HERITABILITY OF MULTIPLE MATING BY FEMALE FIELD CRICKETS *Gryllus integer* (ORTHOPTERA: GRYLLIDAE)

by

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To My Parents

ABSTRACT

The heritability of multiple mating in female Gryllus integer crickets was studied. Two preliminary experiments were conducted to determine when females first mate following the post-imaginal moult and to ascertain whether constant exposure to males affects female mating rate. Female G. integer first mated at an average age of 3.6 days (S.D. = 2.3, Range = 0-8 days). Exposing female crickets to courting males 24 hr daily did not significantly alter mating rates from those females in contact with males for only 5 hr per day.

A heritability value of 0.690 ± 0.283 was calculated for multiple mating behavior in female G. integer using a parent-offspring regression approach. Parental females mated between 1 and 30 times ($\bar{x}$ = 9.8, S.D. = 6.6) and offspring matings ranged from 0 to 26 times ($\bar{x}$ = 7.3, S.D. = 3.4).

Multiple mating is probably a sexually selected trait which functions as a mechanism of female choice and increases reproductive success through increased offspring production. Classical theory suggests that traits intimately related with fitness should exhibit negligible heritable variation. However, this study has shown that multiple mating, a trait closely linked with reproductive fitness, exhibits substantial heritability. These results are in concordance with a growing body of empirical evidence suggesting many fitness traits in natural populations demonstrate heritabilities far removed from zero. Various mechanisms which may maintain heritable variation for female multiple mating in wild, outbred G. integer populations are discussed.

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INTRODUCTION

Alleles advantageous to survival and reproduction will increase in frequency in response to selection thereby depleting underlying additive genetic variance (Maynard Smith 1978, Williams 1975). This process is a corollary of Fisher's (1958) Fundamental Theorem of Natural Selection, which states that "the rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time". Crow and Kimura (1970) formulated a population genetic model which mathematically demonstrated a rate of depletion in additive genetic variance directly correlated with an increase in selection intensity. Traits under sexual selection, such as female mating preference and male secondary reproductive traits, should also exhibit a reduction in genetic variation (Harpending 1979, Howard 1978, Thornhill 1980a). West-Eberhard (1979) suggested that fitness traits such as body size and vigor are under rigorous selection pressures resulting in fixation of responsible alleles and a corresponding reduction in heritable variation.

Hypotheses which predict reduced additive genetic variation over evolutionary time assume constant selection, stable non-fluctuating environments and rely on simple Mendelian genetic models. Selection in nature, however, is almost never constant, environmental fluctuations are the rule and a large proportion of fitness traits are under polygenic control (Futuyama 1979). Cade (1984a), Istock (1983) and Mousseau and Roff (1987) have suggested that additive genetic variation underlying fitness traits is often much greater than theory suggests. They cite numerous examples from the pertinent literature which demonstrate that most quantitative traits studied do indeed exhibit significant levels of heritable variation.

Multiple mating by female insects is a behavior which increases reproductive fitness and may be sexually selected. Female crickets (Gryllidae) mate more than once and are therefore ideal animals to study the adaptive significance of multiple mating. The purpose of this study was to determine the heritability of multiple mating in female field crickets, Gryllus integer, and to discuss the adaptive significance of this behavior.

LITERATURE REVIEW

MEASURING GENETIC VARIANCE

Genetic variance (V_G) consists of an additive component (V_A), a dominance component (V_D) and an epistatic component (V_I), so that

$$V_G = V_A + V_D + V_I.$$

Additive genetic variance, defined as the proportion of genetic variance due to additive gene effects, estimates the extent to which genotypes "breed true" from parent to offspring. Dominance and epistatic effects collectively represent non-additive gene interactions, the former between interactions of alleles at a single locus and the latter between alleles at different loci. When estimating the heritability of a trait V_A can be separated from all other genetic variation by lumping V_D and V_I with environmental variation (non-genetic variation).

Heritability is a statistic used on quantitative characters, which are those exhibiting continuous variation, are thought to be under polygenic control and usually follow a normal distribution. Narrow-sense heritability (h^2) is defined as the proportion of phenotypic variance (V_P) which is due to additive genetic variance such that $h^2 = V_A / V_P$.

Heritability studies may be approached using one of several methods. Directional selection experiments are used to isolate extreme genotypes in a population experiencing constant environmental conditions (Ehrman and

Parsons 1976). Over many generations a shift in the population mean will result providing an estimate of the realized heritability, or the response to selection.

Heritabilities may also be estimated from the degree of resemblance between relatives by performing linear regressions (offspring on parent or offspring on mid-parent, described as mean of both parents, analyses) or correlations (half sib or full sib analyses). Taking as an example the regression of offspring values on parent values, a value for a dependent variable, y (offspring values) is estimated for each independent variable (parent values). A covariance calculated from the cross-products of the paired values then gives the following equation:

$$b = Cov_{x,y} / V_y$$

where b is the slope of the regression line, $Cov_{x,y}$ is the covariance of y on x, and V_y is the variance of y. In the case of the offspring-parent regression the slope will give an estimate of half the variability such that $h^2 = 2b$.

Precise estimates of heritabilities are limited by space, labor and costs. The number of families used can be reduced by increasing the number of individuals per family to arrive at a "compromise between large families and many families that will minimize the sampling variance of the regression or correlation" (Falconer 1981). Standard errors are calculated from these sampling variances. For example, to achieve a standard error of one, 400 parents and 400 offspring must be measured (Klein et al. 1973).

When measures of large numbers of relatives is a limiting factor, repeatability measurements of traits replicated in space or time may be more feasible to estimate an upper limit heritability value.

Heritability estimates do not specify how quantitative traits are inherited but they do assess the proportion of phenotypic variation which is

due to additive genetic variance (Cade 1984a, Futuyama 1979). These estimates are valid only for the particular population under study. Since heritability estimates for metric characters may differ between populations exposed to different environments, heritabilities determined for a specific laboratory-reared population are therefore only valid for that generation at that time. However, a laboratory heritability study is useful since it allows one to eliminate most of the existing environmental variation. Even so, interactions between genotype and environment will vary and large standard errors may result (Falconer 1981).

MAGNITUDE OF GENETIC VARIATION

Fisher (1958) proposed that natural selection depletes additive genetic variance underlying fitness characters. Quantitative traits directly associated with fitness (viability, developmental time and fecundity) should therefore exhibit negligible genetic variation (Maynard Smith 1978, Williams 1975). Fitness-related traits are usually subjected to selection under natural conditions and several mathematical models (Crow and Kimura 1970, Turner 1969), as well as various experimental data (Falconer 1981), support Fisher's prediction. However, most of these models are based on various assumptions which may not be met by natural populations and the experimental data come primarily from domesticated animals and laboratory Drosophila populations which have been exposed to intense directional selection in the past (Istock 1983, Hohenboken 1985).

In wild, outbred populations heritability for fitness-related characters is probably almost always non-zero (Cade 1984a, Istock 1983). This may occur when certain genes act on one character in one direction and on a second fitness character in the opposite direction resulting in a negative genetic correlation between the two characters (Falconer 1981).

These negative genetic correlations are chiefly the result of antagonistic pleiotropy, or genetic "trade-offs" between fitness components (Rose 1982, 1984). Service and Rose (1983) demonstrated a decrease in the strength of negative additive genetic correlations between early-life fecundity and starvation resistance when D. melanogaster flies, reared initially in a standard environment, were introduced and bred in a novel environment. Corresponding reductions in heritability values for both traits in individuals reared in the novel environment led them to suggest antagonistic pleiotropy between fecundity and starvation resistance was responsible for this reduction in heritable variation.

Data from domesticated animals suggest there is a decline of V_A and h^2 as characters more closely related to fitness are studied (Falconer 1981). Traits less directly related to fitness (ie. body size, oviposition site preference, courtship patterns, mate selection and sexual dimorphism) should thus exhibit higher V_A and h^2 values than traits more directly related to fitness such as life-history traits. Roff and Mousseau (1987) and Mousseau and Roff (1987) compiled an extensive data set of heritabilities of traits in Drosophila as well as for other invertebrates and vertebrates from the available literature. They set up four categories of traits: life history traits (fecundity, viability, and development rates), physiological traits, morphological traits and behavioral traits. Analysis of the data demonstrated that, in general and as predicted by Fisher (1958), life history traits exhibit the lowest heritabilities. Morphological traits had high heritabilities, and physiological and behavioral traits had heritabilities which fell between the afore mentioned two. The magnitude of average heritabilities suggests that significant genetic variation is preserved across all traits. Table 1 presents heritability values (and standard errors where given) collected from the literature for various fitness traits in insects.

Table 1. Heritabilities of fitness-related traits in some insect species.

Fitness Component	Species	Method of Estimation[1]	h^2	S.E.	Source
Fecundity	*Drosophila melanogaster*[2]	3	0.31	-	Rose and Charlesworth 1981
	D. melanogaster	2	0.03	-	Tantawy and Rakha 1964
Fertility	*D. melanogaster*	2	0.15	-	Gromko 1987
Productivity	*D. melanogaster*	1	0.28	±0.11	Rose 1984
	D. melanogaster	2	0.05	±0.01	Tantawy and El-Helw 1970
	D. simulans	2	0.11	-	Tantawy and Rakha 1964
Virility	*D. melanogaster*	3	0.25	±0.25	Tucic *et al*. 1988
Copulation Duration	*D. melanogaster*	2	0.46	-	Gromko 1987
	D. pseudobscura	1	0.02	±0.02	Spuhler *et al*. 1978
Repeat Mating	*D. melanogaster*	1	0.30	-	Pyle and Gromko 1981
Oviposition Preference	*Deloyala guttata*[3]	2	0.05	±0.13	Rausher 1983
Developmental Time	*D. melanogaster*	2	0.28	±0.04	Tantawy and El-Helw 1970
	D. subobscura	3	0.33	-	Clarke *et al*. 1961
	Tribolium castaneum[3]	1	0.11	-	Dawson 1965
Larval Feeding Rate	*D. melanogaster*	2	0.20	±0.02	Sewell *et al*. 1974
Adult Longetivity	*D. melanogaster*	2	0.11	-	Tantawy and Rakha 1964
	D. melanogaster	2	0.04	±0.03	Tantawy and El-Helw 1970
	D. simulans	2	0.15	-	Tantawy and Rakha 1964
	Dysdercus bimaculatus[4]	2	0.11	±0.06	Derr 1980
Calling Duration	*Gryllus integer*[5]	1	0.50	-	Cade 1981
Song Characters	*Chorthippus bruneus*[5]	2	0.28	-	Butlin and Hewitt 1986
Body Weight	*D. melanogaster*	2	0.27	±0.07	MacKay 1981
	G. bimaculatus	2	0.25	±0.11	Simmons 1987a
Body Length	*D. melanogaster*	2	0.36	±0.03	Tantawy and El-Helw 1970
	D. simulans	2	0.23	-	Tantawy and Rakha 1964
	G. integer	3	0.39	±0.11	McGowan 1986
	G. bimaculatus	2	0.26	±0.09	Simmons 1987a
Cercus Length	*C. bruneus*	2	0.66	-	Butlin and Hewitt 1986
Wing Dimorphism	*G. firmus*	2	0.62	±0.08	Roff 1986
Diapause Duration	*Oncopeltus fasciatus*[4]	2	0.71	±0.07	Dingle *et al*. 1977
	Hyphantria cunea[6]	2	0.60	±0.01	Morris and Fulton 1970

[1] 1 = selection experiments, 2 = parent-offspring regression, 3 = sibling correlation approach
[2]Diptera, [3]Coleoptera, [4]Hemiptera, [5]Orthoptera, [6]Lepidoptera

and illustrates the generally higher heritabilities for morphological traits and lower heritability values for behavioral and life history traits.

MAINTENANCE OF GENETIC VARIANCE

Classical theory suggests that quantitative characters subjected to stabilizing selection should exhibit a decrease in additive genetic variance. However, Crow and Kimura (1970) proposed that changes in genetic variances in populations acted on by selection will decrease as the number of loci involved increases. Falconer (1981) noted that non-zero genetic variability exists for most metric characters even though they are under stabilizing selection. Bulmer (1971) presented a mathematical model which predicted that polygenic characters (those under the control of many loci) will demonstrate only temporary reductions in genetic variance under stabilizing or directional selection, but "rapidly reversed" under episodes of disruptive selection. An effectively infinite number of loci, with a large number of alleles at each, should thus result in only insignificant changes in heritable variation of quantitative characters involved.

Lande (1976) presented a quantitative model which suggested appreciable input to additive genic variance in fitness each generation from polygenic mutation and recombination effects. He predicted that mating systems have no significant influence on levels of maintained genetic variance (Lande 1977) and suggested that the counter-selection force of polygenic mutations occurring each generation may be sufficient to preserve or maintain additive genetic variance for some fitness components (Lande 1976).

Variable environments reflect different selection pressures on different genotypes and may exert sufficient effects to maintain genetic variability. MacKay (1980, 1981) varied the amount of ethanol (0% to 5%) in the diet of Drosophila melanogaster to determine the effect on heritability

and additive genetic variance of the following morphological traits: sternopleural bristle number, abdominal bristle number and body weight. All traits exhibited increased V_A in spatially and temporally varying environments as compared to that of flies reared on diets without ethanol. In a similar experiment Tachida and Mukai (1985) attempted to determine the cause of genetic variability of viability in D. melanogaster. Various strains, either homozygous or heterozygous for different wild-type second chromosomes, were raised on various combinations of yeasts and media. ANOVA tests showed significantly larger genotype-environment interaction components for homozygotes than for heterozygotes. The authors suggested that diversifying selection was responsible for maintaining genetic variation for viability. However, a third study, which examined the effect of flour type on various components of fitness in the flour beetles, Tribolium castaneum and T. confusum, showed no evidence that environmental variability preserves genetic variance. Dawson and Riddle (1983) suggested that antagonistic pleiotropy between fitness traits may inhibit such responses.

Sexual selection may also affect the maintenance of heritable variation for fitness traits. Arnold (1983) suggested that if a female preference for a heritable male character, which has been acted on by selection so that it has reached an optimal value, were to shift so that "a net force of sexual selection is exerted on the male character, this shift will create genic variance in total male fitness". Therefore a change in additive genetic variance in a sexually selected character could alter the additive genetic variance for fitness itself resulting in either production or erosion of heritable fitness variance within populations (Lande 1982).

Sexual selection and counteracting forces of natural selection may also function in preserving heritable variation for fitness traits. (Lande 1980,

1981). When these forces are not equal and act in opposite directions over evolutionary time heritable variation for fitness components will vacillate.

Finally, varying intensities of sexual selection may contribute to maintenance of heritable fitness variation. McLain (1987) demonstrated that, although sexual and natural selection favor larger body size in the green stink bug, Nezara viridula, the intensity of sexual selection was relaxed when diet quality was poor resulting in a decrease of measurable heritable variation for body size. This led McLain to suggest that environmental factors, such as diet quality, may limit heritable expression for body size which will be masked by increasing environmental variance.

Multiple mating in insects may be a sexually selected trait. If repeated inseminations impart some benefit to female fitness then mating more than once must be adaptive. The next section discusses the phenomenon of multiple mating in female insects and presents various adaptive explanations as to why females do so.

MULTIPLE MATING IN INSECTS

Repeated matings by female insects have been documented in at least some species of most orders (Thornhill and Alcock 1983). Since females are able to store sperm for extended periods of time in a specialized storage chamber, the spermatheca (Chapman 1980), a single complete insemination should thus be sufficient to fertilize all the eggs that a female produces in her lifetime (Parker 1970, Sivinski 1980). There should therefore be some benefit that females derive from mating more than once which outweighs the costs of doing so.

Costs associated with multiple mating by female insects may include the danger of physical damage to the female. For example, female dungflies (Scatophaga stercoria) are often injured or drowned when 3 or 4 males simul-

taneously attempt to mate with her (Borgia 1981). Additionally, time and energy normally allocated to seeking food or oviposition sites may be reduced. Finally, the risk of exposure to predators may be increased. Sakaluk and Belwood (1984) observed gecko phonotaxis to song of male decorated crickets, Gryllodes supplicans. They suggested that "satellite predation" by these lizards may "impose a sex-biased mortality" on female crickets which are intercepted and eaten as they approach calling males.

Selection should favor repeated matings by females if survivorship and reproductive output are increased (Parker 1970). Walker (1980) established several categories of possible benefits and these are discussed in the following paragraphs.

Acquisition of Nutrition. Males may supply females with nutrients necessary for maintenance, egg production and oviposition (Alcock 1984). Male hangingflies, Hylobittacus apicalis, offer dead arthropods to females which the latter feed on while in copula (Thornhill 1976, 1980b). The duration of copulation is positively correlated with prey size and number of sperm transferred. Females encountering males with small or unpalatable prey refused copulation attempts or terminated copulation prior to complete ejaculation. Repeated copulations with males offering nuptial gifts also reduced hazards involved in females searching for their own prey.

Male insects may also contribute nutrients to females by producing body secretions which are ingested by females. Transfer of regurgitated crop contents from males to females has been documented in Drosophila subobscura (Steele 1986a, b). Females mated more frequently with males offering drops and moved away from males without drops. Females which fed on regurgitated drops also had higher fecundity. Similarly, Panorpa scorpionflies produce saliva secretions which they present to females (Thornhill 1981). Females

mate preferentially with males offering these secretions and refuse copulation attempts by males without a nuptial gift.

Males of most cockroach species exude proteinaceous substances from tergal glands (Breed 1982). Nemobine (Mays 1971) and Oecanthine (Alexander and Otte 1967, Bell 1980) crickets produce glandular secretions from tibial spurs and metanotal glands respectively. Bidochka and Snedden (1985) demonstrated that female ground crickets, Allonemobius fasciatus, terminated copulation earlier when mated to males which had their tibial spurs painted than with unpainted males. In the primitive orthopteran genus, Cyphoderris, females actually consume the fleshy hindwings of males while in copula (Dodson et al. 1985, Sakaluk et al. 1987).

Males may also transfer nutritional substances directly into the females reproductive tract during mating. Using radio-tracer studies, Boggs and Gilbert (1979) demonstrated nutrient transfer in male ejaculates of Heliconius spp. and Danaus plexippus butterflies. A large number of other Lepidoptera also show nutritional gains from male ejaculates by copulating repeatedly (Drummond 1984).

Males of the cactophilic desert species, Drosophila mojavensis, also contribute nutrients to females which stimulates oogenesis (Markow and Ankey 1984). This behavior is absent in the more cosmopolitan species, D. melanogaster. Markow and Ankey (1984) postulate that since D. mojavensis occupy a harsh, fluctuating environment, often with limited resources, they require a greater degree of "paternal investment" than do female D. melanogaster which generally occupy less severe environments.

Males may also supply females with nutritious spermatophores. Female ladybird beetles, Harmonia axyridis, eject from the bursa copulatrix and consume male transferred spermatophores following copulation (Obata and Hidaka 1987). Most orthopteran males produce spermatophores which, in some

families, may have evolved as a form of nutrient supplement for females (Eberhard 1985). Increased fecundity due to nutrient transfer has been demonstrated in the grasshoppers, Melanoplus sanguipes (Friedel and Gillott 1977) and Chorthippus bruneus (Butlin et al. 1987), and in the German cockroach (Mullins and Keil 1980).

Male katydids, Requena verticalis, produce a bipartite external spermatophore consisting of a sperm-filled ampulla and a large proteinaceous spermatophylax, which may comprise 20% of the male's body weight. Females feed on the latter post copula. Selection for a large spermatophylax evidently evolved as a mechanism to prevent females from feeding on the ampulla before it has emptied of sperm (Gwynne 1983). Using radioactively labelled protein hydrosylate, Bowen et al. (1984) demonstrated uptake of ampulla contents by ovaries and eggs in R. verticalis. Male-derived nutrients were shown to enhance size and number of eggs laid (Gwynne 1984).

Spermatophore consumption is also common in grylline crickets and has been documented in the following species: Acheta domesticus (Khalifa 1950, Sakaluk 1981), Teleogryllus commodus (Loher and Rence 1978), G. bimaculatus (Simmons 1986), G. integer (Sakaluk 1981, Sakaluk and Cade 1983) and others (Alexander and Otte 1967). Whether or not the relatively small grylline spermatophore plays a nutritional role has not been demonstrated. However, Butlin et al. (1987) demonstrated increased fertility in female grasshoppers, Chorthippus bruneus, when the relatively small spermatophore packet provided by the male was consumed.

Insure An Adequate Sperm Supply. Females may remate if a first mating failed to inseminate the female, if insufficient sperm was transferred or if sperm from a previous mating becomes inviable with elapsed time. Blockage of the genital tract (Taylor 1967) or inability of the male to thread the thin tube of the spermatophore into the female (Loher and Rence 1978) may

account for failures in copulation. Many lepidopterans experience first-time mating failures of as high as 30%. Eberhard (1985) suggested that, with an increase in the complexity of the genitalic structures, the probability of an unsuccessful first time mating is increased.

Sakaluk (1981) and Sakaluk and Cade (1980) found that doubly mated G. integer and A. domesticus crickets produced significantly more progeny than did one time maters. This difference was due in large part to the failure of one time maters to produce any progeny suggesting that first time mating failures may be responsible for the difference.

Pyle and Gromko (1978) demonstrated a positive correlation between remating and increased female fitness (productivity, fertility, and fecundity) in D. melanogaster. They suggested that female flies may remate to replenish spent spermatozoa. Females of D. mojavensis also produce more offspring when paired continuously to conspecific males (Markow 1982).

Genetic Benefits. Females may increase the genetic diversity of their offspring by obtaining sperm from more than one male (Thornhill and Alcock 1983). The spermatheca of many female insects is a spherical structure which has the capability of expanding with successive matings, allowing storage of sperm from numerous inseminations (Alexander and Otte 1967, Eberhard 1985). This allows a degree of sperm mixing to occur within the spermatheca. Females are thus able to control the paternity of their offspring by diluting sperm from previous matings with sperm from a preferred male (Walker 1980). Sperm mixing is likely to occur in mating systems in which females mate solely for genetic reasons (Richmond and Ehrman 1974). Sperm mixing has been documented in chrysomelid beetles (Dickinson 1986, McCauley and O'Donnell 1984), in some drosophilids (Gromko et al. 1984, Markow 1982), in a cockroach (Woodhead 1985) and in the field crickets G.

integer (Backus and Cade 1986), G. bimaculatus (Simmons 1987b) and G. supplicans (Sakaluk 1986a, 1987).

In other insects a different system of sperm competition exists. Sperm precedence by displacement or by "last sperm in, first sperm out" is predominant in odonate (Fincke 1984, Waage 1984), lepidopteran (Drummond 1984), and in many dipteran (Gromko et al. 1986) species. By replacing less desirable sperm from previous mates with sperm from "genetically superior" males (ie. those that exhibit better foraging abilities, survivorship, and resistance to parasites and predators) females may increase the heritable fitness of their offspring (Walker 1980).

Although increased genetic diversity of offspring from multiple matings is a plausible theory, Williams (1975) maintains that a single mating is usually sufficient to provide half the within progeny variance in a population because of spontaneous mutations and cross-over events during meiosis. Therefore the genetic advantages a female obtains are probably slight unless offspring gain genetically in some other way.

Table 2 lists insect species in which females are known to mate multiply and the adaptive reasons for doing so.

Female crickets (Gryllidae) mate multiply and are therefore ideal animals to study the adaptive significance of repeated matings. The following section describes cricket mating behavior.

CRICKET MATING BEHAVIOR

Field crickets (Orthoptera: Gryllidae) are globally distributed, inhabiting a wide range of habitats. They are generally nocturnal, ground dwelling and may be either phytophagus or omnivorous (Vickery and Kevin 1985, Walker and Masaki, unpubl. ms.).

Table 2. Species of insects in which females are known to mate multiply.

Order	Species	Adaptive Function	Source
Odonata	*Enallagma hageni*	access to oviposition sites	Fincke 1984
	Calopteryx maculata	access to oviposition sites	Waage 1984
Orthoptera	*Gryllus integer*	genetic benefits, oviposition stimulation	Backus and Cade 1986, Sakaluk and Cade 1983
	G. bimaculatus	genetic benefits via female choice	Simmons 1986
	Requena verticalis	nutritional benefits	Gwynne 1984a
	Chorthippus bruneus	nutritional benefits	Butlin *et al.* 1987
Mecoptera	*Hylobittacus apicalis*	nutritional benefits	Thornhill 1976, 1980
	Harpobittacus similis	nutritional benefits	Gwynne 1984b
Hemiptera	*Abedus herberti*	access to oviposition sites	Smith 1979
	Nezara viridula	genetic benefits	McLain 1987
Lepidoptera	*Manduca sexta*	correct for faulty 1st mating	Raulston *et al.* 1975
	Atteva punctella	hormonal oviposition stimulation	Taylor 1967
	Danaus plexippus	hormonal oviposition stimulation	Boggs & Gilbert 1979
	Papilio xuthus	hormonal oviposition stimulation	Watanabe 1988
	Papilio polyxenes	replenish spent sperm	Lederhouse 1981
Coleoptera	*Labidomera clivicollis*	genetic benefits	Dickinson 1986
	Monochamus scutellatus	genetic benefits	Hughes & Hughes 1985
Diptera	*Anopheles culiciformes*	correct for faulty 1st mating	Mahmood & Reiser 1980
	Drosophila melanogaster	replenish spent sperm	Pyle & Gromko 1978, Gromko *et al.* 1984
	D. paulistorum	genetic benefits	Richmond & Ehrman 1974
	D. hydei	genetic benefits	Markow 1985
	D. mojavensis	nutritional benefits	Markow & Ankney 1984
	D. subobscura	nutritional benefits	Steele 1986b

Male crickets attract conspecific females by calling from sheltered locations, such as under logs, rocks or leaf debris (Alexander 1961, Ewing 1984). Stridulation by males also functions in aggressive encounters between males (Dixon and Cade 1986), territorial spacing (French and Cade 1987) and in courtship of attracted females (Alexander 1961). Onset of calling is proceeded by initial spermatophore production from two to seven days following the post-imaginal molt (Cade and Wyatt 1984).

Various factors may affect the calling behavior of male crickets. At high conspecific male density, G. pennsylvanicus males call less frequently possibly because of the increased cost of defending a calling site. Instead, males tend to spend more time actively searching for females. At lower densities males call significantly more and variance in male mating success is greater (French and Cade, in press). Male calling and movement is also related to levels of female movement and sexual receptivity (French and Cade 1987), which are under circadian control (Loher and Orsak 1985). Under laboratory conditions male aggressive interactions increase with density (Graham 1985).

Cade and Wyatt (1984) found that male age and body size do not affect calling duration in G. integer, G. pennsylvanicus or G. veletis. However, male aggression to conspecific males is positively correlated with age and size (Dixon and Cade 1986).

Although calling durations differ slightly among species, Cade and Wyatt (1984) found that G. integer call for significantly shorter periods than G. veletis or G. pennsylvanicus. The authors suggest that reduced calling in G. integer may have evolved through selection as a result of a parasitic fly. Female tachinid flies, Euphasiopteryx ochracea, orient to male cricket song and deposit larvae on the male's body. The larvae bore through the body wall and feed on the cricket internally leading to its

eventual death (Cade 1984b). Other males do not stridulate but instead remain close to calling males and intercept attracted females. This "satellite" behavior may result in a lower probability of being parasitized and avoidance of other costs associated with signalling (Cade 1984b, Cade and Wyatt 1984).

Female crickets respond to male song by orienting towards stridulating males either by ambulation (Loher 1981) or by flight (Cade 1979). Onset of phonotaxis corresponds with sexual maturity: within 24 hours of the post-imaginal molt in T. commodus (Loher and Edson 1973) and up to 6 days in A. domesticus (Sakaluk 1982).

The actual mating sequence is fairly ritualized among cricket species (Alexander 1961, Alexander and Otte 1967, Loher and Rence 1978). Once the female locates the male the latter switches from calling to a quieter courtship song. The female mounts the male and receives a spermatophore. The spermatophore consists of a thin tube, which the male threads into her bursa copulatrix, and an external portion. Copulation usually lasts only a few seconds in G. integer (Sakaluk 1981) and up to 3 min in T. commodus (Loher and Rence 1978).

Following copulation the female dismounts and the male may "guard" the female. This behavior may function in preventing other males from mating with the female (Parker 1970). Gwynne (pers. comm.) has offered an alternative reason for why male guarding occurs. He suggested that while large nutritious spermatophores evolved in the tettigonids, male gryllids adapted guarding behavior to insure females do not remove spermatophores before complete insemination has occurred. Graham (1982) found a significant linear correlation between spermatophore attachment time and male guarding duration. Sakaluk and Cade (1980), however, found no difference in the

length of spermatophore attachment between guarded A. domesticus females and females isolated from males immediately after mating.

Female crickets may actively choose males with whom to mate. Hedrick (1986) observed that female G. integer discriminate among males on the basis of calling bout duration, preferring those with longer bouts. Zuk (1987a) placed G. pennsylvanicus and G. veletis males in cages suspended above equidistantly spaced pitfall traps in an arena. Male age was significantly positively correlated with number of attracted conspecific females captured in pitfalls. Male body size, calling time and level of gregarine parasite infestation were not correlated with female attractedness. Since males were kept apart from each other, the results suggest that female choice rather than male-male competition was operating.

Female G. bimaculatus, when given a choice of males to mate with, laid significantly more eggs than females mated with an allocated male (Simmons 1987a). Offspring from the former developed more rapidly and reached reproductive age earlier suggesting a greater long-term reproductive success and offspring fitness. G. bimaculatus females also appear to mate preferentially and more frequently with larger males (Simmons 1986).

Female multiple mating is common in gryllids (Alexander and Otte 1961, Loher and Rence 1978, Sakaluk 1981, Simmons 1986). Female crickets do not exhibit refractory periods between matings and can therefore remate immediately following a previous copulation (Loher and Rence 1978) without ovipositing (Alexander 1961, Sakaluk and Cade 1980).

Graham (1982) found that courtship song apparently stimulates spermatophore removal by females. Females also regularly consume attached spermatophores. Sakaluk and Cade (1983) suggested that a oviposition stimulant may be passed at the time of copulation. They showed that doubly mated G.

integer females mated significantly more times than did females which had only mated once.

If multiple mating tendencies in female crickets are adaptive then it should reflect on the reproductive success of the females and fitness of their offspring. Repeated matings should therefore be a component of fitness and show polygenic variation within and between populations.

METHODS

All data were collected between January 13, 1987 and February 28, 1988 at Brock University, St. Catharines. Three experiments were performed for this study. The first experiment (age at first mating experiment) was set up to determine the age at which post-imaginal females first mate. A second experiment was designed to discover whether the mating rate of female crickets is affected by the time spent in contact with males. The third experiment (heritability experiment) was designed to deduce whether multiple mating in female crickets is heritable. This section describes the techniques and methods used to conduct these experiments.

CULTURING OF CRICKETS

Gryllus integer crickets used in this study were obtained from laboratory stock cultures originally derived from adults collected in the field near Austin, Texas. The cultures were maintained in 45 l garbage cans equipped with a 100W light bulb and maintained on a 12 hr light: 12 hr dark light cycle. Purina Cat Chow°, cotton-plugged water vials, moist fine-grain vermiculite for oviposition, and egg carton shelters were supplied.

Cans were checked daily for newly molted adults which were removed and placed individually into 500 ml plastic tubs. All tubs were supplied with food and water. Adults were allowed to reach sexual maturity (when calling

begins in males and when females become phonotactic) and then used as needed. Sexual maturity is signalled by initial calling by males at an average age of 6.9 days following the post-imaginal moult (Cade and Wyatt 1984) and by initiation of phonotaxis in females (see next section on age at first mating experiment).

Crickets used in the age at first mating and mating rate experiments were taken from a second generation lab culture. Crickets used for the heritability experiment were from a first generation culture derived from crickets collected in the field in Austin, Texas between February 25th and 29th, 1987.

AGE AT FIRST MATING EXPERIMENT

The purpose of this baseline experiment was to determine the average age at which adult female G. integer first mate in order to insure only sexually mature females were used for the heritability experiment.

Female G. integer were removed daily from garbage cans containing stock cultures to insure that newly molted individuals were less than 24 h old. Individuals were marked distinctively on the thorax with Correction Liquid Paper® and introduced into plastic mating chambers (36 x 30 x 17 cm), up to a maximum of 4 females per chamber ($x = 3.1$, Range = 1-4). Food and water were supplied ad libitum. Adult, sexually mature males in equal numbers to the number of females present at any one time were then placed in the chambers.

Females were observed for 5 hr daily to record age at first mating (age here meaning post-imaginal age). Once mated females were discarded. Those females not mating in the 5 hr observation period were removed from the chamber and returned to their individual 500 ml tubs. This procedure was

continued daily until females mated. Mean time to first mating was calculated from the data.

MATING RATE EXPERIMENT

This baseline experiment was conducted to investigate whether 5 h observation periods were sufficient to collect accurate data on mating rates for the purpose of conducting the heritability experiment.

To determine whether the length of time female crickets are exposed to males affects the rate of mating sets of 2 females were introduced into 500 ml plastic tubs containing a calling male, 3 cm of moist vermiculite for oviposition, and cat chow. All females used were between 4 and 11 days old.

Twelve sets of 2 female crickets were exposed to males for 5 hs daily during the light cycle for 10 consecutive days. All matings during the observation periods were recorded. A mating was deemed successful if a spermatophore was attached to the female during the mating sequence.

A further two sets of female crickets were exposed to males continuously for 10 days. A Panasonic WV-3230 color video camera and a Panasonic AG-6010 VHS Time Lapse video recorder were used to monitor number of matings. This system allowed 24 h of continuous recording with a 2 h playback time consisting of 2 sec frames.

During viewing of the tapes the presence of a spermatophore attached to the female was almost never discernible. A mating was therefore considered successful if males did not resume calling after mating and/or if females began ovipositing after a mating attempt. Male G. integer take an average of 20 minutes to produce a new spermatophore and resume calling (Sakaluk 1981). Females, following a successful mating, will not respond to male song and begin ovipositing immediately if a suitable substrate is available (Loher 1981).

The average number of matings over the 10 day period was calculated for sets of females exposed to males 5 hs per day and for those continuously in contact with males. The mating rate per 24 h day was then calculated for both groups of females.

HERITABILITY EXPERIMENT

The purpose of this experiment was to determine the heritability for multiple mating in female G. integer. As in the previous experiments, newly molted adults were removed daily from garbage cans and placed in individual 500 ml plastic tubs.

Observation chambers (36 x 30 x 17 cm) were set up with adequate food and water and with a 500 ml expanded polystyrene tub containing 4-6 cm of moist vermiculite. Four adult males of approximately the same age and size were introduced into each chamber and allowed to acclimate for 24 hs.

Correction Liquid Paper® was used to mark females with either 1, 2, 3, or 4 dots on the pronotum. Four females between 4 and 11 days old were introduced into each chamber. Chambers were then concurrently observed for 5 hours each day (beginning 1 h into the light phase) for 10 consecutive days. Females were checked every 5 minutes for spermatophore attachment indicating a successful mating had occurred. When the spermatophore was removed or consumed (not necessarily observed each time) a mating was considered complete. These observations allowed a complete record of the number of times each female mated over the 5 h observation periods.

Following each observation period individual females were placed in labelled 500 ml oviposition chambers containing 4-6 cm of moist vermiculite. Females were thus able to continue to oviposit when not being observed. Cat chow was replaced daily to prevent mold formation. In total 66 females were observed.

Following the 10 day observation period females were retained in the oviposition tubs an additional 5 days to allow egg-laying to continue. Females were then removed and discarded.

The oviposition tubs were placed in individually labelled hatching chambers (28 x 17 x 13 cm) under 100 W brooder lamps. Temperatures inside the containers ranged from 24°C during the dark cycle to 31°C during the day cycle. Emerging nymphs were given cat chow ad libitum, water in cotton plugged vials, and egg cartons for shelter.

Nymphs were observed daily when they reached the late instar stages to insure any adults were removed within 24 hs of their post-imaginal moult. Newly molted male and female crickets were placed into individual 500 ml tubs and marked as to age and sex. A total of 10 offspring were removed from each of the chambers representing a parental female. All males collected were used for the second generation portion of the experiment.

Observation chambers were set up in identical fashion to those described for the parental females. All F_1 females were again marked with 1 to 4 dots on the pronotum and observed in the mating chambers for 5 hs a day for 10 days. As before females were placed in individual marked tubs containing vermiculite when not being observed. This insured similar environmental conditions and handling procedures for both parent females and their female offspring. Recording of number of matings was as for the parental generation.

An unidentified ailment which caused abdominal bloating, a reduction in observed mating behaviors (calling in males and response to courtship song and mounting in females), and frequent death of individuals resulted in a small sample size of first generation adults. All visibly diseased adults were discarded. To increase the sample size of parental adults additional second generation females from the original stock culture were obtained.

A linear regression of female offspring on female parents was performed using SPSS statistical packages (Nie et al. 1980, Norusis 1986) on a Burroughs B7900 mainframe at Brock University, St. Catharines. The ten offspring values for each parent were averaged prior to the analysis (Falconer 1981).

The heritability of multiple mating in G. integer was then calculated by multiplying the slope of the regression line by 2 so that:

$$h^2 = 2b$$

where b is the slope of the regression line (Falconer 1981).

To calculate the standard error the sampling variance of the regression coefficient, σ_b^2, was computed using the following equation (Falconer 1981):

$$\sigma_b^2 = \frac{k[1 + (n - 1)t]}{nN}$$

where k is the number of parents (either 1 or 2), n is the number of offspring per family, and N is the sample size. The intraclass correlation coefficient, t, which estimates the degree of resemblance between groups (Zar 1984) was calculated as follows:

$$t = \frac{\sigma_B^2}{\sigma_B^2 + \sigma_W^2}$$

where σ_B^2 is the between family variance and σ_W^2 is the within family variance. Finally, the standard error was estimated as follows:

$$s.e.(h^2) = 2\sqrt{\sigma_b^2}.$$

RESULTS

AGE AT FIRST MATING EXPERIMENT

The table in Appendix I gives the ages of female G. integer (n = 32) when first time matings occurred. Four females which died during the course of the experiment were excluded from the sample. On average females mated

for the first time at 3.6 days (S.D. = 2.3, Range = 0-8 days) following the post-imaginal moult. Sixty percent of females mated by day 4, 84% by day 6, and 100% by day 8. This distribution is shown in Figure 1.

In light of the above results all female crickets used in subsequent experiments were at least 4 days old to insure sexual maturity.

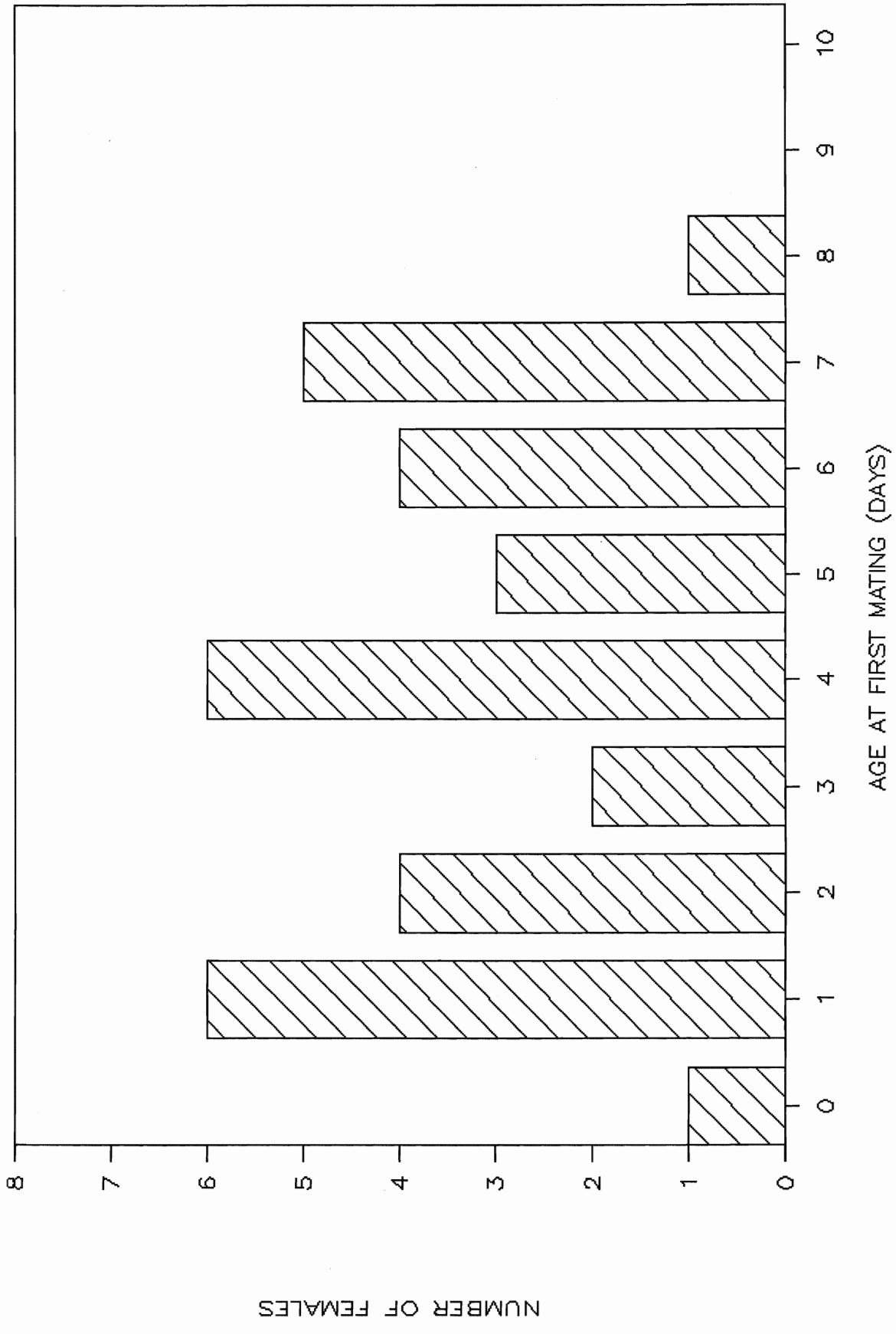
MATING RATE EXPERIMENT

Females continuously exposed to males over the 10 day observation period mated at an average rate of 1.1 times in a 24 h day (S.D. = 0.7, Range = 0-4) (see Appendix II).

In those observations in which female G. integer were in contact with males for 5 hs per day the average rate of matings for females was 1.7 matings per 24 h day (S.D. = 3.5, Range = 0-5) (see Appendix III).

There was no significant difference between the mean rate of mating in females in continual contact with males and in females which had access to males only 5 hs per day ($U = 21.0$, $p < 0.05$, $n_1 = 2$, $n_2 = 12$). It was therefore concluded that a 5 h observation period per 24 h day is sufficient to represent accurately mating rates in these crickets. Therefore all observations for the heritability experiment were 5 hs per day.

Figure 1. Age at which G. integer females first mate following the post-imaginal molt.


NUMBER OF FEMALES
0
1
2
3
4
5
6
7
8
0
1
2
3
4
5
6
7
8
9
10
AGE AT FIRST MATING (DAYS)

HERITABILITY EXPERIMENT

Of the 66 parental females observed 9 produced no offspring and 6 produced less than the minimum 10 female offspring required for the heritability study. These individuals were discarded from the sample. Additionally, 4 more females produced offspring which showed symptoms of the illness described in the methods section. These families were also discarded to prevent any risk of contaminating the other cultures. Finally, 1 female did not mate during the 10 day observation period. A total of 46 parental females and their offspring were thus observed for number of matings.

As described in the method section an apparent illness necessitated use of second generation adults in addition to the first generation adults observed initially. In total, 21 first generation and 25 second generation females were used. A two-tailed F-test showed no significant difference between the variances of the first and second generation parental females ($F = 1.65$, $p > 0.05$).

Appendix IV presents a complete data set for observations on multiple matings in parent females and their female offspring. The number of matings by female G. integer in the parental generation ranged from 1 to 30 times ($x = 9.8$, S.D. = 6.6) and is illustrated graphically in Figure 2. The most times a female mated in a single observation period was 5 times.

Number of offspring matings ranged from 0 to 26 times. When the number of matings by the 10 offspring from each parental female were averaged the range was constricted to 1.9 to 16.2 times ($x = 7.3$, S.D. = 3.4). Figure 3 graphically illustrates average number of matings by offspring from each parent.

Figure 2. Frequency of matings observed in parental G. integer females over the 10 day observation period.

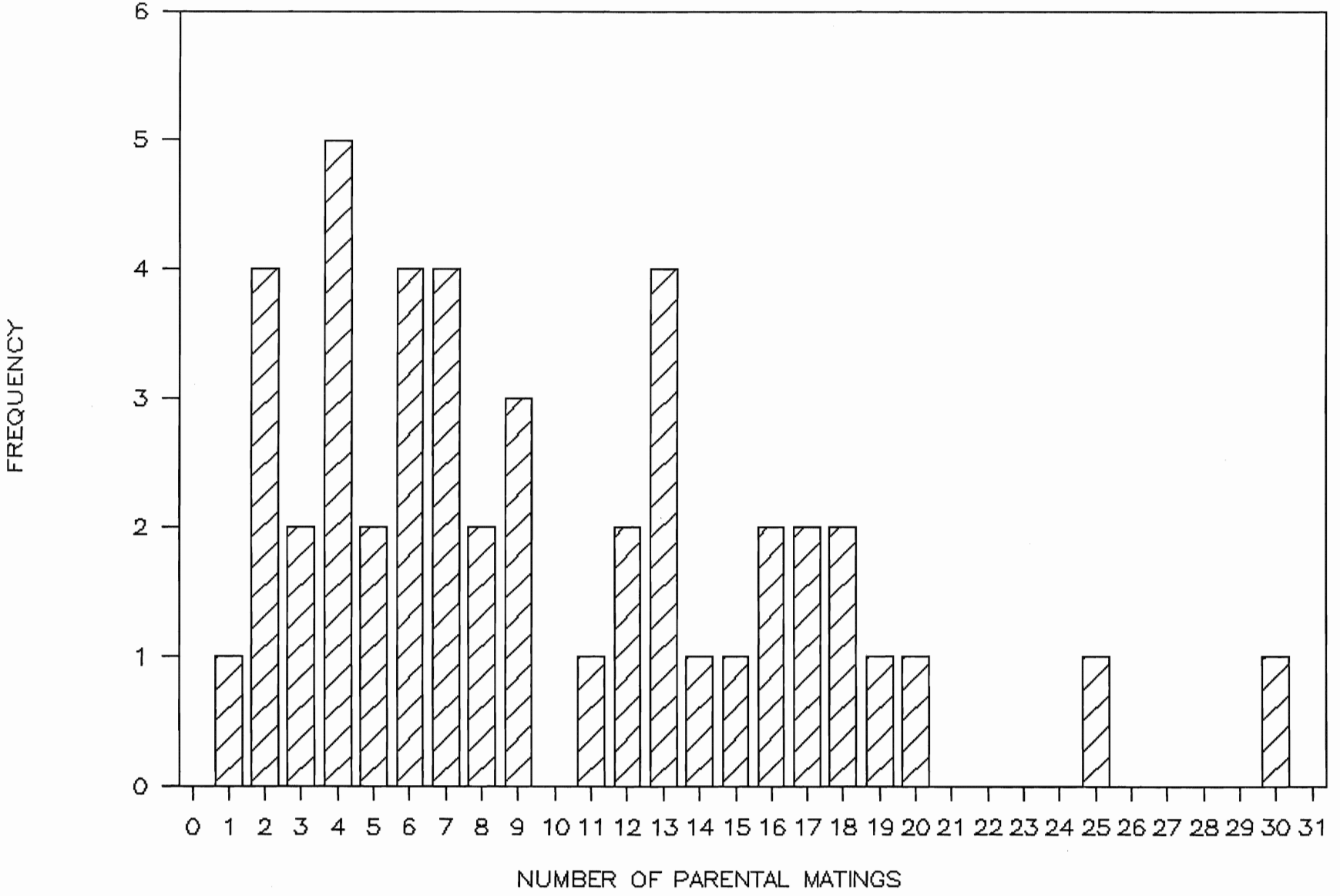
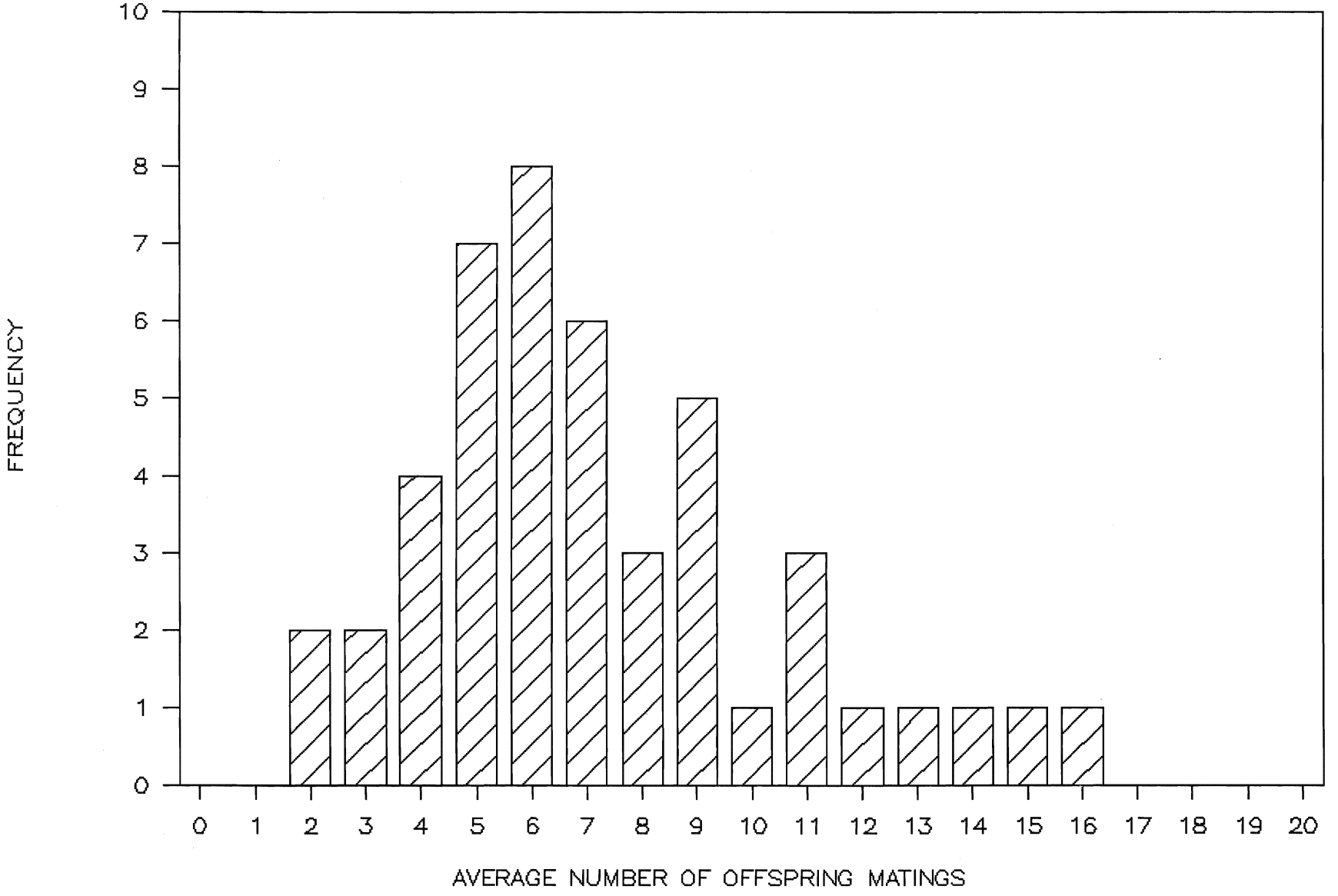

FREQUENCY
0
1
2
3
4
5
6
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
NUMBER OF PARENTAL MATINGS

Figure 3. Frequency of matings averaged for 10 offspring per parental female over the 10 day observation period.


FREQUENCY
10
9
8
7
6
5
4
3
2
1
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
AVERAGE NUMBER OF OFFSPRING MATINGS

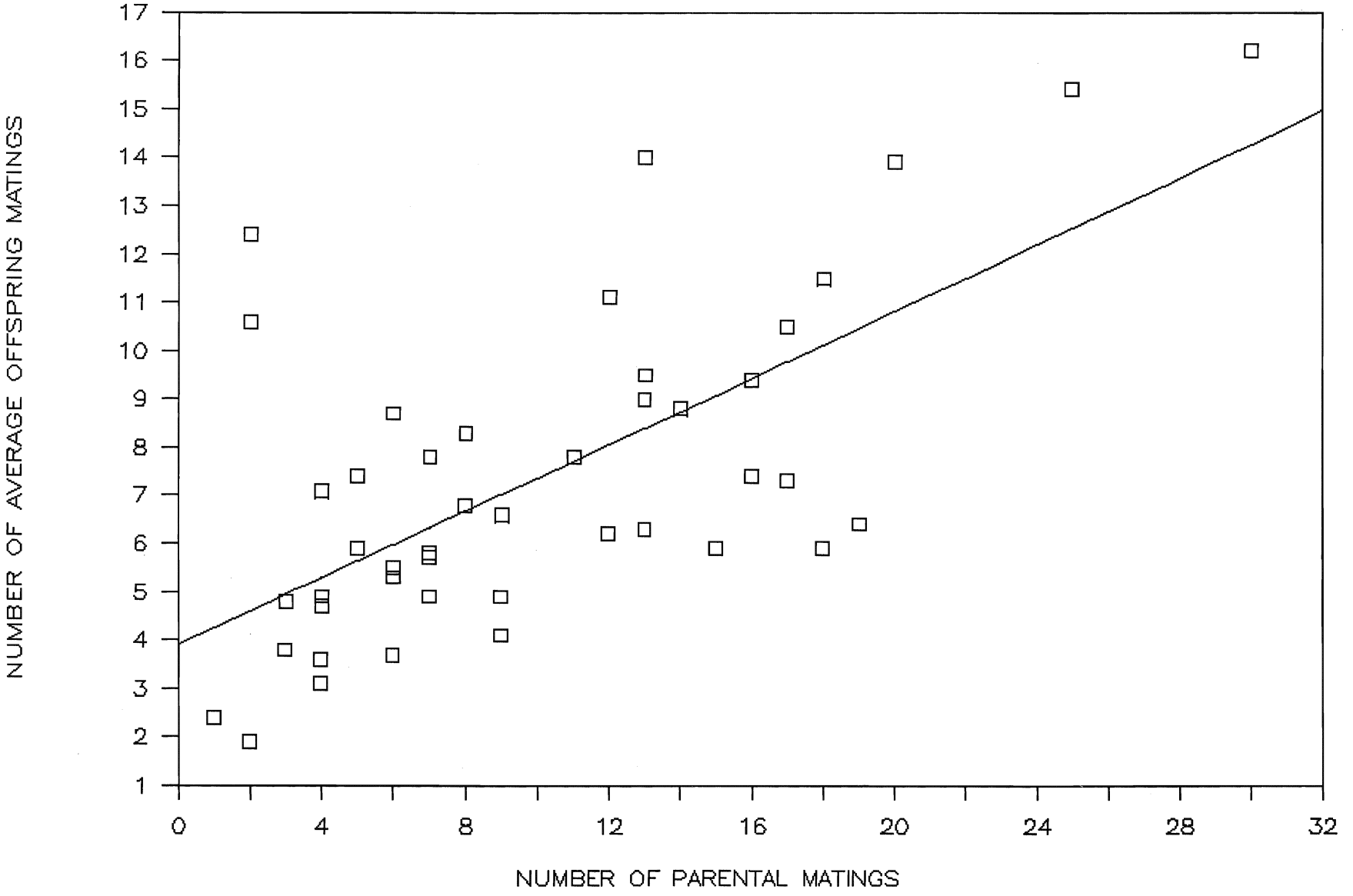
The regression equation for the linear regression of offspring on parent values was:

$$y = 3.908 + 0.345x$$

where the value 3.908 represents the y-intercept and 0.345 represents the slope of the regression line. Figure 4 illustrates the linear regression of average offspring matings on parental matings. The regression was found to be statistically significant ($F = 35.5$, $p < 0.0001$). The heritability of multiple mating was then calculated as twice the slope resulting in a heritability value of 0.690 ± 0.287. Derivations and methods used to calculate the standard error are given in Appendix V.

Several assumptions had to be made in order to conduct a linear regression on the data. The dependent values (offspring data) for each of the independent values (parent data) along the regression line must be homoscedastic, in other words, they should have a common variance, and for any given independent value the dependent values must be independently and normally distributed (Zar 1984). Bartlett's test for homogeneity of variances showed no significant differences in variances of offspring between different families ($\chi^2 = 64.62$, d.f. = 45, $p > 0.05$). A series of Kolomogorov-Smirnoff tests ($p > 0.05$) on the offspring of each parent female for goodness of fit to a normal distribution demonstrated deviations from a normal distribution in only 6 of the 46 families. This is insignificant for the purposes of the regression since these values will average out with the rest of the family values (Ralph, pers. comm.).

Figure 4. Linear regression line depicting relationship of number of times parental matings and average number of offsprings matings.


NUMBER OF AVERAGE OFFSPRING MATINGS
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
4
8
12
16
20
24
28
32
NUMBER OF PARENTAL MATINGS

DISCUSSION

This study has demonstrated that multiple mating is a heritable trait in female G. integer crickets. The heritability value calculated for this behavior ($h^2 = 0.690 \pm 0.287$) is consistent with the findings of Mousseau and Roff (1987). In an extensive review of the pertinent literature they found that life-history traits (such as fecundity, developmental rate and viability) generally exhibit low levels of heritable variation while morphological traits are generally heritable to a greater degree. Behavioral traits (such as multiple mating) generally had heritabilities intermediate between life-history and morphological traits. These data are in contention with the hypothesis that "on the whole, characters with the lowest heritabilities are those most closely related to fitness, while characters with the highest heritabilities are those that might be judged on biological grounds to be the least important as determinants of natural selection" (Falconer 1981), a corollary of Fisher's (1958) Fundamental Theorem of Natural Selection.

It is important to understand that the heritability value obtained in this study is valid only for the particular population employed in this investigation and for the environmental conditions experienced by the experimental population. An effort was made to keep the laboratory environment constant for all individuals used in this study since more variable conditions may decrease the detectable heritability (Falconer 1981). Because "genetic components are influenced by gene frequencies and may therefore differ from one population to another, according to the past history of the population" (Falconer 1981), another sample collected at a different time or place may have yielded heritability values lower or higher than the one obtained in this study.

The heritability value for multiple mating by female G. integer calculated here compares favorably (in terms of magnitude) with the herit-

ability of another behavioral trait in this species. Cade (1981a) computed realized heritabilities of 0.50 and 0.53 for high and low selected lines for male nightly calling duration. However, the heritability value for female multiple mating presented here is substantially larger than heritabilities calculated for various morphological traits in G. integer (McGowan 1986) and other gryllids (Roff 1986, Simmons 1987a). These values are not in concordance with the findings of Roff and Mousseau (1987) who suggest that morphological traits should exhibit greater heritable variation than behavioral and life history traits. Morphological traits in gryllids may be more sensitive to micro-fluctuations in the laboratory environment than behavioral traits resulting in masking of some heritable variation by environmental variation.

A source of environmental variation which is difficult to control in the laboratory, and which may result in inflated values for heritabilities, are maternal effects (Falconer 1981). Maternal effects are pre-natal and post-natal influences of the female parent on her offspring. These influences may be due to nutritional factors, ovipositional factors, and infectious disease factors. Conversely, competition between offspring for resources may increase levels of measurable heritable variation.

The standard error obtained for the estimated heritability of multiple mating in female G. integer was relatively large (S.E. = ±0.287). This is a common problem in many heritability studies since heritabilities themselves are not easily estimated with any great precision (Falconer 1981). The large standard error was a result of the small sample size used. This was partially due to space and labor limitations but mainly due to the apparent illness which affected the parental generation.

Mousseau and Roff (1987) formulated an equation from their collective heritability data from the literature which yields the relationship between the standard error and the estimated heritability value such that:

$$S.E. = 0.172(\pm 0.014)h^2 + 0.088(\pm 0.007).$$

By substituting in the heritability value for multiple mating calculated in this study a standard error range of $0.032 < S.E. < 0.328$ was obtained. The standard error calculated (in the results) by conventional methods (see Falconer 1981) falls well within this range suggesting that it is essentially accurate within the limits of this study.

The remainder of this section discusses various adaptive (and one non-adaptive) explanations for why multiple mating in G. integer females exhibits heritable variation and its effect on female fitness. Possible mechanisms which may maintain heritable variation underlying multiple mating in this species are also presented.

SIGNIFICANCE OF MATING MULTIPLY: ADAPTIVE EXPLANATIONS

Sperm depletion has been suggested as an impetus for remating in insects. Sperm depletion in the spermatheca is correlated with remating in D. melanogaster (Pyle and Gromko 1978). Female flies exhibit decreased fecundity, fertility, and productivity over time. However, in most insects one complete insemination is usually sufficient to fertilize all the eggs a female may produce in her lifetime (Parker 1970) and sperm can be stored in the spermatheca indefinitely (Walker 1980). Loher (1981) demonstrated that a single mating by female Teleogryllus commodus was sufficient for 4 weeks of continuous oviposition. One insemination suffices for a life-time of egg-laying in female A. domesticus (Murtaugh and Denlinger 1985) and G. bimaculatus (Simmons 1986). Depletion of viable sperm is therefore an unlikely explanation for repeated matings by female crickets.

Acquisition of nutrition is also an unlikely function of multiple mating in gryllids. Spermatophores of male crickets represent a very small percentage of total male body weight unlike the large proteinaceous spermatophores of tettigonids which may represent up to 40% of the male's body weight (Bowen et al. 1984, Gwynne 1984a). Production of large nutritious spermatophores probably represents a form of mating effort (Wickler 1984) or parental investment (Sakaluk 1986a) by males. Since males are investing substantial metabolic energy into producing these spermatophores, they should be assured of fathering a large proportion of the female's offspring. Since female G. integer mate with different males and are highly mobile, any male mating effort or nutritional investment in offspring is improbable. The relatively small spermatophores produced by G. integer males may therefore preclude any nutritional value to the female.

Female G. integer may remate in order to receive oviposition stimulants which are passed in the male's sperm. Loher and Edson (1973) and Sakaluk and Cade (1983) suggested that male crickets pass a "mating factor" during insemination which increases oviposition in females. Supernumery matings in other gryllids has been shown to result in increased oviposition (Loher 1981) and increased offspring production (Sakaluk and Cade 1983, Simmons 1986). Destaphano and Brady (1977) found that A. domesticus sperm contains an enzyme called prostaglandin-synthetase which converts arachidonic acid into prostaglandins (specifically PGE and PGE_2). Haemocoelic injections of nanogram amounts of PGE_2 stimulated oviposition in both A. domesticus (Destaphano et al. 1982) and in T. commodus (Loher 1979). Thus a successful copulation triggers PGE_2 activation causing an immediate release of stored eggs (Loher 1981, Loher and Edson 1973) if a suitable oviposition substrate is available (Destaphano et al. 1982). Another "egg-laying factor" may remain active during prolonged periods of substrate deprivation (Murtaugh

and Denlinger 1985) and long term oocyte production may be increased due to elevated JH III titres (Loher et al. 1983). It is therefore possible that female G. integer remate to stimulate egg production and oviposition. However, since the stimulants are passed directly into the bursa copulatrix during sperm transfer the function of spermatophore ingestion by the female, which is common in this species (Acharya 1988; Sakaluk 1981), is not explained by this theory.

Female crickets may ingest spermatophores post-copula as a way of exercising mate choice (Simmons 1986). By controlling the length of time the spermatophore is attached females can control the amount of sperm transferred. In the crickets Gryllodes supplicans (Sakaluk 1984) and G. bimaculatus (Simmons 1987a) spermatophore attachment time is positively correlated with the number of sperm transferred. Simmons (1986) demonstrated that female G. bimaculatus removed spermatophores from small males significantly earlier than those of larger males, and mated more often with males that were burrow residents (Simmons 1987b). Furthermore, females allowed to choose from several males exhibited higher egg production and oviposition than females allocated males at random (Simmons 1987a).

Female G. integer have also been shown to mate preferentially with larger males (Acharya 1988) and remove spermatophores at variable times (Solymar, pers. observ.). Male G. integer used for this investigation were of approximately the same size and age, and were not marked individually. As well, most copulations were not observed and therefore it was not possible to discern whether females were choosing and, consequently, mating more frequently with some males. However, in natural populations males of this species typically call from sheltered areas (Alexander 1968) and it is therefore probable that females remain with these males for extended periods and mate more than once during this time.

Female crickets may demonstrate mate choice by mating with an array of males. Sperm mixing is known to occur in G. integer (Backus and Cade 1986), G. bimaculatus (Simmons 1986), and in G. supplicans (Sakaluk 1986a). In G. integer there is a slight second male precedence (72% of all eggs fertilized) which would suggest that females could increase the genetic diversity of their offspring by mating with different males and ovipositing between inseminations (Backus and Cade 1986). However, if a female remains with a male for extended periods and mates only with that male than genetic diversity of offspring should be negligible. Female G. integer may also increase their offspring's fitness by mating more often with "genetically superior" males thereby flooding the spermatheca with sperm from these males (Borgia 1979). For example, female G. integer mate preferentially with larger males (Acharya 1988), body size being heritable in this species (McGowan 1986).

Female G. bimaculatus , which are given a choice of mates, produce offspring which develop faster, begin their reproductive life sooner, and exhibit higher survivorship than offspring from females mated with an allocated male (Simmons 1987b).

It is important to realize that females probably choose mates by assessing an array of male characters simultaneously (Acharya 1988, Lande and Arnold 1983). If these male characters, and female preferences associated with these characters, exhibit heritable variation then offspring fitness should be increased.

Finally, although empirical evidence is lacking, female gryllids may mate initially with the first conspecific male encountered to insure a ready sperm supply. Subsequent matings may then involve female choice of mates. This would allow females to continue "sampling males throughout their reproductive life without having to commit their total reproductive effort to a single male" (Simmons 1986).

SIGNIFICANCE OF MATING MULTIPLY: A NON-ADAPTIVE EXPLANATION

Halliday and Arnold (1987) have offered an alternative suggestion for the significance of multiple mating by females. They hypothesize that a genetic correlation exists between male and female mating tendency. This genetic coupling would allow for little genetic variation for sexual dimorphism and therefore divergence between the sexes would be extremely slow. The authors make 2 major assumptions: firstly, a genetic correlation due to pleiotropic gene interactions exists between mating tendency in the sexes and this mating tendency has a polygenic basis. And secondly, selection on male mating tendency is more vigorous than on females. They therefore suggest that multiple mating by females is an adaptively neutral trait which occurs due to tight genetic coupling between male and female mating tendency which has "inhibited divergence from male promiscuity". They reinforce their view by pointing out that various morphological traits (such as body size) and some behavioral traits (mating speed in Drosophila) have been demonstrated as having positive genetic correlations between the sexes. Thus, for example, larger males are more apt to sire larger progeny of both sexes and smaller males produce smaller male and female offspring.

Despite the interesting inferences that this hypothesis has on evolutionary theory, the body of evidence for an adaptive function for multiple mating in crickets (female choice for male characters, Acharya 1988 and Simmons 1986; the occurrence of sperm competition suggesting genetic benefits to offspring, Backus and Cade 1986; and increased offspring production by females mating more than once, Sakaluk and Cade 1983) is solid. The remainder of this treatise therefore treats the subject in the context of multiple mating by female G. integer as being an adaptive behavior.

MECHANISMS MAINTAINING HERITABLE VARIATION FOR MULTIPLE MATING

If multiple mating is adaptive then heritability for multiple mating in female G. integer is probably preserved by varying selection forces, genotype-environment (g-e) interactions and underlying antagonistic pleiotropy between multiple mating tendency and other fitness components.

Arnold (1983) suggested that sexual selection in the face of countervailing natural selection can preserve additive genetic variance for fitness traits. This can occur when opposing selection forces act on fitness components in different directions (Arnold 1983) or at varying intensities (Arnold and Wade 1984a, b). Since these forces are not always constant in space or time, either between or within populations, their strength and direction can vary due to temporal or spatial fluctuations in the environment. Nevo (1976) suggested that "magnitude of genetic variation for fitness traits can be regarded as an adaptation to environmental heterogeneity and selection as the tendency to adapt individuals to different environments".

As discussed earlier in this paper, female crickets derive benefits from mating more than once through increased offspring production and mating multiply may be a mechanism of female choice. Since greater reproductive success signals greater fitness this behavior is likely a sexually selected trait. And if multiple mating is considered as a mechanism of female choice, then heritable variation underlying this trait should deteriorate rapidly if sexual selection forces are strong (Williams 1975). However, if the intensity of sexual selection acting on multiple mating in female G. integer varies over evolutionary time then significant and substantial heritable variation could be preserved.

Fluctuations in sexual selection intensities may occur due to shifting male densities, varying availability of food resources and acceptable ovi-

position sites , seasonal parasite-host interactions and other environmental factors. French and Cade (In press) found that sexual selection acting on several correlated male characters (mating frequency and nightly calling duration) was more intense at low male densities of G. pennsylvanicus. At high male densities sexual selection pressures on these correlated traits were relaxed. In low male density populations of G. integer sexual selection forces acting on multiple mating behavior in females may be relaxed. Under high density male situations a greater array of males are available to choose from and sexual selection intensity on multiple mating may intensify.

Seasonal predation and parasite pressures may also cause a shift in heritable levels of variation for multiple mating in female G. integer. The parasitic fly, Euphasiopteryx ochracea, is acoustically attracted to calling males (Cade 1975). Female flies deposit larvae on and around calling males. The larvae burrow into the male and consume it from within resulting in eventual death of the male (Cade 1981a). Parasite levels fluctuate widely throughout the summer (Cade, pers. comm.) and the number of healthy, unparasitized male crickets available to females may therefore also fluctuate with fly density. The reduced availability of healthy males due to widespread parasitism during certain times of the year may therefore decrease the opportunity for sexual selection forces to act on female choice of mates. This may limit the expression of heritable variation for female multiple mating behavior during certain times of the year. It should, however, be noted that no evidence exists suggesting females are able to discriminate healthy males from parasitized males.

Another mechanism which may preserve heritable levels of variation for multiple mating are g-e interactions (Berven 1987, Dingle et al. 1979, Via 1984). Individual genotypes are thought to have different ranks in phenotypic value in different portions of the environment occupied by a

population (Dawson and Riddle 1983, Via and Lande 1985). The magnitude of the interaction affects additive genetic variances and covariances between fitness traits and provides a means of quantifying g-e interactions so that responses to selection may be predicted (Via and Lande 1987). Thus, additive genetic covariance between characters or character states (the same character expressed in 2 or more environments) measures the extent to which they have the same genetic basis (Falconer 1981). For example, a high genetic correlation between characters (or character states) suggests that all genotypes react in the same manner to changes in the environment. Conversely, a low genetic correlation suggests that different genotypes react differently to environmental variation (Falconer 1981).

Heritable variation for multiple mating by female G. integer in different environments may be masked to varying degrees if significant g-e interactions exist between multiple mating and one or more environmental variables (such as quality and type of food available, ambient temperature, relative humidity, light cycle, or oviposition substrate). The presence of such interactions could be tested by conducting an investigation in which female crickets, originally from the same parent population, are introduced and reared for successive generations in different environments. Heritability values for multiple mating and additive genetic correlations with other fitness traits (such as fecundity and productivity) calculated from the parent populations and the populations from the different environments would then demonstrate the presence of g-e interactions and their effect on levels of heritable variation for multiple mating behavior.

The importance of genetic correlations for fitness traits to heritability studies was discussed earlier in this paper. However, the genetic correlations considered were positive ones between fitness components. Negative genetic correlations between multiple mating and other fitness

traits may protect underlying heritable variation for multiple mating tendency.

The primary genetic cause of negative correlations is antagonistic pleiotropy, or "genetic trade-offs" in fitness (Rose 1982). Genes which exhibit antagonistic pleiotropy affect one character in one direction and a second character in the opposite direction resulting in a negative genetic correlation between them (Service and Rose 1983). Thus, at equilibrium substantial heritability in fitness components may exist without any net change in the heritability of fitness itself (Rose 1982).

The antagonistic pleiotropy hypothesis is generally expected to reveal correlation patterns between early- and late-life fitness components and, as such, may be looked at as trade-offs between reproduction (early-life fitness) and survival ability (late-life fitness) (Rose 1984, Schnebel and Grossfield 1988). Rose and Charlesworth (1981) found significant negative genetic correlations between early fecundity and lifespan and between egg-laying rate and longevity. Service and Rose (1985) attained similar results between early-life fecundity and starvation resistance. However, Schnebel and Grossfield (1988) cautioned that "the hypothesis is only relevant to the evolution of life history differences among individuals in the same breeding population confronted by the same environmental constraints" and does not apply to studies of life-history differences between species.

Multiple mating, if regarded as an early-life (reproductive) fitness component, may be negatively correlated with some late-life (longevity) fitness component. The probability of parasitism may, for example, be considered a late-life fitness component affecting longevity of G. integer females. As described earlier in this treatise, the tachinid fly, E. ochracea, deposits larvae on and around calling male G. integer (Cade 1984b). At times of the year when fly densities are high female G. integer

may experience increased parasitism risks. As female crickets orient towards calling males fly larvae deposited on grass or other material near the male may crawl on the female and burrow into her thereby decreasing her reproductive lifespan. Hamilton and Zuk (1982) suggested that parasite-host cycles may maintain significant levels of heritable variation and that females should choose healthy, vigorous males over parasitized males. Cade (1984b) demonstrated that parasitism by E. ochracea reduces the duration of calling by male G. integer thus limiting their ability to attract females. Fluctuating selection pressures and underlying antagonistic pleiotropy between multiple mating tendency and parasite avoidance could therefore affect heritable expression for repeated matings in female G. integer during times of the season when fly densities are high.

SUMMARY

Multiple mating by female G. integer was shown to have a heritability of 0.690 ±0.287. Supernumery copulations in gryllids have elsewhere been shown to be closely linked to reproductive fitness and increased offspring production (Sakaluk and Cade 1983, Simmons 1987b) and to be a form of female choice (Simmons 1986). The results of this study refute the contentions of classical theory which suggest that traits closely related to fitness should exhibit low or zero heritable variation because of strong selection pressures over evolutionary time. The findings in this study are, however, in accordance with a growing body of empirical evidence which demonstrate that even traits closely linked with fitness can have significant levels of heritable variation in natural populations.

Repeated mating by female G. integer may be adaptive and has been shown here to exhibit significant and substantial heritability. It is suggested that multiple mating in this species is a mechanism of female choice in

which females control the amount of sperm transferred from each male mated with. "Preferred" males are allowed to donate larger amounts of sperm than "non-preferred" males resulting in flooding of the spermatheca with the "preferred" male's sperm. Additionally, male sperm may contain egg production or oviposition stimulants.

Finally, several mechanisms which may act to preserve heritable variation for multiple mating in female G. integer were presented. Intensities of sexual selection may change due to temporal or spatial fluctuations in the environment. Differential responses by different genotypes to different environmental conditions may give rise to substantial genotype-environment interactions which may maintain heritable levels of variation. And, finally, antagonistic pleiotropy between reproduction and survival may play a significant role in the preservation of heritable variation for multiple mating in this species.

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APPENDICES

Appendix I. Observational data on when female G. integer first mate after the post-imaginal moult (N = 32).

Female No.	Age at First Mating
1	1
2	5
3	5
4	1
5	8
6	6
7	2
8	7
9	4
10	7
11	4
12	7
13	6
14	4
15	6
16	7
17	4
18	6
19	7
20	3
21	2
22	1
23	1
24	5
25	1
26	4
27	3
28	4
29	2
30	5
31	1
32	2

Appendix II. Observational data on the number of times female G. integer under 24 hr. continuous observation mated in 10 days (N = 4).

Female No.	No. of Matings
1	7
2	15
3	10
4	12

Appendix III. Observational data on the number of times female G. integer mated during 5 hr. daily observation mated over a 5 day period (N = 24).

Female No.	No. of Matings
1	3
2	2
3	5
4	0
5	1
6	2
7	3
8	5
9	2
10	2
11	4
12	5
13	4
14	1
15	2
16	4
17	5
18	3
19	1
20	2
21	3
22	2
23	4
24	3

Appendix IV. Observational data on the number of times parental females and 10 of their offspring mated over the 10 day observation periods.

Female No.	No. of Matings by Parental Female	No. of Matings by Each of 10 Offspring
1	11	13,9,6,22,3,10,4,5,4,2
2	12	14,8,5,14,7,9,8,15,7,6
3	2	17,14,11,7,5,3,11,13,14,11
4	6	3,3,8,15,3,10,9,12,11,13
5	13	12,13,10,5,9,4,17,9,2,20
6	2	4,14,11,10,9,13,15,26,10,12
7	20	12,11,21,17,17,5,15,15,5,21
8	25	21,15,23,15,10,18,12,14,17,9
9	16	25,10,4,12,7,11,14,2,6,3
10	30	16,10,21,16,15,15,17,12,23,9
11	4	8,15,11,7,2,3,7,3,4,11
12	17	10,14,21,16,8,7,4,9,14,2
13	14	9,12,17,4,8,4,10,3,9,12
14	6	9,5,4,3,3,3,3,5,6,14
15	18	10,7,7,17,14,8,21,13,11,7
16	17	14,5,5,4,2,9,4,15,8,7
17	5	0,9,3,3,5,3,12,2,6,4
18	8	3,9,9,7,1,19,4,3,6,7
19	13	4,9,2,7,14,5,10,18,12,9
20	4	6,4,3,7,4,8,6,5,4,5
21	7	6,9,5,5,5,10,12,8,11,7
22	4	1,1,6,2,4,13,3,2,0,4
23	13	4,6,1,6,2,10,7,8,10,9
24	9	4,1,6,7,7,1,3,7,3,2
25	6	7,12,11,2,2,4,5,4,4,2
26	7	11,12,6,9,2,6,7,1,2,1
27	15	5,22,3,4,1,2,5,2,6,9
28	2	2,1,1,3,2,4,3,1,1,1
29	18	3,10,9,6,2,4,8,6,3,8
30	19	10,5,4,11,4,8,5,4,10,3
31	7	2,7,4,6,5,10,3,5,7,9
32	12	4,3,3,4,7,12,4,8,10,7
33	5	5,9,11,3,13,3,8,2,10,10
34	9	3,4,5,5,7,7,11,8,8,8
35	3	6,1,4,6,7,3,0,3,4,4
36	9	1,1,6,3,5,7,5,5,4,12
37	4	7,7,2,4,3,0,2,3,7,3
38	2	5,1,1,1,4,2,1,5,3,3
39	16	10,6,5,7,11,5,7,4,9,10
40	6	1,4,4,1,5,7,2,3,7,3
41	4	5,7,3,7,4,5,1,7,7,3
42	13	9,12,9,8,6,9,15,7,8,12
43	1	1,4,3,2,1,2,4,4,1,2
44	7	5,2,5,3,5,5,3,11,4,5
45	3	3,4,4,8,5,6,2,4,10,2
46	8	8,8,9,2,12,8,9,9,9,9

Appendix V. Calculation of standard error for computed heritability of multiple mating by female G. integer (from Falconer 1981).

1. Calculation of intraclass correlation coefficient:

$$t = \frac{\sigma_B^2}{\sigma_B^2 + \sigma_W^2} = \frac{\text{groups MS - error MS}}{\text{groups MS + error MS}} = \frac{234.12 - 6.56}{234.12 + 6.56} = 0.945$$

where σ_B^2 is the between groups variance, σ_W^2 is the within groups variance, and MS is the mean of squares.

2. Calculation of sampling variance of the regression coefficient:

$$\sigma_b^2 = \frac{k[1 + (n - 1)t]}{nN} = \frac{1[1 + (10 - 1)0.945]}{10(46)} = 0.02066$$

where k is the number of parents (1 or 2), n is the number of offspring per family, and N is the sample size.

3. Calculation of the standard error:

$$S.E.(h^2) = 2\acute{U}_b = 2\sqrt{\sigma_b^2} = 2(0.1437) = 0.287$$