	F_2 Genotypes	Frequency
975	Released T+/+sty	.791
69	F_2 T+/+sty	
71	T+/++	.054
104	++/+sty	.079
72	+sty/+sty	.055
28	++/++	.021
1319		1.000

b. F_2 mating ratios were calculated by cross multiplying expected genotypic frequencies as follows:

(1) F_2 MATING RATIOS F_1 - 1 Population C

1319 ♂ / ♀ 268	T+/+sty .791	T+/++ .054	++/+sty .079	+sty/+sty .055	++/++ .021
T+/+sty .202	~~.160~~	~~.011~~	.016	.011	.004
T+/++ .207	~~.164~~	~~.011~~	.016	.011	.004
++/+sty .302	.239	.016	.024	.017	.006
+sty/+sty .208	.164	.011	.016	.011	.004
++.++ .081	.064	.004	.006	.004	.002

(2) These were corrected for non-viable crosses as follows:

F_2 MATING RATIOS

1319 ♂ / ♀ 268	T+/sty	T+/++	++/+sty	+sty/+sty	++/++
T+/+sty			.025(.51)	.071(.51)	.006(.51)[a]
T+/++			.025(.51)	.017(.51)	.006(.51)
++/+sty	.367(.59)	.025(.59)	.037	.026	.009
+sty/+sty	.252(.158)	.017(.158)	.025	.017	.006(.25)
++/++	.098(.59)	.006(.59)	.009	.006	.003

[a]Numbers in parentheses are productivity rates for these types of crosses. Other rates are equal to one.

(3) Effective frequencies of mating types were calculated using previously measured productivity rates for the respective crosses and using the wild type productivity rate as equal to one.

F_2 Effective Mating Ratios

1319 ♂ / ♀ 268	T+/sty	T+/++	++/+sty	+sty/+sty	++/++	Totals
T+/+sty			.027	.019	.006	.052
T+/++			.027	.019	.006	.052
++/+sty	.444	.029	.076	.053	.019	.621
+sty/+sty	.082	.006	.012	.008	.003	.111
++/++	.119	.008	.019	.012	.006	.164

6. Genotypic frequencies of productive F_2 females were obtained by adding the above frequencies from left to right.
7. Genotypic frequencies of productive F_2 males were determined by multiplying the mating ratios in 5b(1) times the total number of females and then converting the numbers to frequencies as follows:

F_2 Effective Genotypic Frequency of Males

♀ \ ♂	T+/+sty	T+/++	++/+sty	+sty/+sty	++/++
T+/+sty			4	3	1
T+/++			4	3	1
++/+sty	64	4	6	5	2
+sty/+sty	49	3	4	3	1
++/++	17	1	2	1	1
Total	125	8	20	15	6
Frequencies	.718	.046	.115	.086	.034

8. Expected genotypic frequencies for the F_3 generation originating from population C F_1-1, F_2(1-1).

a. Gametic frequencies

(1)

Productive Genotypic Frequencies F_2 Males				
T+/+sty	T+/++	++/+sty	++/++	+sty/+sty
.718	.046	.115	.034	.086

(2)

Gametic Frequencies F_1 Males[a]		
T+	+sty	++
.382	.503	.115

[a]Calculated from the above genotypic frequencies

(3)

Genotypic Frequencies Productive F_2 Females				
T+/+sty	T+/++	++/+sty	++/++	+sty/+sty
.052	.052	.621	.164	.111

(4)

Gametic Frequencies F_2 Females[a]		
T+	+sty	++
.052	.4475	.5005

[a]Calculated from above genotypic frequencies

b. Expected Genotypic frequencies for F_3

(1)

	T+ .382	+sty .503	++ .115
T+/ .052	.02 T+/T+	.026 T+/+sty .027	.006 T+/++ .006
+sty .4475	.171 T+/+sty .174	.225 +sty/+sty .230	.051 ++/+sty .052
++ .5005	.191 T+/++ .195	.252 +sty/++ .257	.058 ++/++ .059

(2) Adding the resulting frequencies from above gives the following:

Genotypic Frequencies				
T+/+sty	T+/++	++/+sty	++/++	+sty/+sty
.201	.201	.309	.059	.230

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USE OF A TRANSLOCATION AND RECESSIVE DELETERIOUS GENE TO RETARD POPULATION GROWTH IN Blattella germanica (L.)

by

Timothy Holland Dickens

(ABSTRACT)

Successive releases of male German cockroaches heterozygous for the translocation T(8;9) and the recessive deleterious gene sty were made into laboratory populations of Blattella germanica to study the effect of this genetic load on population growth.

Five experimental populations and one control were followed by monthly census for eight months. Individual progeny groups were held in separate containers. Various aspects of reproductive behavior of different genotypes were evaluated in separate experiments including fecundity, competitiveness and assortative mating. Linkage between T(8;9) and sty was also measured.

The translocation T(8;9) and sty were successfully introduced into the experimental populations by the introduction of heterozygous males. Experimental populations were only 50% the size of the control at the F_1 generation and only 25% as large by the F_2 generation. At the F_3 generation, experimental populations were only 15.4% as large as the control. Cross connected contingency table analyses of population data showed a significant retardation of population growth from releases of T(8;9)sty males. T(8;9) provided a successful mechanism for driving the deleterious gene, sty, into the normal segment of the population. The frequency of sty/sty females in F_2 groups was

predicted at 0.20. Observed frequencies approached the expected frequency at 0.11 to 0.22. This deleterious gene provided additional genetic load by reducing possible F_3 progeny by approximately 15%. Linkage tests of T(8;9) with sty showed cross-over frequencies of less than 1% for both males and females.

Results were less than optimum due to the following: a possible reduction in competitiveness of released males; higher than expected fecundity in the sty homozygote female; possible shift in the frequency of alternate disjunction in T(8;9) sty heterozygote males; possible assortative mating between non-translocation bearing wild-type males and T+/+sty females in the population as well as T+/+sty males and non-translocation bearing wild-type females; fewer T+/+sty males and more sty males released than planned due to phenotyping errors in larger releases.

Laboratory studies of the reproductive behavior of three genotypes involved in the experimental populations evaluated competitiveness among males, initial productivity, maximum number of matings per male, and assessed the prospect of assortative mating among the genotypes. Competitiveness of the T+/+sty males in small number tests was consistently better than wild-type males but in later assessments by mass mating and population studies, they demonstrated equal competitiveness with wild-type males. A statistically significant tendency toward assortative mating between VPI wild-type males and T+/+sty females was observed. The feasibility of techniques for mass rearing of semi-sterile males for releases of up to 10,000 males per month was demonstrated.