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    AGONISTIC BEHAVIOR, DOMINANT-SUBORDINATE
    RELATIONSHIPS, AND A POSSIBLE SOCIAL STRESS
    RESPONSE IN THE FIELD CRICKET, GRYLLUS INTEGER.
    (ORTHOPTERA: GRYLLIDAE)

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SOCIAL STRESS RESPONSE IN THE FIELD CRICKET, Gryllus integer

(ORTHOPTERA: GRYLLIDAE)

A DISSERTATION

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AGONISTIC BEHAVIOR, DOMINANT-SUBORDINATE RELATIONSHIPS, AND A POSSIBLE

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(ORTHOPTERA: GRYLLIDAE)

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CHAPTER I

INTRODUCTION

The homeostatic modifications symptomatic of stress have been
well elucidated by Hans Selye. According to Selye (1950) an organism's
reaction to stress involves a syndrome which is both general and adap-
tive (General-Adaptation-Syndrome or GAS), indicating that the particular
manifestations of the stress are both integrated and partly interdepen-
dent. The implication is that the syndrome is evoked by stresses which
affect large portions of the body resulting in a generalized defense
reaction which aids in maintaining the normal homeostatic state.

The GAS is a phenomenon consisting of three successive stages:
the Alarm Reaction, the Stage of Resistance, and the Stage of Exhaustion
(Selye, 1950). Commonly employed measures to indicate an organism's re-
sponse to stress are studies of the morphology, histology and chemistry
of various body organs. This procedure is most accurate for the syn-
drome's first and third stages as the Resistance Stage generally involves
a return to normalcy. Selye (1950) showed that several of the more
apparent and reliable changes occurring in stressed mammals are adrenal

hypertrophy, atrophy of the thymico-lymphatic system, atrophy of the gonads and sexual accessory organs, and gastro-intestinal ulcers.

Among the stressing agents capable of evoking the Alarm Reaction Selye (1950) listed: extreme temperature, X-rays, intense solar radiation, infections, climatic changes, electric injury, trauma, excessive muscular exercise, and nervous stimuli, including emotional stress. In considering Selye's GAS it should be understood that any changes affecting a living organism are stressors if they evoke mild manifestations of the Alarm Reaction; and secondly, that the Alarm Reaction is not necessarily a pathologic condition, but rather the first stage of a GAS which will eventually occur in three successive stages if the organism is continually exposed to severe systemic stress.

Christian (1950) suggested the existence of a relationship between stress and mammalian population dynamics and enumerated eight stress factors which he believed were probably responsible for fluctuations. These were: (1) food scarcity, (2) lack of proper cover, (3) increased muscular exertion resulting from longer food forage trips, (4) fighting resulting from territorial encroachment, (5) non-specific fighting, (6) predation, (7) exposure, and (8) nutrition. Christian believed that as population density increased the physiological stress on individual members of the population would increase as a result of crowding, competition, and the forced utilization of less favorable marginal habitats. If the stressing factors continued and/or were severe enough, exhaustion of the adreno-pituitary mechanism resulted and animals succumbed with symptoms of adrenal insufficiency. Subsequently, Christian (1955, 1960, 1961) crystallized his thinking to the point where he thought that

social factors (i.e., competition, aggression, territoriality, etc.) and the stress resulting from social interactions became of predominant importance in helping to explain the 'natural regulation' of animal numbers, finally stating that "each population has an upper asymptote of growth based on its socio-behavioural structure which will operate even in the presence of a great superfluity of all environmental needs" (Christian, 1963a: 572).

In time, the interpretation of many changes within an animal population in terms of the social interactions within that population and their import were commonly alluded to as Christian's Theory of Social Stress. The application of this controversial theory has been limited primarily to animals in one mammalian order -- the Rodentia. Recently, Christian (1970) has suggested that the forced emigration of subdominant individuals into marginal habitats because of increasing social pressure might be the most important factor in the evolution of some mammalian species.

There is much information available which suggests or confirms the existence of a relationship between social factors and the physiology, behavior, and population dynamics of mammals. By way of introduction a few pertinent studies are worth mention.

Christian (1955) grouped albino and wild-stock Mus musculus and found that adrenal weight increased and the weights of the preputial glands, seminal vesicles, testes, and thymus decreased as density increased. Changes were more pronounced for the wild Mus, probably attributable to their more active and aggressive nature in comparison to the docile albino laboratory strain. When the experiment was repeated

using cages with 42 times more area, comparable adrenal weight increases resulted, indicating that factors of density per se were not alone inducing the organ weight changes. Christian concluded that the presence of other mice, thus social factors, were working along with density to produce the results. Other workers (e.g., Clarke, 1953; Southwick and Bland, 1959) also indicated the importance of considering social factors, rather than mere density. Barnett (1958b) noted that adrenal weights of male Norway rats in all-male groups in large cages and in control males from small cages containing pairs were not significantly different; but, adrenal weights of males from male-female colonies in large cages were significantly higher. Males added one at a time to already established male-female colonies usually died; however, those dying were either unwounded or only superficially injured. This difference between male-female and all-male colonies seemed to indicate that crowding was not the entire cause for conflict, and that social factors were involved. However, in a previous study, Barnett (1958a) observed that in some male-female colonies composed of litter mates there was no observable conflict.

Bronson and Eleftheriou (1963) hypothesized that the reaction of a given species to a stress situation involving density depends on the temperament and behavior of the particular species involved. When male Peromyscus maniculatus bairdii and a C57BL/10J Mus strain were stressed by one of three methods -- maintenance at various densities, exposure to cold, or subjection to daily attacks by trained fighter mice -- there were expected adrenal weight increases in both species exposed to cold or to fighters. Of those mice exposed to varying densities, the more aggressive C57 Mus showed increased adrenal weight and adrenal ascorbic

acid depletion; <u>Peromyscus</u>, however, showed no significant differences from their isolated controls. Bronson and Eleftheriou implied that species differences in behavior, temperament, aggressiveness and other genetically-determined traits must be considered heavily in experiments involving factors of stress and that the particular role of density in affecting adrenal response may be nothing more than the degree of social adjustment necessitated by grouping the particular species.

Dominant-subordinate roles are evident in rodents. Davis and Christian (1957) grouped wild-stock <u>Mus</u> in populations of six; each population was composed of individuals with body weights approximately equal, and social rank was determined by observation of fighting. After ten days together, adrenal weight was least in the dominant animal, greatest in the most subordinate mouse, and a significant relationship existed between adrenal weight and social rank. Dominant animals in rank one gained weight during the experimental period, rank two mice remained nearly constant, while the mice in the four lowest ranks tended to lose weight in proportion to their rank. Since low-ranking mice had larger adrenals than high-ranking mice they concluded that the subordinates had been exposed to more physical and psychological stress. Welch and Klopfer (1961) housed adult male albino mice in groups of 1, 2, 4, 8, 16, and 30, and confirmed Christian's results by noting that low-ranking mice in the dominance hierarchy of each group had the heaviest adrenals. The hierarchical phenomenon was most evident in the cages containing two animals, where a dominant-subordinate relationship was very evident. Barnett (1955) found that dominant male Norway rats which had fought just as much as, and probably more than, subordinate males, showed no

signs of the adrenal hypertrophy characteristic of subordinates. Smith

and Ross (1951) subjected eight groups of three male C3H mice each to

a vitamin-free diet and found that in each group the socially dominant

animal outlived the other two mice, even though the dominant animal was

not always the mouse with the heaviest initial body weight. In studying

distribution patterns of bisexual pairs of Peromyscus released into $2\frac{1}{4}$

acre fields supplied with nestboxes, Terman (1960) obtained results

which suggested the existence of a direct relationship between spatial

distribution and the amount of social interaction (as evidenced by

adrenal hypertrophy) to which each mouse had been exposed during a

3-week experimental period.

Mus, Microtus, Rattus and Peromyscus have been studied most, but

'social stress' is not a phenomenon unique to them. The hypothetical

relationship between natural social 'conventions' and population homeo-

stasis has been thoroughly discussed by Wynne-Edwards (1962) for a wide

variety of animals, especially arthropods and vertebrates. Errington

(1957) noted varying degrees in the expression of intraspecific tolerance

from year to year among muskrat (Ondatra zibethica) populations, and

suggested the possibility that muskrats living in good marsh habitat may

act crowded only when they feel crowded, regardless of density; he thus

stated, in essence, that in natural muskrat populations the chief

influence on population density involves social interactions among the

rats themselves. Kalela (1957) attributed fecundity regulation in the

vole, Clethrionomys rufocanus, to intraspecific intolerance with increas-

ing numbers. Christian et al. (1960) concluded that hierarchical be-

havioral phenomena, or some other factor associated with high density,

induced physiological disturbances and contributed to die-offs in a herd
of Sika deer, _Cervus nippon_. Bronson (1962), studying social pressure
in a natural population of woodchucks, found that the combination of two
factors -- high density and a high level of aggression -- resulted in a
high interaction rate which, in turn, induced depression of the home
range size and behavioral responses of subordinate animals. Similarly,
Myers (1966) described the behavioral and physiological changes induced
by rising population densities in outdoor enclosures containing wild
rabbits, _Oryctolagus cuniculus_. Holst (1969) in a comprehensive study
has shown the ethological and physiological effects of intraspecific
social stress in the tree shrew (_Tupaia belangeri_) and implicates hor-
monal changes, _à la_ Selye, as probable explanations for his results.
Even _Homo sapiens_, particularly the modern 'civilized' variety, surrounded
by his technological trappings and increasingly sensing the physiological
and psychological pressures resulting from his own increasing biomass,
appears susceptible to the effects of social stress (Morris, 1969).

Many studies make reference to 'density', yet for clarification it
should be remembered that density "in terms of mammalian populations is
related only indirectly to numbers of mammals per unit of area, being
more directly related to intraspecific competition, social strife,
socio-psychologic pressures or whatever other comparable designation
one may choose to use for the interactions between mammals in the same
population" (Christian, 1963b: 326).

The preceding references and many more not included serve to express
or suggest the important regulatory role which social factors play in
natural animal populations. Necessarily, most of the inferences have

been drawn from experiments using caged animals under laboratory conditions, but since the basic physiological mechanisms for both laboratory and natural populations are presumably the same there is little reason to question whether such inherent genetically-fixed responses could occur in nature. The question resolves itself to one of degree, not conceivability!

To date, "social stress" has been largely considered a mammalian phenomenon, and with few exceptions (e.g., Wynne-Edwards, 1962) rarely have factors of social interaction, etc. been considered to help explain or better understand the natural population dynamics of arthropods or other invertebrates. In considering the findings of Christian, the feasibility of population regulation by a set of negative natural controls (Wynne-Edwards, 1962), or the phenomenon of the "behavioral sink" (Calhoun, 1962), the question occurs as to whether there are responses among certain invertebrates that suggest a phenomenon equatable with the mammalian situation. Strongly provocative evidence exists.

In describing the insect 'retrocerebral gland system', consisting of corpora allata innervated by nerves leading from neurosecretory cells in the protocerebrum which traverse the corpora cardiaca en route, Wigglesworth (1965) describes how neurosecretory granules pass from the brain along axons to the corpora cardiaca and then to the corpora allata.[*] Wigglesworth (1965: 179) observes that "there is a striking similarity between this system -- consisting of a neurosecretory part (corpus cardiacum) and a glandular part of ectodermal origin (corpus

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[*]For a clear, understandable account of neurosecretion, and insect endocrine and neuroendocrine organs, see Tombes, A. S. 1970. An Introduction to Invertebrate Endocrinology. Academic Press, New York. 217 p.

allatum) innervated by neurosecretory cells in the brain -- and the
association in vertebrates of the neurohypophysis and the glandular
hypophysis, supplied by neurosecretory cells in the hypothalamus."
He further suggests that the corpora cardiaca may be involved in the
secretion of a pharmacologically active substance or substances compa-
rable to those produced by the pituitary or adrenals of vertebrates
(Wigglesworth, 1954, 1965). Recently, the pathways leading from neuro-
secretory cells in the brain to the corpora cardiaca and corpora allata
have been well illustrated for three insects -- eight species of noctuid
moths (Hinks, 1970), the house cricket,' Gryllodes sigillatus, and the
green cotton bug, Nezara viridula (Awasthi, 1968, 1969a, 1969b).
Awasthi (1969a) cites references for related studies on other insects,
especially Orthoptera; and Hinks (1970) reports probably the first
discovery of a direct nerve connection between the corpora cardiaca
and insect sensory organs.

Beament (1958) observed that cockroaches that were mechanically
restrained, exposed to short periods of electrical stimulation, or
exposed to prolonged mechanical stimulation by enforced activity for
4-12 hours in rotating jars, characteristically exhibited symptoms of
paralysis before death. Parabiotic experiments suggested that the
paralyzing agent responsible was blood-borne and Beament postulated the
existence of a neurotoxin secreted by a hyperactive nervous system.

Heslop and Ray (1959) noted that mechanically restrained roaches
showed signs of paralysis similar to the late stages of DDT-poisoning,
but did not exhibit the violent convulsions and tremulous appendages
symptomatic of DDT-poisoned insects; they suggested that "whenever a

lethal dose of a convulsant insecticide is applied to a roach, unless

toxic action is rapid, a generalized stress syndrome will be superimposed

on the specific response to the insecticide and may even obscure it"

(Heslop and Ray, 1959: 400). They further suggested that any stimulus,

either DDT or bodily stress, which is sufficiently strong, will trigger

reactions initiating the stress syndrome.

Hodgson and Geldiay (1959) found that electrical shocks or forced

hyperactivity caused a significant decrease of two neurosecretory sub-

stances in the corpora cardiaca of female roaches, Blaberus craniifer,

and concluded that the release of these neurosecretions might be

analogous to adrenalin secretion during mammalian responses to stress.

Colhoun (1959) observed that roach corpora cardiaca were depleted

of neurosecretory materials during stress induced by DDT-poisoning and

later (Colhoun, 1960), during parabiotic experiments in which one member

was poisoned with a low dose of insecticide, he noted that the untreated

animal became paralyzed. No insecticide was recovered in the untreated

roach, and the paralysis was not preceded by symptoms of hyperactivity

or convulsions. These results supported those of Beament (1958) and

Heslop and Ray (1959) in implicating blood-borne factors, probably of

nervous origin, as the materials responsible, wholly or in part, for

symptoms of paralysis in stressed roaches.

Studies published up to early 1962 pertinent to the topic or chemi-

cally or physically induced stress and its effects on insect behavior

and physiology have been reviewed by Sternberg (1963). Nearly all of

these involve roaches, and many are primarily concerned with attempts

to locate the source or determine the chemical identity of the active

substance(s) involved. In most cases neuroactive materials from the corpora cardiaca are studied and discussed. Little mention is made of the possible importance of stress resulting from intraspecific social interaction, although this aspect may have been implied by some authors (e.g., Heslop and Ray, 1959) when emphasizing the possible importance of any stressor of sufficient strength in triggering a stress response.

Proceeding on the assumption that the GAS and stress responses might be common to insects, especially those of higher social orders, Pence et al. (1963) observed that preventing the expression of normal habitat-maintaining behavior in foraging worker honey bees by forced confinement leads to hyperactivity, followed by prostration and subsequent death. The stressful effects of confinement were magnified and the onset of prostration hastened by any of the following factors: presence of light, increasing the area of confinement, removal of antennae, and absence of honeycomb or hive odor. Experimental evidence suggested that increased energy expenditure resulting from hyperactivity was not alone responsible in determining how long a worker bee endures forced confinement. They hypothesized that confinement stress, if not relieved by escape, triggers an autointoxicating mechanism that accelerates the onset of exhaustion, prostration and death; they suspect that the toxic substances involved are released into the haemolymph, as evidenced by the deleterious effects on the behavior and physiology of normal bees injected with small haemolymph samples from 'stressed' bees.

Discussing the existence of two or more known cardio-accelerator substances in roach corpora cardiaca extracts, Davey (1964: 230) considered the significance of experiments showing the release of

materials from stimulated ganglionic areas to the phenomenon of insect stress, but concluded that there is "no evidence that these materials play a role in the normal physiology of the insect."

Clarke (1966: 169) stated that "emptying of the anterior lobes of the corpora cardiaca always seems to be associated with the action of some stressor on the insect." He observed that exposing young adult locusts (Locusta migratoria) to varying temperature regimes induced histological changes in the corpora cardiaca and corpora allata with increasing amplitude of temperature fluctuation resulting in increasing depletion of neurosecretory material from the glands. Aware that other forms of stimulation can induce similar changes in the neurosecretory system, Clarke (1966) maintained that the changes were evidence for a GAS, presumably analogous to the vertebrate GAS elucidated by Selye, rather than specific responses to the imposed temperature regime. Awasthi (1969a) described seasonal differences in the neurosecretory systems of hibernating and active house crickets, Gryllodes sigillatus; from studies of the green cotton bug, Nezara viridula, he concluded that temperature is a major factor influencing insect neurosecretory activity (Awasthi, 1969b).

Cook (1967) isolated a neuroactive substance from whole animal extracts of American roaches (Periplaneta americana) that elicited excitatory responses in roach nerve cord and motor nerves. Chromato-graphic studies and chemical analyses suggested a biogenic amine with biological and chemical properties similar to Factor S, previously iso-lated from the crayfish Cambarus by Van der Kloot (1960). Cook believed the two substances to be closely related chemically, if not identical.

He isolated Factor S from <u>Cambarus</u> <u>clarkii</u> and <u>Periplaneta</u> <u>americana</u>;
the roaches, <u>Leucophaea</u> <u>maderae</u> and <u>Blaberus</u> <u>giganteus</u>; the grasshopper,
<u>Schistocerca</u> <u>vaga</u>; and the housefly, <u>Musca</u> <u>domestica</u>. In <u>Periplaneta</u>
the substance was found in the head, ventral nerve cord and legs (Cook,
1967). Later, Cook <u>et</u> <u>al</u>. (1969) noted two-fold increases in Factor S
titres for mechanically stressed roaches and discussed the possible
relationship between increasing Factor S concentrations and progressive
stages of stress paralysis. They maintain that intensive CNS stimulation
such as occurs under stress, results in the release of neuroactive sub-
stances into the haemolymph, a conjecture supported by their findings of
increased levels of Factor S in stress-paralyzed insects, highest concen-
trations of Factor S in the CNS (brain and nerve cord), and the appearance
of Factor S-like compounds in perfusates from electrically stimulated
nerve cords. Injection of a saline solution containing various concen-
trations of roach extracts containing the neuroactive agents consistently
induced rapid paralysis when injected into houseflies, <u>Musca</u> <u>domestica</u>.

In Chapter 7 of his book, <u>The</u> <u>Cockroach</u>, dealing with the nervous
system and endocrine activity, under the subtitle "Nerve Toxins", Cornwell
(1968) briefly considered the production of paralyzing and death-inducing
autocatalytic metabolites following exposure to stressful stimulation,
and in a recent paper Flattum and Sternberg (1970: 67) discuss and cite
much of the evidence for the release of pharmacologically active sub-
stances with neuroactive properties from the tissues of insects exposed
to varying forms of physical or chemical stress. They note that the
liberation of such substances "must presumably have a normal function,
and under ordinary conditions were probably necessary for the proper

integration of biochemical and physiological events in the insect.
These factors when released in greater than normal amounts would then
account for abnormal behavioral characteristics or even paralysis and
death."

Nearly all studies concerned with the effects of stress on insects
have been artificial and contrived, involving confinement, or chemically-,
electrically-, mechanically-, or temperature-induced stress situations.
However, Highnam (1961) noted that adult female desert locusts (Schisto-
cerca gregaria) killed during and after their first observed copulation
showed changes in the neurosecretory system identical to changes observed
following high-frequency electrical stimulation or enforced activity.

The first experimental evidence for the applicability of stress
phenomena to the natural biology of an insect was provided by Ewing's
(1967) study of fighting behavior among adult male lobster cockroaches,
Nauphoeta cinerea. As part of her experimental design Ewing studied
paired males confronted once daily with a test male. Ewing does not
state the length of exposure time, which apparently varied, but she
found that this daily social exposure to a test male induced increased
mortality rates compared to isolated controls or paired males left
untouched; early mortality was especially common for the subordinate
animal of the pairs, and was accompanied by a state of semi-paralysis
affecting the abdomen and limbs from which the roaches did not recover.
She noted the similarity of these results to social stress studies
in mammals and hypothesized that internal changes affected by the corpora
cardiaca were involved. Pence and Viray (1969) state that German
cockroaches (Blatella germanica), though gregarious, normally maintain

individual distances from one another at a distance determined by antennal length, and that increasingly belligerent behavior and potentially fatal stress may result when normal distance-maintaining behavior is inhibited by the loss or impairment of extremities following exposure to dodecyl alcohol.

To test the possible existence of a social stress response in an insect the following experiments similar to, but modified from, those of Ewing (1967) were conducted. Since the effects of social interaction and fighting on longevity and hierarchical relationships were to be studied, the field cricket, _Gryllus integer_, was chosen, because of its availability and the known aggressive nature of gryllids (Fabre, 1915; Laufer, 1927; Alexander, 1961).

In addition to the main stated purpose of experimentation, i.e., testing for a social stress response, two other aspects were studied and are reported here: (1) a detailed account of agonistic behavior, and (2) aspects of the general biology of _G. integer_, including courtship and mating, hatching, and the growth, molting and mortality of developing nymphs.

CHAPTER II

METHODS AND MATERIALS

The present study was conducted over nearly a $2\frac{1}{2}$ year period from June, 1968 to November, 1970.

On 7-22-68, 18 adult field crickets, Gryllus integer, (15 females 3 males), were captured on sidewalks and in grass beneath street lights near the Zoology building on the University of Oklahoma campus at Norman, Oklahoma. The females, placed in a 5 gallon terrarium containing damp sand, began ovipositing soon thereafter. Hatchlings first began appearing 12 days later. Beginning 10-1-68, 40 crickets (8 females, 32 males) in late instars were individually isolated in quart Mason jars and left undisturbed except for periodic addition of food and water until death. Longevity data for these F_1's indicated the feasibility of using $\underline{G}$. integer for the laboratory experiments to be described. The males showed a mean adult longevity of 120 days (range: 27-169); the females 95 days (range: 18-138) (Table 1).

On 10-13-68, 23 adults (16 females, 7 males) were captured beneath the same campus lights. Numerous immatures, the result of July-August matings, were also seen at this time. One pair was isolated in a quart jar with damp sand; courtship, mating and oviposition followed and on 11-3-68 hatchlings first appeared. Hatchlings were separated into gallon

Table 1. Life table for 40 F₁ generation crickets (32 males; 8 females) maintained in isolation in quart jars since late nymphal stages, and undergoing adult molt between 10-4-68 and 11-1-68. Age expressed in days from the date of adult molt. X = age interval in days, l_x = number surviving at beginning of age interval stated in X column, d_x = number dying during age interval stated in X column, q_x = mortality rate per 1000 alive at beginning of age interval, L_x = no. of crickets alive between ages X and $(X + 1)$, T_x = no. of cricket days, i.e., number of days still to be lived by all crickets of age X, e_x = mean life expectancy for those crickets attaining age interval stated in X column.

X	l_x	d_x	q_x	L_x	T_x	e_x
0-10	40	0	0	40	4460	111.5
11-20	40	1	25	39.5	4160	104.0
21-30	39	1	25.6	38.5	3765	96.5
31-40	38	0	0	38	3380	89.0
41-50	38	2	52.6	37	3000	79.0
51-60	36	1	27.8	35.5	2630	73.1
61-70	35	0	0	35	2275	65.0
71-80	35	0	0	35	1925	55.0
81-90	35	1	28.6	34.5	1575	45.0
91-100	34	3	88.2	32.5	1230	36.2
101-110	31	5	161.3	28.5	905	29.2
111-120	26	8	307.7	22	620	23.8
121-130	18	5	277.8	15.5	400	22.2
131-140	13	5	384.6	10.5	245	18.8
141-150	8	1	125.0	7.5	140	17.5
151-160	7	4	571.4	5.0	65	9.3
161-170	3	3	1000.0	1.5	15	5.0
171-180	0	0		0		

Males: $\overline{Y}$ longevity (days) = 120.1
Females: "   "   = 95.2

jars according to hatching date, and late instar males were isolated
in quart jars. Of 16 isolated adult males, eight were designated con-
trols and eight as experimentals, and on 4-21-69 experiments were begun
to test for results that would in any way suggest (1) that aggression
reduces longevity, or (2) the existence of a social stress response.

Experimental males were exposed to intruder males for 10-15
minutes approximately every two days, all behavior during the inter-
actions recorded, and the intruders then returned to their own jars.
Intruders were either laboratory raised adults of known ages, or wild
caught. All interactions were staged between 8 p.m. and midnight.
Handling of intruders was facilitated by a short length of thread em-
bedded in a small wax block attached to the pronotum. Results of this
preliminary experiment indicated a stress response among experimental
males, and accordingly further experiments were conducted. Experiments
2 to 6 (Table 2) were replicates of preliminary Experiment 1, but were
modified in several ways as described below.

As hatchlings appeared in breeding jars they were transferred to
quart or gallon rearing jars according to hatching date. These jars
were checked daily to record molting and mortality data. At the stage
(usually 9th instar) when small wing pads appeared and females were
distinguishable by the small developing ovipositor, all males were
removed, assigned identification numbers, and placed in jars according
to one of three groups — controls, experimentals, and permanently
paired males. This procedure was modified for the F_4's in Experiment
4 which were communally reared in a 5 gallon terrarium containing wood,
rocks, wire screening, etc., then isolated at late nymphal stages.

Table 2. Summary of pertinent data for male Gryllus integer used in Experiment 1, and replicated Experiments 2-6.

No. Expt.	Crickets	Parents	Dates of Hatching	Dates of Final Molts	Dates of Experiment	Controls N	Exptls. N	Paired N
1	F_1's	wild caught 10-13-68	11-3-68 to 11-22-68	3-1-69 to 4-14-69	4-21-69 to 7-21-69	8	8	-
2	F_2's	F_1 female #5 male #35	1-12-69 to 1-28-69	5-12-69 to 6-27-69	6-4-69 to 11-23-69	18	18	30
3	F_3's	F_2 female #58 male #68	6-22-69 to 8-10-69	7-31-69 to 2-18-70	9-9-69 to 5-31-70	61	61	34
4	F_4's	several F_3's offspring of F_2 female #60 male #68	9-25-69 to 10-14-69	3-2-70 to 5-30-70	3-24-70 to 10-14-70	13	13	12
5	F_1's	wild caught female #421 male #423	1-17-70 to 2-4-70	4-13-70 to 5-12-70	4-16-70 to 11-3-70	10	10	8
6	F_1's	wild caught female #422 male #423	2-1-70 to 2-10-70	5-12-70 to 5-31-70	5-14-70 to 9-23-70	6	6	8
					Totals =	116	116	92

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Jars were examined daily and the date of last nymphal and adult molts recorded. Jars containing adults were scanned at least twice daily (morning and afternoon) to check for dead or dying animals.

Species Identification

The taxonomic status of many North American field crickets is unclear. The two species involved in the present study were identified on the basis of behavioral information, life cycle observations, song, and morphology, especially file tooth counts, according to published reports (Alexander and Walker, 1962; Alexander and Meral, 1967; Alexander, 1968a). Final decision on identification, in large measure, was based on opinions and information from R. D. Alexander (personal communication).

Gryllus integer males were used in all three treatments (i.e., controls, experimentals, and pairs) and as intruders in all six experiments; several Gryllus alogus males, as described later, were used as intruders in Experiment 3.

Housing and Maintenance

All jars were quart wide-mouth Mason jars with 15 holes punched in the metal lid. Each contained a layer several inches deep of fine-grained sand, a two dram water vial with an absorbent paper wick, a piece of screening as a vertical resting site, and a cap for a six dram vial in which food was provided (Fig. 1). All crickets used in this study, including ovipositing females and developing nymphs from the time of hatching, were fed exclusively on Gaines dog meal (pellet form). This diet proved quite satisfactory. Numerous broods were raised in the laboratory solely

on this diet, and the ranges of variation in size, color, wing development, etc. of laboratory-raised animals appeared to differ in no significant way from randomly caught samples of wild crickets. Luckey and Stone (1968) reported that house crickets, Acheta domestica, failed to grow when fed a laboratory diet which supported growth and reproduction in the roach, Blatella germanica. They found sodium to be the deficient factor and supplemented the crickets' diet with grass. However, A. domestica raised in our laboratory on Gaines meal alone, under identical conditions as G. integer, have quickly matured, successfully reproduced, and survived considerably longer (i.e., 3 months or more as an average) than previously reported in the literature (Nowosielski and Patton, 1965). Water was added to the vials at least weekly (more often during summer months) and old pellets removed and new food added at least once weekly.

Laboratory Conditions

Experiments 1 to 4 were conducted under uncontrolled environmental conditions on the third floor of the Zoology building (Richards Hall) on the University of Oklahoma campus. Jars were on shelves lining the north wall of the laboratory (Fig. 2). Blind-covered windows facing the east were left partly open most of the year and with the exception of heat waves in July 1969 and August 1970 yearly room temperatures remained within the author's comfort range, not falling below 65° F nor exceeding 85° F (Fig. 5). Daily temperatures from 8 a.m. to midnight rarely fluctuated more than 5° F throughout the year. Humidity varied considerably, and no set light regime was established. Controlled environmental chambers were not available and without ques-

tion the varying environmental conditions influenced cricket behavior
and physiology, especially Experiment 2 conducted during the warm summer
months of 1969. No direct environmental effects on mortality were
evident, however, and since all animals in any experiment were exposed
to the same varying conditions, the importance of these differences
are minimized as regards the purpose and basic aims of the experiments.

Secondly, one of the most consistent criticisms leveled against
laboratory behavior studies is their 'unnaturalness' and artificiality
as compared to the 'real' world where the animal normally lives. With
no controls over the physical factors of temperature, humidity and light
the laboratory, in a sense, became more natural. If consistent results
occurred under such varying conditions they would constitute more re-
liable proof to support any conclusions drawn concerning the validity
of findings as representing real phenomena and not artifacts of
'unnatural' controlled laboratory conditions.

Experiments 5 and 6 were conducted in an insectary under more
controlled conditions of temperature (67°-73° F) and relative
humidity (61-65%).

In Experiment 3, many of the hatchlings appearing last were
transferred to a cool room (66°-72° F) where growth and development
were retarded. These males, of course, were much older at the time
of adult molt than their siblings and are noted on the F_3 data sheets
(see Table 23, Appendix I).

Time of Experiments

During Experiment 2 interactions were staged between 1-2 p.m.,
and the crickets were more active and spent less time resting motionless

compared to Experiment 1 conducted in the late evening. Since contact
between experimentals and intruders, preferably occurring early during
the interaction period, was essential in order to ascertain aggression
levels and dominance relationships all remaining experiments were con-
ducted between 9 a.m. and 3 p.m.; most interactions were completed
before noon.

Molting and Mortality

Jars were checked several times daily to determine the day or
exact time of final molt or death. If actual molting was not observed,
molting time could often be approximated, because 3-4 hours, depending
on temperature, are required for cuticular tanning. Thus, quite accu-
rate determinations of longevity were obtained. When it became apparent,
during Experiment 2, that experimental animals frequently died in a
paralyzed state, records were kept of death postures and of behavior
of dying crickets whenever possible.

Isolated Experimentals and Controls

Assignment of male G. integer as experimentals or controls was
randomized as much as possible, after taking all factors for equaliz-
ing the two groups into consideration -- e.g., hatching date, rearing
jar in which cricket developed during early nymphal stages, date of adult
molt, size of adult, etc. In most instances experimentals and their
appropriate controls represented animals from the same rearing jar that
molted to adults on or about the same day. Since different numbers of
hatchlings appeared daily over the hatching period, the density of
nymphs in the rearing jars varied considerably -- from 2 to 20+.
Taking experimentals and controls from the same rearing jars was done

to control for possible density effects or group effects on longevity patterns as reported for _Acheta_ _domestica_ by Nowosielski and Patton (1965).

Beginning at 0 to 47 days adulthood, experimental males were exposed to 15-20 minutes of social interaction with intruder males placed in their jars. Interactions were staged on alternate days (T, Th, Sat, and alternate Sundays). Intruders were placed in each jar at a distance from the resident experimental which prevented immediate contact. Behavioral responses during and after initial contact were observed from two feet away and recorded, including incidence of aggressive and court-ship calling, chasing, mandible-locking, etc. Duration of fighting bouts was timed. Initially, only one jar was observed at a time; however, with practice, it became possible to observe as many as six jars at once. Letter symbols representing the repertoire of behavior patterns were used for rapid recording of data (Table 3). Because nearly all inter-actions were characterized by considerable periods of inactivity, with bouts of continual activity or chasing being exceptional, the observer was rarely pressed to record observations and the data accurately re-flect the behavioral responses that occurred.

After initial contact, dominance was usually quickly established during a relatively short bout, varying in level of aggressive intensity. All behavioral responses commencing with initial contact and ending with submission and retreat by one individual were emphasized when recording data. Alexander (1961) distinguished five types of encounters between male field crickets based on the intensity or level of aggression expressed. In assigning agonistic encounters I found Alexander's

Table 3.   Letter symbols used in recording observations of behavior
patterns of male field crickets, Gryllus integer, during
experimental-intruder interactions.

A   = approach
AC   = antennal contact (mutual)
AC$_s$ = antennal contact (single)
AF   = antennal fencing
ACG   = attempting to climb glass sides of jar
ADS   = attempting to dislodge spermatophore
ATS   = attempting to transfer spermatophore
ACa   = aggressive call
CoCa = courtship call
Ca   = calling
Ch   = chase
Ch+   = brief chase (i.e., 1-2 seconds)
F   = following
FO   = face-off
J   = jerking (of body)
J'   = exaggerated or pronounced jerking
K   = kicking with hind legs
LM   = locking of mandibles
M   = mount
DM   = dismount
M/DM = mount with almost immediate dismount
MA   = moving away
OM   = open mandibles
R   = retreat
T   = turn
WA   = wings arched (but no calling)

—   = brief passage of time (i.e., no more than several seconds)
⌣   = longer period of time
⌣⌣   = period of time exceeding two minutes

res. = resident experimental
intruder designated by number

classification convenient, but it was necessary to expand and/or make more explicit Alexander's original categories to facilitate identification of all types of interactions observed (Table 4).

Following establishment of a dominant-subordinate relationship, usually at initial encounter, the remainder of the interaction period invariably consisted of one of several possibilities:

1. Both males inactive and resting, usually apart but frequently in body or antennal contact.

2. Both males inactive with occasional or frequent aggressive calling by the dominant animal.

3. Mild activity with the subordinate moving away and otherwise maintaining distance from the dominant.

4. Dominant chasing the subordinate, ranging from bouts characterized by a quick charge and short chase (i.e., less than one turn around the jar) and usually terminated by aggressive calling, to bouts of intense chasing, characterized by the subordinate running, jumping, or energetically attempting to climb the sides of the jar.

This particular experimental design is of the type proposed by Bronson and Eleftheriou (1963) for mammalian studies. They believe that such an experimental procedure has much worth for laboratory investigations of relationships between population density and physiology. Many mammalian studies have either involved freely-growing caged populations or continuously caging animals for varying time periods, and often at extreme densities, seldom, if ever, occurring under natural conditions. In this study the field crickets were behaviorally isolated except for short periodic groupings, a situation probably more closely approximating conditions of social interaction likely to occur in nature between territorial burrow-inhabiting males.

After 15-20 minutes each intruder was removed and returned to its

Table 4.   Agonistic behaviors characteristic of the 5 level of
           aggressive encounters exhibited by adult male field
           crickets (modified from Alexander, 1961).

Inactivity or one-sided aggressive encounters

Level 1:
   1. Both attempt to climb glass sides of jar (ACG).
   2. Both aggressive call (ACa), but no contact.
   3. ACa by one or both males after initial contact, followed by
      inactivity (i.e., no moving away or retreat).
   4. Both move away after initial contact, or remain together immobile.
   5. Mutual or one-sided courtship calling (CoCa).

Level 2: (typical behavior = antennal fencing, followed by retreat)
   1. Some ACa, but no open mandibles (OM) or chasing. One male
      retreats or quickly moves away.
   2. No OM, but brief chasing (i.e., less than one turn around the jar).
   3. One male OM - other male retreats or moves away.
   4. OM, followed by a brief charge (but no chasing).
   5. One male approaches and other moves away as if in retreat.
      Approaching male may jerk body or turn and kick with hind legs.
      Retreat preceded by antennal fencing or lashing. Brief aggressive
      calling may also occur.

Level 3: (typical behavior = open mandibles and aggressive calling)
   1. OM and some aggressive calling.
   2. OM and some chasing.
   3. OM and both males aggressive calling, but no face-off, followed
      by one male retreating.
   4. No OM, but considerable chasing (i.e., two or more distinct bouts
      of chasing around the jar or several discrete brief chasing bouts).

      If any two of the following three agonistic behaviors occurs —
      (1) aggressive calling, (2) considerable chasing, or (3) open
      mandibles, then the aggressive encounter was considered at least
      Level 3 in intensity.

Reciprocal or two-sided aggressive encounters

Level 4:
      Both males have open mandibles, or both call aggressively during
      a face-off.

Level 5:
      FO with OM and eventual locking of mandibles (IM).

own jar. To determine the stability of dominant-subordinate relation-
ships over time, experimental males were continually exposed to the
same intruder males, until the death of one or the other. Because each
experimental animal was consistently exposed to the same intruder, and
intruders were exposed to only one experimental animal during any given
period, experimental males and their associated intruders were exposed
to equal amounts of social contact.

Intruders

During May to November male G. integer (adults and occasionally late
instar nymphs) were captured under street lights at night and housed in
isolation. When wild males were unavailable, laboratory-raised animals
were used; most were siblings of experimentals and controls. Soon after
the capture of wild males or the final molt of laboratory-reared males,
crickets designated as intruders were placed in an ice-bottomed container
next to the freezer compartment of a refrigerator (41°-50° F) for approxi-
mately five minutes. Thus inactivated, the cricket was placed on ice
while a small wax block with protruding thread was attached to the pro-
notum in a way not to restrict wing or head movements; attachment was
accomplished in less than one minute. In a few instances cold treatment
or wax attachment appeared to have adverse after-effects; males so
affected were not used. The wax blocks seemed not to affect behavior
nor place intruders at a disadvantage during their encounters with
experimental males (Fig. 3). Alexander (1961) reached similar conclu-
sions for cardboard crests attached to crickets in his experiments.

Thus fitted, intruders were easily transferred to and from the
jars of experimentals by holding the thread with forceps (Fig. 4).

Fig. 1.   Quart jar containing water vial, screening and food cup.

Fig. 2.   Quart jars containing controls, experimentals, and permanently paired male field crickets, _Gryllus_ _integer_.

Fig. 3.   Antennal fencing during a face-off between an experimental male (_G_. _integer_) and a conspecific intruder male.

Fig. 4.   Transfer of intruder male to the experimental male's jar.   (Photographs by F. J. Sonleitner)
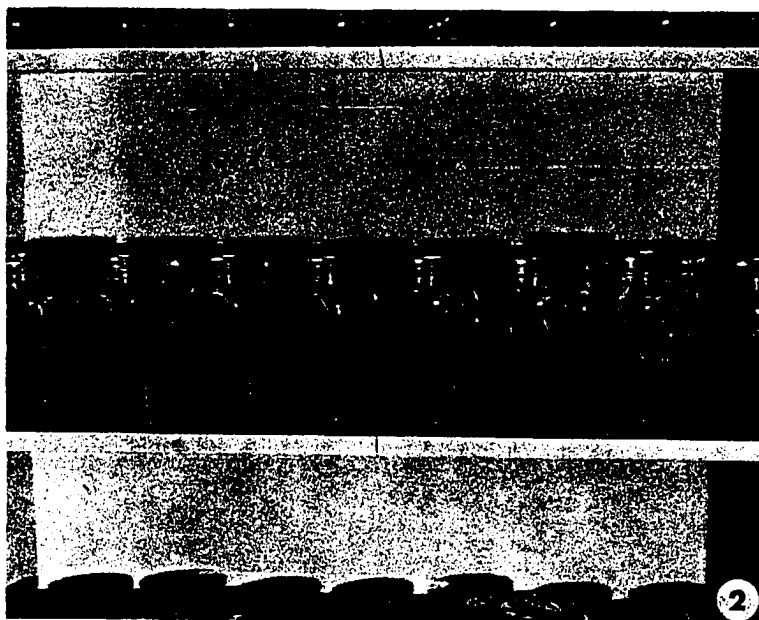
Fig. 5.   Average monthly temperature (F) of laboratory recorded
          each morning at 8 a.m. from January, 1969 to September,
          1970.

DEGREES (F°)

MONTH

1969

1970

32
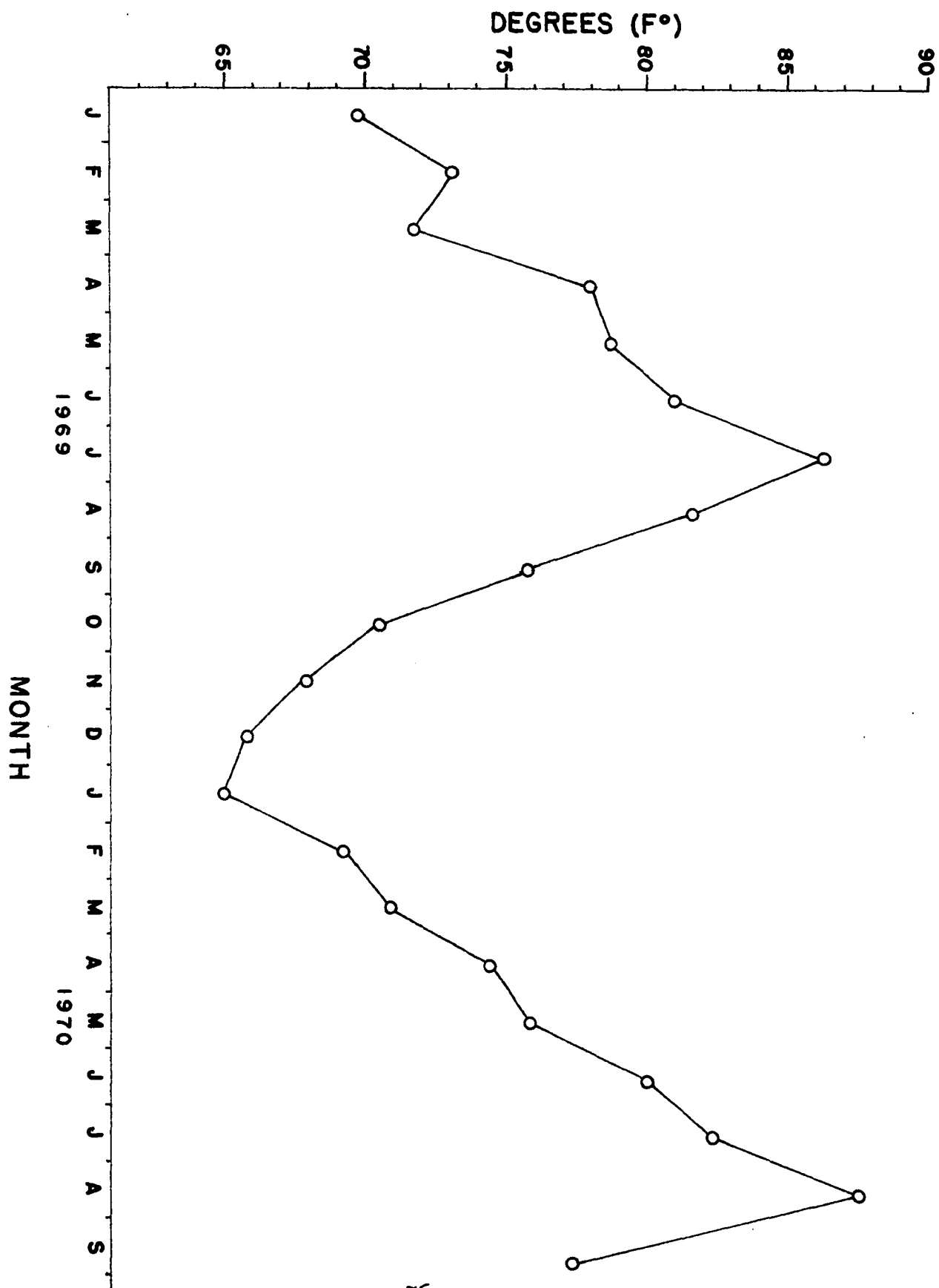
The wax did influence mating behavior in tests where block-fitted males were exposed to females. A receptive female mounts a courting male from behind and remains on top of his body, her head above his, or, in larger females, in front of his, during spermatophore transfer and attachment. Initially, aborted matings resulted as the female prematurely dismounted or fell off before spermatophore attachment was accomplished. The wax did not prevent mating, however, for after numerous mounts successful matings were often achieved when the female oriented sideways rather than lengthwise on top of the male.

Permanently Paired Males

In jars housing G. integer males permanently paired since the small wing pad nymphal stage (occasionally large pad stage) the right cercus of one male in each pair was partially cut off for identification purposes. Pairs were usually observed at various unscheduled times at least once daily between 8 a.m. and midnight. All observations of agonistic behavior were recorded on tape and transposed at a later date. Also, the jars were scanned frequently and whenever an aggressive encounter was observed, combatants were identified, and the time and pertinent information tape recorded. All agonistic encounters were counted. However, among paired males one-sided or mutual courting occurred more frequently than aggression. Most, but not all, courtship behavior was recorded, although all courtship sequences terminating with mating attempts were tabulated.

CHAPTER III

RESULTS

General Biology

Mating and Oviposition

Successful reproduction was easily achieved in laboratory populations of G. integer used in these experiments.

Female #5 was first observed with an attached spermatophore five days following initial exposure to male #35. Eighty minutes later a second spermatophore was visible and 40 minutes later the male commenced courtship calling; the female quickly approached and mounted. Mounting lasted 22 seconds and resulted in successful mating, with the attachment of a fresh spermatophore and dislodgement of the two older ones. Subsequently female #5 was observed with two spermatophores simultaneously attached on three different occasions until the male's removal and isolation of the female in a jar containing dry sand. The jar originally housing the pair was set aside to await hatching of the eggs oviposited by the female in damp sand. Dry sand in the new jar apparently inhibited further egg-laying by the female whose abdomen was still bulging with eggs following laying of the first egg batch. Ten days later a patch of dry sand was moistened; the female investigated

and began ovipositing within a minute after the labial palps first contacted the moisture.

During mating male G. integer exhibit three characteristic movements exclusive of directing the phallic complex at the tip of the abdomen and the spermatophore to the female's subgenital plate; these are (1) continuous vibration of the anal cerci while the female is mounted, (2) rotation of the head from side to side, and (3) antennal lashing. Following copulation the female quickly dismounts and remains immobile near the male. The longest time recorded for post-copulatory immobility was 34 minutes for female #58. A male may occasionally lash a female with his antennae following mating or jerk his body if she attempts to move away. These observations of mating and post-copulatory behavior in G. integer agree with previously described reports for other species of field crickets (Alexander, 1961; Alexander and Otte, 1967).

Whereas the absence of damp substrate apparently inhibited egg-laying in female #5, resulting in two distinct egg batches and oviposition bouts, isolated G. integer females (both mated and unmated) with egg-swollen abdomens were observed making oviposition movements in dry sand or into the wet paper wick of the water vials.

On 2-19-69 adult F_1 female #71 in a terrarium containing courting males was observed on a wire screen lying half-submerged in a water-filled cup. The female periodically backed down the screen, lowered the ovipositor into the water, jerked the body slightly and withdrew the ovipositor -- motor patterns identical to oviposition movements. When removed and isolated in a jar containing damp sand this female

began ovipositing within two minutes. When the cup was examined 104 submerged eggs were found. Water and eggs were transferred to a jar and covered with wet sand; from 3-18-69 to 3-21-69 26 hatchlings appeared, 12 of which survived to adulthood.

On 10-18-69 at 12:34 p.m. an adult female wild caught on 10-16-69 was placed with F_3 intruder male #10 which was spontaneously courtship calling in isolation in his jar. Mounting with successful spermatophore attachment was observed at 12:40 p.m., at 1:20 p.m., and again at 2:50 p.m. in spite of the wax on the male's pronotum. Alexander (1961) believes that an important function of post-copulatory behavior in field crickets is that it allows territorial males to monopolize females and mate with them repeatedly; he has observed male G. pennsylvanicus monopolizing females and copulating at hourly intervals or less. The relative rapidity with which male G. integer in this study could produce spermatophores and mate successively lends support to this belief. On 5-30-69 F_2 male #68 successfully copulated at 11:15 a.m. and 15 minutes later a fresh spermatophore was partly visible which the male proceeded to protrude and withdraw over a dozen times in succession.

Generally, a sexually responsive male field cricket commences courtship calling following antennal contact with another cricket of either sex if it responds with immobility in the characteristic manner of most adult females. To ascertain (1) the latency period between initial contact of male and female and the commencement of courtship calling, (2) the latency period from the beginning of courting to female mounting, and (3) the duration of mounting, an adult sexually active F_2 male (#68) was exposed to four naive adult F_2 females (#57-#60)

maintained in isolation since a late nymphal stage. The male was grouped with each female for two days then removed and directly transferred to the jar of another female. For all four naive females, courtship calling and successful mating occurred within one hour after initial contact (Table 5). The male was directly transferred back to some jars a second or third time before it was returned to its own jar on 6-11-69. One day after mating, female #67 made oviposition movements in dry sand. When the sand in each jar was wetted three of the four females began ovipositing within the hour. Numerous instances such as this were noted in which females that had successfully mated days earlier failed to oviposit until the sand was moistened. Invariably, once they detect moist sand with their palps, oviposition commences within minutes.

One of the most consistent mating behavior patterns was the rapidity with which most sexually mature females approached and mounted courting males (Table 5). Beginning 11-28-69 F3 naive female #419, maintained 79 days in isolation since adult molt on 9-10-69, was exposed to an F3 male. After each successful mating the male was removed and returned to its jar. Five encounters were staged and in each (see Table 5) the male commenced courting within minutes after initial contact and the female quickly approached and mounted soon after.

Alexander (1961) reports that after successful spermatophore attachment the male's antennae and cerci cease vibrating and drop slowly, and the female dismounts following release by the male. This was true for most G. integer matings. However, on 12-2-69 a successful copulation occurred between F3 female #420 and F3 male #404, and when the female dismounted with spermatophore attached, after 27 seconds,

Table 5. Reproduction data for various adult female G. integer (previously maintained in isolation) following initial exposure to a sexually mature male, including latency (in minutes) after contact before male began courting (C), latency (in seconds) from courting to first mounting (M), and latency (in days) from first oviposition to appearance of first hatchling (H).

Female	Male	Exposure	C. (min.)	M. (sec.)	Mount duration (sec.)	H. (days)	No. Hatchlings
F₁#5 (e)	F₁#35	12-8-68	?	?	22	30	113
"	"	12-30-68				23	114
F₁#71(e)	?	?	?	?	?	27	26
F₂#59	F₂#68	5-30-69	< 1	1380	30	16	164
F₂#58		6-1-69	25	<10	28	16	972
F₂#60	"	6-3-69	22	<10	25	17	50
F₂#57(e)		6-5-69	42	<10	25	19	42
F₂#59	"	6-6-69	2	<10	28		
F₂#60		6-7-69	10	40	40		
F₂#59	"	6-9-69	7	< 60	?		
WC#422	WC#423	11-29-69	120+	<20	?	49	68
WC#421(e)	"	11-25-69	120+	?	?	45	69
F₃#420	F₃#404	11-29-69	420+	26	21 (x)		
"	"	12-2-69	< 1	<60	27		none
F₃#419	F₃#245	11-28-69	2	<10	27		
"	"	11-29-69	2	50	26		
"	"	11-30-69	< 2	< 5	11		
"	"	12-2-69	1	< 5	20		
"	"	12-8-69	20	< 5	37		none
F₄#466	F₄#452	3-20-70	5	60	19 (x)	29	1
F₄#465(e)	F₄#451	3-14-70	67	< 10	20 (x)		none
"	F₄#456	3-26-70	?	?	21 (x)	29	1
F₄#467	F₄#456	3-20-70	< 2	< 10	13 (x)		none
WC#561	?	5-17-70	?	?	?	20	1425

(e) = female excavated depression in sand during oviposition; (x) = unsuccessful mating

the male remained for 10 seconds with its abdomen pointed high in the air, anal cerci vibrating, as if still engaged in mating. This phenomenon was observed on two other occasions for different F_3 males.

Table 5 summarizes the reproduction data for various females at different times of the year. With the exception of F_1 #5 all matings represent the first mating occurring after placement of the male in the female's jar. Some data for subsequent matings and for unsuccessful matings are included. Several encounters summarized in the Table are described below in more detail.

Minutes after F_4 male #451 contacted F_4 female #465 it began protruding and withdrawing a spermatophore. Courtship calling commenced 67 minutes later at which time the female oriented to the male, approached and mounted; unsuccessful spermatophore transfer occurred. During the next 40 minutes, 21 more aborted matings were observed. In each instance the female mounted within seconds after the male commenced courting, but in each case the male was unable to attach the spermatophore before the female dismounted or fell off. Old overly dried spermatophores incapable of smooth transfer or attachment were largely responsible for unsuccessful mating attempts. Males in isolation or maintained in all-male groups and given no access to females frequently dragged their abdomens in the sand to dislodge old spermatophores. Infrequently, once dislodged, males were observed to seek out and eat the spermatophores.

Wild caught female #421 isolated for 20 days after capture and heavily egg-laden was mated several times with male #423; one week later the sand was moistened and the male removed. The female inspected the damp area, continually palpating and maneuvering over the wet sand.

In less than a minute preliminary ovipositor thrusting occurred, and for over five minutes the female positioned herself with head and thorax over a damp area, palpating the sand continually and thrusting the ovipositor (and perhaps ovipositing?) in dry sand. Then the female reoriented so that her head was over dry sand and the ovipositor thrusted into damp sand. Several eggs were seen deposited next to the glass $\frac{1}{2}$-inch below the surface. Alexander (1961) has described females with palpi contacting dampness repeatedly stabbing the ovipositor into dry sand, and states that although inseminated females given no access to moist sand will probe dry surfaces with the ovipositor, no eggs are deposited. He believes failure to oviposit in dry areas is probably explained by sensory receptors located on the ovipositor that must encounter moisture before oviposition can occur. This seems reasonable, and yet I have observed eggs lying on the dry sand surface in some jars containing isolated G. integer females, both mated and unmated, never given access to wet sand.

On the second day of egg-laying, female #421 excavated a depression one inch deep next to the glass and oviposited frequently during the next several days. Within minutes after exposure to a damp substrate female #561 began egg-laying and continued sporadically for over two weeks; oviposition bouts exceeding four hours in length were noted on several occasions. Although most ovipositing integer did not excavate, five females representing two F_1's, and F_2, an F_4 and a wild caught individual, oviposited in excavations (Table 5). In some instances a new depression was excavated each morning, several days in succession.

On 3-20-70 a 14 day old adult F_4 male and a 29 day old F_4 female

previously isolated were permanently paired. Successful matings were never directly witnessed for this pair, but beginning 3-27-70 and up to 4-10-70 when the male was removed, the female had a recently-attached fresh spermatophore every morning at 8 a.m. when the jar was checked. Oviposition occurred but only one hatchling appeared, which eventually molted to an adult male 81 days later on 7-12-70. Four other F_4 mated pairs were established, and in all cases successful matings occurred as evidenced by females with attached spermatophores, but for only one pair did hatching occur, and in this instance it was again only a single offspring, which did not survive. Nearly all mating experiments with G. integer resulted in successful reproduction and more offspring than could be feasibly housed. With the exception of several attempts to mate F_3's that were old (i.e., adult ages of three months or more) or showed stunted growth or retarded development accomplished by rearing under crowded conditions in a cool room (66°-72° F) mating experiments with F_4 generation integer were the only unsuccessful reproduction attempts during the $2\frac{1}{2}$ year study period.

Male G. integer were first heard calling in Norman on April 22 in 1969 and on April 23 in 1970. Adult males in the laboratory called year round and successful reproduction, with the exception of cases mentioned above, occurred year round indicating no obligate diapause in this species. Beginning mid-May, adults began congregating under street lamps on the University campus at night and were easily captured; females taken at this time had egg-swollen abdomens. Observed numbers declined until early June when very few or no adults were found near the lights at night. Beginning approximately the second week in July

adults once again oriented towards the lights, with peak numbers appear-
ing in late July and August. During these months large accumulations
of crushed adult carcasses were in evidence on sidewalks, etc. These
'invasions' obviously represented the progeny of adults heard calling
and seen congregating beneath lights from April-June.

Male G. integer called on campus on November 19, 1969, two weeks
after a cold wave and the first frost. On 11-17-69, three days after
the first killing frost, at 8 p.m. and a temperature of 55° F, courtship
calling was heard at the base of a lamp post. The grass was slowly
pulled back revealing a courting integer male and an adult female one
inch away. The persistence of G. pennsylvanicus beyond first heavy
frosts, as evidenced by chirping, has previously been reported for a
population in Michigan (Alexander and Meral, 1967). Both adult integer
were captured and housed together in the laboratory. The male courted
frequently and on 11-23-69 mounting and successful mating occurred;
the female dismounted with an attached spermatophore after 35 seconds.
The male was subsequently removed and successfully mated with two other
wild caught females (#421 and #422), both of which laid eggs that
produced the F_1 generation hatchlings used in Experiments 5 and 6 (see
Table 5). Male G. integer were heard calling in Norman as late as
December 17, 1970 at a temperature of 59° F.

Hatching

Depending on room temperature and other varying environmental
factors, first hatchlings appeared from 12 to 49 days after the first
observed ovipositions. In many cases eggs were not deposited near the
glass sides of the rearing jar, so it is not known whether actual egg-

laying occurred during the first observed ovipositions or sometime later.

The hatching of an F_2 whose development was followed as it developed next to the glass was witnessed on 1-22-69, 23 days after laying. The "larva" worked its way to the surface by undulating movements, still enclosed in a transparent membrane and freed itself once at the surface. The head emerged first and worked free of the membrane, then the entire body emerged with antennae and legs, previously flattened against the ventral body surface, popping out quickly. Cricket hatching is thus similar to the hatching of grasshoppers (Uvarov, 1966). Uvarov described hatching from the egg pod and the subsequent active wriggling movements of the larva working its way up through the soil to the surface surrounded by a thin transparent membrane called the provisional cuticle (referred to as 'embryonic cuticle' by Wigglesworth, 1965). Once at the surface the head of the hopper larva penetrates, the sac-like enveloping cuticle is shed, and the hatchling or first instar emerges.

Cursory examination of the sand in several breeding jars after the passage of three or four days with no further hatchlings appearing, suggested that egg mortality was high. Aside from many eggs showing no indications of embryonic development, numerous others were found which had developed but failed to hatch, or in which the egg case was broken, but the nymph failed to emerge completely or reach the surface. On several occasions hatchlings emerged in air pockets beneath the surface and did not survive. Failure to escape the provisional cuticle was a cause of early mortality. Of the 68 G. integer nymphs that surfaced from the egg batch laid by female #422, four (6%) were hopelessly entangled in the membrane. Likewise, two of 69 hatchlings from female

#421 were unable to free themselves and did not survive. In nearly all cases the head and distal segments of all appendages, especially the hind legs, were surrounded by adherent membrane.

For female #58 which began ovipositing on 6-6-69 and continued until the last observed ovipositions on 7-22-69 before dying on 8-2-69, the daily hatching data for the 972 successfully emerging offspring are shown in Table 6, along with the hatching records for the progeny of eight other females. For some broods large numbers of offspring appeared during the first several days, then emergence tapered off. In other cases daily numbers emerging peaked after only a few hatchlings during the first several days. These inconclusive data suggest the existence of individual variability in egg-laying by adult female G. integer, probably attributable to a number of environmental, and possible genetic, factors.

Greatest hatching success (1425 hatchlings) was recorded for wild caught female #561 captured 5-17-70, placed in a gallon jar with several males for four days, then isolated in a breeding jar where she oviposited off and on for 31 days until seven days before her death.

Molting and Number of Instars

Successful G. integer hatchlings undergo a series of molts and instars leading to the adult winged stage. In the last two instars wing buds are present and females are easily distinguished from males by the developing ovipositor (approx. 2 mm. long in the small wing bud instar; 5 mm. in the large wing bud instar). First instars removed from breeding jars with an aspirator and placed in rearing jars according to the date of hatching were checked daily to record molting and

Table 6. Number of hatchlings emerging daily for ten different egg batches, representing the progeny of nine different female *Gryllus integer*.

Day	F1's #5/#35 Batch#1	F1's #5/#35 Batch#2	F1's #71/?	F2's #57/#68	F2's #58/#68	F2's #59/#68	F2's #60/#68	WC#421 WC#423	WC#422 WC#423	WC#561/?
Day 1 =	1-12-69	1-22-69	3-18-69	6-25-69	6-22-69	6-22-69	6-23-69	1-16-70	1-28-70	6-10-70
Day 1	2	24	16	1	35	12	1	2	1	27
2	7	39	2	0	23	10	1	5	1	147
3	14	9	2	1	18	11	1	4	1	40
4	17	7	6	8	29	11	4	9	1	78
5	12	20	0	12	32	16	8	16	2	133
6	15	12	0̲	16	15	10	11	3	2	126
7	10	1	26̲	1	12	9	10	1	1	198
8	9	0		3	11	17	10	3	7	101
9	16	3		0	26	20	0	0	8	161
10	5	3		0	21	13	3	14	11	115
11	4	2		42̲	15	16	1	6	15	55
12	2	2			30	7	0	0	10	43
13	0	3		sand	10	12	0̲	0	2	17
14	0̲	2		drying	6	0	50̲	1	2	0
15	113̲	1		out	11	0̲		1	1	9
16		0			17	164̲	sand	2	3	37
17		0̲			33		drying	0	0	57
18		114̲			36	sand	out	1	0̲	7
19					26	drying		0	68̲	37
20					32	out		1		7
21					41			0		17
22					48			0̲		10
23					29			69̲		2
24					28					1
25					18					0
26					11					0̲
27					17					1425̲
28					10					
Week 5					146					
Week 6					168					
Week 7					46̲					
					972					

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mortality data. Particularly close checks and careful records were
kept for the developing offspring of five different females -- F_1's
#5 and #71, F_2 #58, and wild caught #421 and #422 (Table 7).

From 9 to 11 instars (rarely 12) in G. integer are required
before the final adult molt. Ten to eleven instars and longer devel-
opment times were generally characteristic of crickets reared at cooler
temperatures (e.g., progeny of F_1 #5), whereas ten instars, frequently
nine, and shorter development times were characteristic of crickets
hatched and reared at higher temperatures. Possible genetic effects
may account for the differences between the offspring of F_1 #5 and
wild caught #421, hatched during the month of January in 1969 and 1970
respectively (Table 7). Among grasshoppers and locusts variations in
instar number have been found in practically every species closely
studied (Uvarov, 1966), and Wigglesworth (1965) has noted the effects
of temperature and other factors on variable instar number in a variety
of insect species.

Nearly all males designated as controls, experimentals or perma-
nently paired animals were removed from rearing jars and isolated, or
(in the case of pairs) housed together, within 24 hours after the small
wing bud instar molt. This reduced crowding and helped prevent the
development of stunted adults or excessive mortality from cannibalism.

Molting occurred either on the sand or with the cricket head
downward on the vertical screen. In nearly all of the molting sequences
observed, the molted cricket, or in some instances another cricket in
the jar, consumed the ecdysed skin. Tanning and total darkening of
the cuticle was usually completed within 3-4 hours after molting.

Table 7. Development data for the progeny of five different G. integer females, including number of instars required before final adult molt.

Female Parent	No. Reaching Adulthood	Quickest Development Time (Days)	Instar Prior to Final Molt			
			9th	10th	11th	12th
F₁ #5	81	105	2	31	44	4
F₁ #71	12	74	2	7	3	
F₂ #58	259	36	39	214	6	
WC #421	43	80	11	32		
WC #422	41	82	10	28	3	

Data for four observed final molts are included in Appendix II.

Growth of Nymphs

Growth rates varied greatly for nymphs in different experiments, probably largely due to varying temperature effects in the laboratory throughout the year. One F_3 female, hatched 6-22-69 and maintained under laboratory conditions underwent final molt 37 days later, one of the most rapid development times recorded. Average daily laboratory temperature during the 37-day development period at 8 a.m. was 87° F. An F_3 male sibling (#439) hatched 8-1-69 and maintained under crowded conditions in a gallon jar for several months in a cool room (66°-72° F) final molted 230 days later on 3-19-70, one of the longest development times recorded.

Sibling crickets raised under nearly identical environmental conditions, with the exception of differing initial densities in the rearing jars, showed variable growth rates. The F_2 offspring used in

Experiment 2 began hatching 1-12-69 and were isolated in quart jars according to hatching date. All jars were identical, with crushed Gaines meal always in excess, except Jars I and J which were gallon jars housing a larger number of hatchlings. The original density of crickets per jar varied from 7 to 41 (Table 8). On the 63rd day, nine weeks after hatching, the crickets in each jar were removed, placed individually in one-dram vials of known weight (desiccator-dried), and weighed to the nearest one-tenth mg. on a Metlar balance. All weighings were made between 10 p.m. and midnight. Length to the nearest one-tenth mm. was determined by placing the vial on a ruler under a dissecting microscope and measuring snout-vent length after each cricket assumed a resting posture. Similar measurements were recorded for the 26 hatchlings from the 104 eggs oviposited in water by F_1 female #71.

It is readily seen (Table 8) that growth rates varied between the two broods and between jars housing siblings from the same brood, as evidenced by differences in weight, length, and instar reached by the 63rd day. A t-test comparing mean weight of the crickets in Jar A from female #5 with that of progeny from female #71 showed differences significant at the .001 level of probability (t-value = 6.01). This difference is largely due to the higher room temperatures during development of crickets in the latter brood (see Fig. 5). More interesting is the difference between the siblings in Jars A and B from female #5, separated by only one day of hatching. Comparison of the mean weight of crickets in the two jars at Day 63 showed differences significant at the .01 level of probability (t-value = 3.01). Other jars showed comparable degrees of growth rate variability but the differences were not checked for significance.

Table 8. Growth data for F_2 generation developing G. integer nymphs, progeny of females #5 and #71, reared in quart jars on the 63rd day post-hatching.

Rearing Jar	Hatching Date	N Day 1	N Day 63	Weight (mg.) $\overline{Y}$	SE	Range	Length (mm.) $\overline{Y}$	Range	4th	5th	6th	7th	8th	9th
F2's from F1 female #5:														
A	1-13-69	7	7	9.60	1.34	4.6-14.9	5.5	4.5-6.5	1	6				
B	1-14-69	14	11	22.44	3.26	9.2-39.9	6.9	5.2-8.2		4	7			
C	1-15-69	17	9	10.02	0.70	6.7-12.6	5.8	4.6-6.4	1	8				
D	1-16-69	12	4	18.05	2.68	13.0-25.0	6.9	6.5-7.5		3	1			
E	1-17-69	15	8	16.31	1.40	9.9-22.2	6.4	5.0-6.8		6	2			
F	1-18-69	10	5	20.32	3.21	11.2-28.3	7.3	6.3-7.8		3	2			
G	1-19-69	9	7	16.10	0.99	10.7-18.8	6.7	5.8-7.0		7				
H	1-20-69	16	9	14.13	1.85	9.1-23.9	6.1	5.0-7.2	2	7				
+I	1-22-69	33	27	18.95	1.36	6.6-41.8	6.7	4.8-8.9	1	15	11			
+J	1-23-69	41	33	23.85	1.58	7.1-51.0	7.3	4.7-9.8	1	17	15			
K	1-24-69	9	0	-	-	-	-	-						
L	1-25-69	7	7	25.06	2.77	18.8-35.3	7.2	6.5-8.1		3	4			
M	1-26-69	20	16	20.53	2.39	6.9-42.3	6.8	5.0-8.3		10	6			
N	1-27-69	12	9	9.38	1.31	3.3-15.3	5.5	3.8-6.6	2	7				
O	1-28-69 to 2-5-69	17	5	45.16	5.89	28.3-58.3	9.2	7.4-10.8			5			
F2's from F1 female #71:														
	3-18 to 3-21-69	26	12	230.38	27.67	101.9-430.4	15.3	12.0-20.0				0	3	9

t-tests of sig. diff. betw. mean weights (mg.):	t-statistic	df
Jar A (#5) vs. Jar B (#5)	3.01 **	16
Jar A (#5) vs. #71	6.01 ***	17

Significant **P< 0.01   ***P< 0.001   + = gallon rearing jar   SE = standard error

Time of Molting

Close checks were made of isolated males used in Experiments 3-6 and for the female siblings of the males in Experiments 5-6; for many animals exact molting times were recorded or accurately estimated. The data (Table 9) suggest that molting occurs with equal frequency throughout the daylight hours, with most molting occurring during periods of darkness.

Mortality in Developing Nymphs

For those nymphs that reach the sand surface and escape the provisional cuticle, mortality is high, especially for early instars (Table 10). Of the five broods closely studied, nearly half (48.5%) of the first instars failed to achieve adulthood. Highest mortality (44%) occurred before and during the molt to the 2nd instar; mortality tended to progressively decrease with later instars (Table 10).

Approximately 12% mortality was due to cannibalism and 9% to entrapment during molting. With few exceptions nearly all mortality beyond the 4th instar was attributable to these two causes.

Dead crickets showing no evidence of external damage comprised 6% of the observed mortality. Drowning accounted for nearly 12% mortality in very young crickets and was almost entirely limited to nine F_3 rearing jars where vials with paper wicks were used as water sources; in all other jars moisture was supplied by placing several drops of water on a leaf and water vials were not added until the crickets had achieved larger sizes. Most mortality (60%) could not be directly accounted for, as no traces remained of missing animals.

Table 9. Time of the late instar and final molts for <u>Gryllus</u> <u>integer</u> in Experiments 3-6. Exact times were ascertained for nearly all molts occurring between 7 a.m. - 8 p.m. Others were closely approximated from degree of cuticular tanning or were unknown (?). No animals in the unknown column molted during the light hours from 8 a.m. to 5 p.m.

Crickets	Total N	4-8 a.m.	8-10 a.m.	10 - Noon	Noon-2 p.m.	2-4 p.m.	4-6 p.m.	6-8 p.m.	Late p.m.- Early a.m.	?
Expt. 3: Males										
Lg. wing bud molt	98	13	7	4	6	2	2	6	3	55
Final molt	98	11	7	7	5	5	8	11	4	40
Expt. 4: Males										
Lg. wing bud molt	55	3	4	4	4	6	1	3	10	20
Final molt	55	6	3	6	6	7	5	1	10	11
Expt's 5 & 6:										
Males										
Sm. wing bud molt	49	1	5	5	2	5	3	4	2	22
Lg. wing bud molt	49	2	1	2	4	2	5	2	18	13
Final molt	49	10	1	4	5	1	2	2	22	2
Females										
Sm. wing bud molt	35	3	4	3	0	2	2	0	3	18
Lg. wing bud molt	35	3	0	2	3	0	3	1	2	21
Final molt	35	2	0	2	2	0	3	3	10	13
Total Observations	558	54	32	39	37	30	34	33	84	215
Percentage		9.7	5.7	7.0	6.6	5.4	6.1	5.9	15.1	38.5

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Table 10. Mortality data for the developing offspring of five different _Gryllus integer_ females.

Female Parent	No. First Instars	Mortality up to and Including Instar								Late Instar	No. Surviving to Adulthood
		2	3	4	5	6	7	8	9		
$F_1\#5$	167	39	9	6	17	7	1	4	1	7	76
$F_1\#71$	26	8	1	1	0	1	3	0	0	1	11
$F_2\#58$	504	110	51	19	28	11	13	8	4	2	258
WC#421	67	12	3	4	0	2	3	0	0	1	42
WC#422	64	8	1	1	3	5	2	3	0	2	39
Total	828	177	65	31	48	26	22	15	5	13	426
Total Percentage		21.4	7.8	3.7	5.8	3.1	2.7	1.8	0.6	1.6	51.5
Total Occurrence of Mortality		44.0%	16.2%	7.7%	12.0%	6.5%	5.5%	3.7%	1.2%	3.2%	48.5%

The jars were escape-proof, and mortality was attributed to cannibalism or entrapment in the ecdysed molt only when cannibalistic behavior or entrapped or partly cannibalized animals were observed by the experimenter. Nearly all crickets entrapped during molting were consumed by cage mates and entire carcasses were seldom evident. Small crickets, especially, were quickly eaten, with only occasional traces of antennae or legs to suggest their fate. Consequently, it is likely that most of the mortality attributed to unknown causes resulted from cannibalism or entrapment followed by cannibalism.

Stridulatory Behavior

Adult male field crickets produce three distinctive sound patterns: (1) the calling song, (2) aggressive or rivalry song, and (3) courtship song (Huber, 1962; Alexander, 1961, 1968b; Kutsch, 1969). The normal acoustic repertoire may also include transitional sound patterns incorporating components of the three basic calls, apparently largely determined by the degree of involvement of antennal and/or cercal stimulation (Alexander, 1968b). Stridulation patterns not produced under natural circumstances can also be experimentally produced by electrical stimulation of certain brain areas (Huber, 1955, 1962).

On the underside of each tegmen there is a stridulatory file and a scraper. In most Gryllidae the right tegmen usually overlies the left, and during stridulation when the tegmina are raised and rubbed together, the stridulatory file on the right tegmen strikes against the scraping edge on the inner margin of the left tegmen (Alexander, 1961). The morphology of the stridulatory file (e.g., number of teeth, length

in mm., number of teeth/mm.) is one of the most important characters used in field cricket taxonomy (Alexander and Walker, 1962; Walker, 1969). The three basic songs reflect patterns of wing movement and differ in several ways: (1) position of the tegmina, (2) length of pulses (i.e., number of teeth striking scraper), (3) number of pulses per chirp, (4) chirp sequence, and the (5) intensity and (6) frequency of the sounds (Huber, 1962).

Patterns of neuromuscular activity involved in the calling and aggressive songs are similar (Bentley and Kutsch, 1966; Kutsch, 1969) although the aggressive song contains a greater number of pulses. Aggressive chirps in the European field cricket (Gryllus campestris) contain up to 30 pulses compared to only four or five in calling chirps (Bentley, 1969). The courtship song is composed of two phases consisting "of several pulses ('ticks') representing reduced calling chirps, which interrupt a series of softer sounds" (Kutsch, 1969: 335).

Considering the structural relationships between the calling and aggressive songs and the phylogenetic sequence in which the three distinct songs evolved Alexander (1961: 68) suggested that:

> ...the aggressive sounds of crickets and the aggressive stridulation itself have evolved as modifications and intensifications of milder interactions among males in which the calling song was principal signal, just as the calling function must have evolved as an elaboration of the courtship function.

Calling Song

The calling song is usually produced by undisturbed males and functions primarily in attracting sexually responsive females, though it has undoubtedly evolved biological significance for other males (Alexander, 1961). The calling song can elicit fighting behavior

and enhance attack readiness in nearby males. Acoustically provoked aggressive encounters occurring with sufficient frequency could effectively space the males within a population, thus increasing the chances of all available females' being mated (Heiligenberg, 1969). The similarity of the calling song to aggressive stridulation suggests its possible importance in reinforcing retreat and the maintenance of distance and spacing by a mechanism of acoustic repellence (Alexander, 1961).

It is known that males within hearing range of one another exhibit alternating chirping, a phenomenon largely determined by mutual inhibition (Jones, 1966). Nearby males engaged in alternating acoustical interactions may mutually increase their chirp rates, increasing the chance of visitation by either females or nearby rival males leading to aggressive encounters which would function to establish or help stabilize spacing (Heiligenberg, 1969). Field crickets exhibit territorial behavior (Alexander, 1961) and the calling song may also have territorial significance (Jones, 1966; Wynne-Edwards, 1962). The principal purpose of calling may be that of an epideictic display whereby the total audible volume directly or indirectly supplies an index of population density leading to dispersive behavior and the "natural regulation" of numbers (Wynne-Edwards, 1962).

Adult male Gryllus integer in isolation (experimentals and controls) or in pairs in the laboratory called at all times, with the largest numbers calling during the early morning light hours; at 7-8 a.m. most adult males were calling in their jars.

The earliest known occurrence of calling by an adult male in

isolation was noted for F_3 #172 which molted to adulthood on 8-5-69 and commenced calling five days later, at which time it called continuously for over one hour. The oldest surviving F_2 male (#159) called for extended periods on 10-20-69 at 9 a.m. (80° F) at adult age 122 days, and for shorter periods on 11-7-69 at 8 a.m. (70° F) at 140 days of age, 16 days before death. Several F_3 males chirped when over 120 days of age, including F_3 control #325 which called continuously for over an hour on 2-7-70 (72° F) as a 140 day old adult, four days before death.

Courtship Call

The courtship call, associated with mild sensory input usually provided by tactile cercal stimulation, generally precedes copulation and may be necessary to induce female mounting in some species (Alexander, 1961; Bentley, 1969). A sexually responsive male approached from behind may commence courting within seconds after contact. Approached from the front, following initial antennal contact, a male with a spermatophore primed for mating usually turns away and commences courting if the other cricket responds non-aggressively and exhibits the common female response of immobility.

Isolated males courtship-called, both when the anal cerci were mechanically stimulated by some object in the jar and when no extrinsic source of stimulation was apparent. Males resting in their jars frequently became alert and started courting when their cerci were lightly stroked with a probe; knowledge of this fact was exploited during attempts to capture field crickets calling at night. When closely approached in the field a calling G. integer retreated into its burrow, making capture difficult. When shining a light down the burrow

the male was frequently seen resting an inch or more below the surface

facing the burrow entrance. By lightly stroking the antennae with a

broom straw, plant stem, etc., the male was slowly induced to crawl

up the burrow. On several occasions as the male rested in the burrow

opening, the straw was inserted in the opening opposite the male and

the cerci lightly stimulated. Whenever this was tried the male quickly

left his retreat and was easily captured. On most occasions males

lured from their burrows by these tactics acted mildly aggressive,

lashing their antennae about the area and/or jerking their bodies;

twice, however, males responded by immediately beginning to court.

Mutual or one-sided courting was frequently observed among

continuously paired males (see Table 12), and during the 15-20 minute

interactions between experimentals and intruders courting often occurred

either in the absence of aggression or before, during, or immediately

after agonistic encounters, some of intense degree (see Table 16).

Rapid switches from aggressive calling to courtship or vice versa

were frequently observed during experimental-intruder interactions.

Aggressive Calling

The aggressive call is usually elicited during intense acoustical

stimulation or mechanical stimulation of the antennae, and is character-

istically accompanied by other agonistic behaviors -- e.g., antennal

lashing, rearing of body off the ground and jerking, etc. (Bentley,

1969; Alexander, 1968b; Huber, 1962). Head-on approach and antennal

contact between two males generally leads to aggressive stridulation,

especially if accompanied by agonistic displays, unless one of the males

exhibits the passivity characteristic of antennated females (Alexander,

1961). Aggressive chirping is indicative of a male's aggressive state
(Alexander, 1961) and was particularly evident for G. integer males
during aggressive encounters of Levels 3-5 (see Table 38). Naive males,
isolated since their adult molt, frequently responded to initial con-
tact with a female by aggressive chirping prior to eventual courting.

Alexander reported several interesting aspects of aggressive
calling in field crickets. All of the following observations have
been verified or supported by behavioral observations of G. integer
described in the next sections. According to Alexander (1961: 164-67):

> .....an encounter in which the retreating male is the only
> one to chirp constitutes an indication of impending change
> in the relationship of the two males......there is also a
> correlation between the amount of chirping and the winning
> or losing of encounters...Aggressive chirps may be produced
> either during an encounter or after contact has been lost
> through retreat. Nearly every case in which a losing male
> was the only one to chirp was an instance in which the loser
> chirped during the encounter. The loser practically never
> chirped after contact was lost following an encounter, while
> the winner almost invariably did so......aggressive sounds
> re-inforce the subordination of a male which has just lost
> a fight.

Permanently Paired Males

Although much activity occurred in jars containing paired males,
interactions resulting in agonistic displays were infrequently observed.
Usually, when not moving and mutually avoiding contact with each other,
males rested in separate areas of the jar (one usually on the vertical
screen) or with antennae or other body parts in contact.

Most aggressive encounters recorded were Level 2 where, upon
contact, one male usually retreated and the other exhibited a mild
agonistic response (e.g., jerking of body, brief chasing, aggressive

chirping, etc.). Level 2 encounters were not included in the tabulations (Table 11, Appendix I) although they were considered when calculating the number of runs (i.e., changes in dominance). An encounter was recorded when part of one male (usually the antennae) touched some part of the other. Most of the aggressive and courtship sequences recorded (Tables 11 & 12, Appendix I) represent encounters separated by at least 24 hours. However, since some pairs were observed up to three or more different times throughout the day, for periods occasionally exceeding several hours, it was arbitrarily decided for tabulation purposes that behavioral interactions for any given pair would be considered as discrete encounters only if separated by over an hour. Many of the common behavior patterns and a few unusual ones for some male pairs in Experiments 2 & 3 are described in Appendix III.

Close observations were made for paired males in Experiments 3-6. From 9-11-69 to 12-10-69 jars housing F_3 pairs (Experiment 3) were usually observed several times daily. Greatest activity occurred in the morning from 7 a.m. to noon; at these times, movement, contact, and social encounters were frequently noted in most jars. Calling, courtship, antennal fencing, jerking, and brief chases were commonly observed. Although activity levels were high, aggressive encounters exceeding Level 2 infrequently occurred, as was true for the F_2 generation paired males in Experiment 2 (Table 11). Table 11 reflects only the relative aggressiveness of paired males during the observation period from 7 a.m. to 6 p.m. and occasionally later. No observations were made after midnight or in the dark, although from several late visits to the laboratory (3-5 a.m.; lights not turned on) it is known

that the crickets were active and calling at these hours. Although active during the day, field crickets are considered largely nocturnal in habits (Alexander and Meral, 1967; Alexander, 1968a).

In contrast to paired males in other experiments, F_4 generation animals in Experiment 4 showed comparable incidences of courtship behavior, but significantly reduced aggression levels (Table 11). Daily observations from 4-13-70 to 7-6-70, nearly three months, revealed only one Level 4 (dominance uncertain) and two Level 3 aggressive displays. Most agonistic encounters were Level 2 and these were observed for any given pair no more than three times (e.g., pair #473-476), only once (e.g., #481-483), or not at all (e.g., #493-494) (Table 11). It was common to observe F_4 paired males resting quietly in antennal or body contact, feeding amiably off the same food pellet, or contacting, antennating or palpating one another, then moving apart with no evidence of jerking, aggressive calling, or other agonistic responses. Interestingly, in spite of the reduced aggressiveness, average adult longevity was lower for the F_4's than for other paired males (Table 14). Both these findings may reflect reduced viability from increased inbreeding.

The F_1 paired G. integer males in Experiments 5 & 6 were observed from 4-17-70 to 8-13-70. Only two aggressive encounters, both involving antennal fencing and jerking and terminating in uncertain dominance, were recorded for non-aggressive pair #535-536. During one mating attempt #535 remained mounted for 30 seconds while #536 protruded a spermatophore and attempted transfer. When #535 dismounted, #536 immediately resumed courtship calling. Non-aggressiveness also

characterized pair #547-548; whenever observed, both males were usually inactive in different parts of the jar, or resting in antennal contact.

Interestingly, the four F_1 pairs in Experiment 5 exhibited several Level 3-5 and many Level 2 aggressive encounters, whereas the four pairs in Experiment 6 showed much reduced aggressive levels -- rarely higher than Level 2 encounters and few of these (Table 11). The only exception was pair #553-554, for which a single Level 5 encounter lasting 70 seconds and involving aggressive calling and four mandible lockings, occurred early during the pair relationship. The encounter ended when both males turned away with dominance undetermined; following this encounter no further aggression was evident for this pair.

The only difference between the males in the two experiments was their female parent (see Table 2), suggesting possible genetic influences on aggressiveness. Although five of the eight males in Experiment 6 lived longer than the longest-lived male in Experiment 5, the differences were not significant (Table 13).

Mean adult longevity varied considerably between paired males in different experiments and most of the differences were highly significant (Table 14). Some differences were undoubtedly due to environmental conditions in the laboratory or insectary, with genetic differences contributing an unknown amount of variability.

Agonistic Behavior

Permanently paired males exhibited infrequent aggressive encounters of reduced intensity (Table 11). Level 5 encounters were noted for only eight of the 46 male pairs studied, and only one time for seven of the eight (Table 11). The most intense Level 5 encounter ever

Table 13. Mean adult longevity (days) of paired male G. integer in Experiments 5 & 6 reared and maintained under identical environmental conditions and differing only in the female parent. Males in Experiment 5 exhibited noticeably more aggression.

Expt.	N	Adult Longevity (Days)			t-statistic		df
		$\overline{Y}$	SE	Range			
5	8	70.8	1.54	63-76	1.72	NS	14
6	8	80.8	5.59	57-100			

NS = not significant using a paired t-test

Table 14. Analysis of variance of mean adult longevity (in days) of paired male G. integer in Experiments 2-6. Significance of difference between means determined by an a posteriori Student-Newman-Keuls (SNK) test.

Expt.	N	Adult Longevity (Days)			MS error	F-value
		$\overline{Y}$	SE	Range		
2	30	75.4	2.93	48-114		
3	34	98.2	2.80	61-133	227.45	24.43 ***
4	12	59.9	3.32	47-79		
5 & 6	16	75.8	3.09	57-100		

SNK tests:	Result	LSR
Expt. 2 vs. Expt. 3	***	14.12
Expt. 3 vs. Expt. 4	***	19.89
Expt. 3 vs. Expts. 5/6	***	15.63
Expt. 2 vs. Expt. 4	**	13.59
Expt. 4 vs. Expts. 5/6	*	13.75

Significant *P< 0.05   **P< 0.01   ***P< 0.001
LSR = Least Significant Range

witnessed involved five mandible-lockings during a face-off lasting over two minutes.

Among the crickets in Experiments 2, 3, 5 and 6, there were eight pairs for which relatively high aggression levels were recorded. It was arbitrarily decided to consider any pair a "high-aggression" pair if ten or more Level 3 or Level 4 encounters (pairs #101-102, 111-112, 266-267, 515-516, 519-520, and 531-532) or more than one Level 5 encounter (pair #97-98) had been observed. Most other pairs exhibited considerably less aggression.

Comparison of the adult longevity of "high-aggression" males with that of other paired males revealed a tendency for males known to have exhibited and experienced more aggression to show reduced longevity. Differences, however, were not significant at the .05 probability level (Table 15). Because of their consistent low aggression levels and reduced longevity, for whatever reason, the F_4 generation G. integer in Experiment 4 were not included in the calculations.

The reduced aggressiveness of permanently paired G. integer males compared to experimental and intruder males exposed to one another for short interaction periods every 48 to 72 hours is well illustrated by comparative behavioral responses during Level 4 encounters. During a face-off, G. integer males antennal-fence, spar with the fore legs, jerk the body, and frequently butt their opponent or stridulate aggressively; often, head to head, they reciprocally palpate head and mouth parts with the palpi. During Level 4 encounters between experimentals and intruders, open mandibles, a behavioral indicator of high aggressive state, were nearly always observed; open mandibles were

Table 15. Mean adult longevity (days) of F_2 male G. integer pairs
#97-98, #101-102 and #111-112, F_3 pairs #266-267 and
#276-277, and F_1 pairs #515-516, #519-520 and #531-
532 for which high levels of aggression were consis-
tently and frequently observed, and the other F_1, F_2
and F_3 male pairs. Data for the F_4 paired males are
omitted.

| Paired Males | N | Adult Longevity (Days) | | | t-statistic | | df |
		$\overline{Y}$	SE	Range			
"High-aggression"	16	78.3	4.57	61-133	1.63	NS	78
"Others"	64	86.9	2.37	48-126			

NS = not significant

infrequently noted in face-offs between paired males. Likewise, open

mandibles were often exhibited by the dominant animal during and/or

after Level 3 encounters between experimentals and intruders, but

rarely occurred during similar encounters between permanently paired

males.

Aggression between Paired Male Nymphs

Aggressive encounters were not limited to male G. integer adults.

On 4-18-70, F_4 male #487 briefly chased #488 during a Level 2 en-

counter when both were large wing bud nymphs one week before their

final molt. The highest aggressive encounter ever recorded for paired

male nymphs was noted for F_1 pair #519-520 on 4-17-70 when both were

ten days before final molt. A short bout of antennal-fencing led to

a face-off with occasional open mandibles lasting over 10 seconds,

after which #519 turned away and #520 gave brief chase.

Actual mandible locking was never observed among immature paired males, but was witnessed once during the most intense fight between G. integer male nymphs ever seen in $2\frac{1}{2}$ years of observation — a Level 5 encounter in a rearing jar between a 9th instar with small wing pads and an 8th instar without wing pads. When first observed both were antennal-fencing during a face-off; there then occurred in quick succession a brief locking of mandibles, several seconds of continued antennal-fencing, and jerking by the 8th instar, following which both males turned and moved away. With the exception of this and the Level 4 encounter outlined above, the few aggressive encounters witnessed between male G. integer nymphs did not exceed Level 2 in aggressive intensity.

Social Dominance

Over half of the 46 pairs studied (Table 11) showed either (1) no evidence of a dominant-subordinate relationship (6 pairs), or (2) a relationship that gave all indications of complete stability (19 pairs). When dominance switches occurred, the new alpha-omega relationship usually remained constant for several days at least (see pair #87-88, Appendix III). The greatest number of dominance switches known to have occurred was six, for pair #515-516.

Pair #266-267 was exceptional in that, following a reversal in social rank, #266 maintained dominance only for a short period of approximately 24 hours, before reassuming subordinate status (see Appendix III). Five Level 4 encounters resulting in unclear dominance were witnessed for pair #266-267 and certainly many others were not observed. More obvious jostling for dominance was noted for this pair

than for most others. Both males were probably evenly matched in aggressiveness, fighting ability, etc., and two dominance switches (Table 11) is probably a greatly underestimated approximation of the actual dominant-subordinate relationship for this pair.

Social rank, easily determined for most interactions between experimental G. integer males periodically exposed to intruders, was difficult to ascertain for several permanently paired integer males. Pair #111-112 was the most active of all the F_2 pairs, and although clearcut dominance was recorded for only #111, numerous Level 3-5 encounters (Table 11) occurred where dominance was unclear -- e.g., five Level 4 encounters were witnessed at widely separated times throughout the experiment during which both males faced-off, jerked the bodies while antennal-fencing and aggressive calling, then separated and moved apart, frequently to commence courting. (See also F_3 pair #252-253, Appendix III).

For 40 of the 46 pairs studied, some evidence of dominance, though slight in some instances, was observable. Examination of the data shows no strong evidence to suggest that dominant males outlived subordinates. In only 22 out of 40 jars was the oldest male at death the same animal that was always observed dominant, or the male that won most encounters and dominated the last observed agonistic bout. The data are insufficient to justify any conclusions on this point, since in 10 pairs, both males died within 72 hours of one another. Also, the data reflect at best only a fair determination of social rank relationships, since only a small fraction of the total pair relationship was observed at random times, mostly between the hours

of 7 a.m. to 4 p.m.

The data recorded for several pairs (e.g., #106-107, Appendix III) well illustrate that (1) larger size, (2) ability to stridulate, and (3) possession of all body parts, are not necessary requirements for the achievement and maintenance of dominant rank. For all aggressive encounters observed for pair #106-107 (i.e., one Level 5, one Level 3, and many Levels 2) (Table 11), #106 dominated, yet it was considerably smaller in size, had non-functional wings, and was missing its right hind leg. Alexander (1961: 171) discussed the importance of "general fighting ability" in the Gryllidae. Regardless of what it be called -- individual variability in innate aggressiveness, aggressive perseverance, etc. -- it is apparently an important factor for consideration in under-standing the determinants of dominance in male field crickets.

Pair #106-107 and F_4 pair #493-494 serve as good examples for another paired male phenomenon. Male #106 died at approximately 9 p.m. on 7-17-69; male #107 was found dead at 8 a.m. the next morning. Rapidly occurring mortality of the remaining male following the death of one pair member was a common occurrence among paired males, too frequently observed to be explainable by chance factors alone. Aggressive behavior was never observed for F_4 pair #493-494. Indeed, except for one courtship calling sequence, activity was minimal. Yet, of all F_4's, this pair showed the shortest adult longevity. On 6-15-70 at 9:30 a.m. #494 was found paralyzed with hind legs off the substrate and stiffening. Male #494 was removed, and at three different times later in the day #493 was seen attempting to climb the glass sides of the jar; at 4:30 p.m. it too was paralyzed on the sand with hind legs

held aloft.

Courtship Behavior

Courtship between permanently paired males (Table 12) was observed more frequently than aggression (Table 11). Courting sequences frequently led to mounting which in turn often terminated with a mating attempt by the mounted male. Of the ten mounts observed for pair #111-112 which ended with mating attempts (Table 12) most did not exceed 10 seconds in length, although one lasted 35 seconds.

Mutual courtship calling (see pairs #93-94, #95-96, #111-112, Appendix III) occasionally observed among paired males (Table 12) was induced or facilitated by mutual cercal stimulation.

Paired males frequently dragged their abdomens in the sand attempting to dislodge old spermatophores. At one time male #93 had two dried darkened spermatophores visible in the ampulla mold of its reproductive apparatus.

Alexander (1961) reported that sexual activity (i.e., recent mating) increases the aggressiveness of male field crickets. Based on several observations of aggressive bouts preceding G. integer courtship encounters (e.g., see F_2 pair #99-100, Appendix III) it may also be that sexual state is of significance in accounting for changes in the dominant-subordinate relationship among permanently paired males.

Courtship-Agonistic Encounters

Sexual-aggressive ambivalent behavior was frequently observed among paired G. integer males (e.g., see pairs #101-102, 111-112, Appendix III), and rapid changes from sexual to agonistic behavior for one or

both males were noted for several male pairs.

During mounting sequences the mounted male assuming the female mating position frequently responded aggressively by opening mandibles and calling aggressively while mounted (see pair #87-88, Appendix III).

Twice, on successive days, #267 mounted #266 and courtship-called while mounted. In one instance #266 resumed courting as male #267, still courting, dismounted, and both males mutually courted back to back for nearly 30 seconds. This curious phenomenon of courtship calling by the mounted male was observed on one other occasion for F3 pair #270-271.

At 2 p.m. on 10-26-69, #271 mounted and called aggressively while #270 attempted spermatophore attachment. When #271 dismounted it began courting, and both males reciprocally called back to back until #270 oriented in front of #271, then stopped calling and attempted to back under. As #270 moved backward, #271 moved forward and mounted, continuing to courtship call as it did so, not stopping until it dismounted 8 seconds later.

During one chasing bout between pair #151-152, #151 continually courted as #152 chased. Then for several minutes #152 followed #151 around the jar, occasionally stopping to call aggressively as #151 maintained its distance, courtship calling the entire time. Continuous courting by a retreating submissive male was also noted for F3 pair #272-273.

Generally, pairs showing considerable courting behavior -- i.e., ten or more witnessed courting sequences and two or more mating attempts (Table 12) (F2's #85-86, #87-88, #93-94, #111-112, F3 #270-271, and

F_1 #531-532) -- also exhibited considerable aggression (Table 11).

The occurrence of paired male behavioral sequences involving rapid switching back and forth between agonistic and courtship behavior are noteworthy in view of Huber's (1955) belief that a close relationship probably does not exist between priming for courtship and priming for aggression in the European species, Gryllus campestris.

Age at Courtship Calling

Male #146 in pair #145-146 courted on 6-9-69 (Table 12), one day after its adult molt, and again on 6-11-69. Huber (1955) reported that pressure exerted by the spermatophore is the stimulus initiating courtship and calling in males of some cricket species. Whether field crickets can successfully copulate within 48 hours after adult molt is not known, although Alexander and Otte (1967) reported that females mate only after several days adulthood. Tests to determine the earliest possible age for successful mating in G. integer were not conducted, but since the first observed courtship calling for other paired males rarely occurred within one week of the adult molt (Table 12) the early adult age of male #146 would suggest either premature reproductive maturity or more probably that courtship calling is not necessarily indicative of a state of reproductive readiness. Alexander (1961) removed spermatophores from courting G. pennsylvanicus with tweezers and noted that the males usually resumed courting again within 15 minutes, before another spermatophore was present.

Experimental-Intruder Interactions

A well-illustrated discussion of male field cricket behavior
during early and later stages of aggressive encounters is given by
Alexander (1961: 134-135). All of the behavior patterns he describes
occurred during G. integer experimental-intruder interactions in the
present study; the variety of possible behavioral responses following
an encounter between two males are best stated by Alexander himself:

> .....If neither individual retreats upon contact, one or both
> may behave aggressively or begin to court, or the two individuals
> may remain in contact (or barely apart) and stand immobile (or
> nearly so) for several minutes.
> A male approached from behind, unless he is calling, most
> often turns quickly about and plays his antennae across the other
> individual. This puts the pair in about the same situation as
> if they had initially contacted by touching antennae together.
> A male approached from the rear may also shake or jerk his body,
> rear up his hind end, and then kick with his hind legs. These
> kicks sometimes repel the advancing individual, and rarely they
> flip an approaching male back several inches. Most often they
> only kick up sand and cause a temporary withdrawal by the approach-
> er. Occasionally a male approached from the front turns about
> and displays these reactions, which seem best described as a
> mild and non-specific form of aggression.......................
> When two aggressive males meet head-on and neither retreats
> with the initial antennal contact, each then begins to 'lash'
> his antennae rapidly upon the other. This is generally associated
> with (1) rearing the forebody, (2) drawing the palpi up and back,
> (3) spreading the mandibles, and (4) stepping forward. The an-
> tennal lashing is interpreted here as the initial act of aggress-
> ion in head-on encounters. If two males are not closely matched,
> the contact is usually terminated at this point. If the males
> are closely matched, or if the normally subordinate individual
> (1) is behaving territorially, (2) has just copulated, (3) has
> just been in isolation, or (4) has just won an intense battle,
> then neither male retreats at this point, and one or both indi-
> viduals may lift the tegmina and stridulate distinctively, jerk
> or shake the body, rear up further, or dash forward....If nei-
> ther individual retreats, the antennae are pressed together as
> the two crickets move forward..., and the two males begin 'spar-
> ring' with the forelegs.....The two may stand head-to-head and
> battle in this manner for several minutes. If neither individual
> retreats, the mandibles are eventually locked together and there
> is a sort of wrestling activity in which either male or both can
> be flipped or thrown sideways.

Courtship Behavior

Among field crickets courtship behavior may be elicited if one male is approached and stimulated from behind, or if it encounters a male that responds passively in female fashion; during homosexual encounters males may perform all aspects of a courtship sequence except successful spermatophore transfer (Alexander, 1961).

Courting by one or both G. integer occurred frequently during experimental-intruder interactions. Of a total of 3523 interactions in Experiments 1-6, 608 (17.3%) involved some courtship calling (Table 16, Appendix I). Incidence of courting by one or both males ranged from 10% of the interactions in Experiment 1 to approximately 27% of the interactions in Experiment 4 (Table 17). In all experiments most courtship behavior (55-78%) occurred during interactions involving Level 3-5 aggressive encounters (Table 17).

Males that courted before aggressive encounters tended to become dominant, and most post-fighting courtship was by the dominant. Courtship behavior was not independent of social rank and subordinate males showed a significant (P < 0.01; Chi-square value = 7.27) reduction in the tendency to courtship call after an aggressive encounter (Tables 16, 17). The tendency for males exhibiting courtship behavior at initial contact with other males to achieve dominant status during subsequent aggressive encounters leads to speculation. Interpreted ethologically, it may be that priming for sexual behavior and priming for aggression in male field crickets is not as distinct as Huber (1955) believes. A male primed for sexual encounters is apparently primed for fighting as well, and the action-specific energies involved in both behavior

Table 17. Incidence of courtship calling before and after Level 3-5 aggressive encounters for dominant and subordinate $\underline{G}$. $\underline{integer}$ during experimental-intruder interactions in Experiments 1-6.

| Experimental Males | Percentage of Interactions during which CoCa Occurred | Percentage that were Levels 3-5 | CoCa - Level 3-5 Interactions | | | | Chi-square Value |
| | | | Before | | After | | |
			Dom.	Sub.	Dom.	Sub.	
F_1's - Expt. 1	10.0%	55.0%	72.7%	0%	45.5%	0%	
F_2's - Expt. 2	15.1%	78.1%	52.6%	21.0%	31.6%	7.0%	
F_3's - Expt. 3	13.0%	62.0%	36.6%	19.0%	42.3%	14.8%	
F_4's - Expt. 4	26.9%	58.3%	41.8%	28.3%	37.3%	4.5%	
F_1's - Expts. 5/6	25.9%	62.0%	49.1%	17.9%	41.5%	5.7%	
Total	17.3%	63.0%	44.4%	20.1%	39.7%	8.9%	7.27 **

Significant **P < 0.01

Note: For complete data on courtship calling from which these percentages were determined, see Table 16, Appendix I.

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patterns may conceivably be drawn from the same neurological reserves.

In 37 (6.1%) of the 608 courtship interactions the courting male was approached and mounted, and in seven, mounting was sustained long enough to enable the courting male to elicit the entire mating sequence by first vibrating its cerci, then protruding a spermatophore and finally unsuccessfully attempting spermatophore transfer (Table 18).

Six (1%) of the 608 courtship interactions (Table 16) involved mutual courtship calling with reciprocal cercal stimulation by both males simultaneously courting back to back; five mutual courting encounters preceded or were interspersed between aggressive bouts of Level 4-5 intensity. Details for three of these encounters are outlined below.

F_2 #149 vs. F_2 intruder XI - Interaction 22 - 8-5-69

> XI approaches - antennal contact - #149 moves away and begins courting - XI approaches from behind, antennates #149 then turns away and also courtship calls. Both courting back to back for 20 seconds, then #149 stops, turns, opens mandibles and jerks body - XI continues courting, slowly backing toward #149 - #149 mounts XI and opens mandibles and jerks slightly as XI attempts spermatophore transfer - #149 dismounts and XI moves away and chirps. Several seconds later antennal contact leads to antennal fencing and a face-off with open mandibles lasting 30 seconds; only XI aggressive calls - locking of mandibles (LM) - #149 retreats as XI jerks body, calls aggressively and chases.

F_3 #165 vs. F_3 intruder 59 - Interaction 12 - 10-2-69

> A face-off with open mandibles lasting 8 seconds with two LM's - retreat of #165 followed less than one minute later by mutual courting back to back - then another face-off lasting 26 seconds with 3 LM's - retreat of #165 and frequent bouts of chasing and aggressive calling by intruder.

F_3 #400 vs. F_3 intruder 90 - Interaction 25 - 12-9-69

> Antennal contact and fencing - intruder aggressive calls and #400 turns away and begins courting. Within seconds intruder turns and courtship calls - mutual courting back to back. After several seconds #400 turns and approaches with open mandibles and

jerks - intruder, responding to contact of #400's antennae, increases rate and intensity of calling - #400 opens mandibles and partially mounts - intruder moves away - #400 begins courting, then stops and approaches intruder from behind - intruder begins courting, then stops. Inactivity for several seconds, then antennal contact and fencing lead to a face-off with open mandibles; intruder aggressive calls (Level 4) - #400 suddenly turns away and begins courting - intruder jerks and opens mandibles. After several seconds #400 turns away and approaches - face-off with open mandibles lasting 8 seconds; only #400 aggressive calls - IM (Level 5) - intruder retreats - #400 chirps, then slides into courtship and calls for 10 seconds. Male #400 approaches and follows intruder around jar - intruder turns - face-off with open mandibles for 5 seconds; both calling aggressively (Level 4) - intruder suddenly stops calling, turns and retreats.

Rapid switches from fighting to courting behavior and vice versa such as this were frequently observed during interactions between intruders and resident experimentals. As noted by Alexander (1961), courtship calling occurring shortly after initial contact of two males is usually elicited in response to inactivity and immobility of the animal encountered by the male presumably primed for courtship and mating with a ripe spermatophore ready for transfer.

Sexual-Agonistic Ambivalent Behavior

Often during Level 3-5 interactions involving courtship, one male, and occasionally both, vacillated between agonistic and sexual behavior. A dramatic illustration of this occurred during a Level 5 encounter between F_1 #541 and F_1 intruder 28, in which both males faced-off with open mandibles on opposite sides of the climbing screen during a bout lasting over seven minutes with three mandible-lockings. During the entire encounter the intruder vigorously jerked its body and alternately called aggressively and courted until #541 retreated.

In many instances commencement of courting by one male appeared to function as the immediate stimulus initiating agonistic responses

Table 18. Number out of 3523 experimental-intruder interactions involving courtship calling (CoCa) terminating in mounting, including the male that mounted in Level 3-5 encounters and the incidence of attempted spermatophore transfers (AST).

No. Exptl.	Interactions with CoCa leading to Mounting			Mounting Male (Levels 3-5)	
	Levels 1-2	Levels 3-5	AST	Dom.	Sub.
114	0	2	1	2	
149	0	1	0		1
156	0	1	0		1
167	0	2	0	2	
170	0	1	1	1	
171	0	1	1		1
194	0	3	3		3
199	0	1	0	1	
207	0	3	0		3
238	0	1	0		1
239	0	1	0		1
241	1	1	0	1	
400	1	1	0	1	
401	0	1	1		1
412	0	1	0	?	
443	1	0	0		
445	1	1	0		1
470	0	1	0		1
480	0	1	0	?	
490	1	0	0		
500	0	1	0		1
508	0	2	0	1	1
514	1	0	0		
518	2	0	0		
524	2	0	0		
Total	10	27	7	9	16

by the other. Several examples follow.

F_3 #239 vs. F_3 intruder 50 - Interactions 47-48 - 12-11/12-13-69

> During both interactions the males alternately aggressive-
> chirped and courtship-called as they continually oriented towards
> and antennated one another; in both instances Level 5 encounters
> followed.
> In interaction 47 over a minute of fighting with 4 LM's termi-
> nated when the intruder moved away. Male #239 followed and upon
> antennal contact the intruder turned and began courting and back-
> ing into #239 which responded by jerking and aggressive calling;
> the intruder retreated and continued courting several inches away.
> In interaction 48 the intruder aggressive-chirped and courted,
> then became inactive. Male #239 approached and antennated; the
> intruder remained inactive, and #239 turned and began courting.
> The intruder immediately became alert and approached with open
> mandibles. At mandible-locking the intruder was thrown off
> balance and retreated as #239 called aggressively.

F_3 #165 vs. F_3 intruder 59 - Interaction 14 - 10-5-69

> During the last two interactions the intruder dominated after
> Level 5 encounters. In this interaction the intruder commenced
> courting at initial contact and #165 immediately approached,
> mounted with open mandibles, dismounted, and charged the intru-
> der, dominating the remainder of the grouping period, frequently
> chasing the intruder and chirping aggressively afterward.

F_4 #480 vs. F_4 intruder 10 - Interaction 38 - 7-4-70

> After initial contact the intruder moved away and began
> courting; #480 rapidly turned and approached with jerking move-
> ments. At antennal contact #480 rushed forward with open mandi-
> bles and after a face-off with aggressive calling and two LM's,
> #480 retreated; the intruder charged and chased several times,
> stopping to chirp after each chasing bout.

In some instances a courting male chased by an aggressive opponent

continued to court, as in the case of F_3 intruder 92 which frequently

courted as it retreated during chases by F_3 experimental #322.

In three interactions (No's 35 and 40 for experimental #48; No.

26 for experimental #154) the courting intruder, initially charged by

the resident experimental, continued courtship calling during the

chase, then turned and defeated the resident in a Level 5 encounter.

Even energetic chasing did not prevent some mating attempts preceded

by courtship e.g., experimental #508, dominant in its last 15 encounters

with three different intruders, began courting during interaction 19

and was charged and chased by the intruder; #508 continued courting the

entire time it was chased, and at one point attempted to back under and

mate with the attacking intruder.

In several instances a change in the social dominance relationship

of an experimental male and its intruder occurred soon after a courtship

sequence. In view of the high degree of social rank stability (see

Stability of the Dominant-Subordinate Relationship) for most experimental-

intruder pairings, courtship behavior appears an important factor in

explaining the causes for some situations involving changing social

rank. Two examples are outlined below.

Case 1: During its 19 successive interactions with experimental
#500, F_4 intruder 14 dominated all encounters except interaction
10. Six of the first nine interactions involved hard-contested
Level 5 aggressive matches with one to six IM's, and in none was
courtship or mating behavior expressed.
     In interaction 10 after a face-off with open mandibles #500
suddenly turned away and kicked with its hind legs. The intru-
der approached and mounted, and after several seconds of cercal
vibration and protrusion of the spermatophore apparatus as occurs
during mating, #500 kicked the intruder off, rapidly turned, and
charged with open mandibles. Several chasing bouts and two more
Level 4 encounters occurred, but in both cases the intruder re-
treated after several seconds and #500 maintained dominant rank
for the duration of the interaction.

Case 2: In its first eight interactions with F_1 intruder 5, experi-
mental #518 dominated. After initial antennal contact in inter-
action 9, #518 turned away and started courting. Immediately
the intruder approached with open mandibles and chased #518
around the jar several times. Initially, #518 continued court-
ing during the chase, but soon stopped briefly and frequently to
aggressive chirp; the intruder, however, appeared to have gathered
a momentum and continued actively chasing #518 for most of the
remaining interaction period. The succeeding 19 interactions
between this pair were characterized by see-sawing dominance
(see Table 28, Appendix I).

Chasing

After an aggressive encounter defeated males were frequently chased. Most chasing was limited to a short charge and/or chases not exceeding one or two turns around the jar, after which the dominant usually stopped to call aggressively, or become inactive. Most chasing in Level 3-5 encounters involved no more than several short bouts after which the dominant climbed the wire screen or remained stationary on the sand, frequently chirping during the remainder of the inter- action while the subordinate maintained its distance, either resting or moving about the jar, frequently attempting to climb the glass sides.

A few subordinates reacted to defeat by excitedly jumping, running, or moving about the jar, frequently bumping into or otherwise contact- ing the dominant; such behavior usually elicited frequent charges and chases by the alpha male. As activity and excitability of the submiss- ive animal decreased, a proportional decrease in frequency of attack, chasing, and other agonistic behavior (e.g., jerking of body, chirping) by the dominant usually followed.

Individual differences in aggressiveness were a factor influencing the frequency of unprovoked attacks by dominants following aggressive bouts. Some males frequently sought out and chased subordinates; other males rarely or never did so.

Some chasing sequences were subjectively classed as "active", according to the number of discrete chasing bouts observed and their intensity and duration. Generally, interactions with four or more distinct chasing bouts in each of which the subordinate was pursued two or more times around the jar were classified as "active chase"

interactions (see Table 25, Appendix I).

Active chasing bouts were particularly characteristic of inter-
actions in which dominance (1) was decided after a long-contested
encounter between two aggressive males, or (2) was achieved by a
male that had been subordinate in previous interactions.

Occasionally during a chasing bout subordinate animals stopped
running and turned to face the dominant before resuming their retreat.
Only rarely during any given interaction (see Dominance Switches) did
a submissive animal re-engage the dominant.

Infrequently, chasing was so persistent and intense that the
subordinate tired, was unable to outdistance its pursuer, and became
prostrate. In such situations the dominant jerked and called aggress-
ively nearby, adjacent to, or partly mounted on the prostrate subordi-
nate until either (1) the dominant moved away, or (2) the subordinate
became active and chasing continued.

Interestingly, after active chasing bouts, presumably involving
equal energy expenditures by both contestants, only subordinate animals
exhibited pronounced abdominal pumping movements.

Kicking

Kicking back with the hind legs during aggressive encounters was
noted for experimental males in all experiments on occasion, but only
the F_4 generation males in Experiment 4 consistently exhibited this
behavior (Table 19). Kicking was also noted for 42 different intruders,
both wild caught (different years, months, campus locations) and labora-
tory-raised from different stocks, but was only expressed regularly
by the 16 F_4 generation males used as intruders in Experiments 4-6.

In view of the high incidence of kicking among these F_4 intruders and their siblings used as experimentals in Experiment 4, and the reduced expression or absence of this behavior in other G. integer intruders and experimentals of different parentages, the possibility occurs that significant genetic variability exists at the loci for this behavior in the G. integer population at Norman. Selander's recent findings with gel electrophoretic techniques of extensive genetic heterogeneity in samples of G. integer from the Norman population and five localities in Texas are noteworthy in this regard (R. Selander, in preparation).

Climbing Attempts

Crickets propped up against the sides of the jar, moving fore- and mid-legs actively up and down in apparent attempts to climb the glass were frequently observed; these abortive climbing attempts were considered a manifestation of escape behavior. The observation that this behavioral response was frequently expressed by defeated animals after an aggressive encounter supports this interpretation (Table 20).

During chasing bouts subordinates often stopped to make climbing movements before continuing to retreat when the dominant approached or charged. Although a common response of defeated or retreating males, some dominant animals attempted to climb also (Table 20), and on several occasions both males simultaneously attempted to climb the glass, often side by side, after an aggressive encounter. These apparent attempts to escape the jar were observed less frequently under other circumstances and do not necessarily reflect attempts to avoid intraspecific agonistic social encounters although this seems the best explanation for most of this behavior observed during experimental-

intruder interactions. Controls and non-aggressive paired males, for example, only occasionally exhibited this behavior.

Table 19.   Incidence of 'kicking' behavior by experimental male
G. integer during Level 3-5 aggressive encounters
with intruder males.

| Expt. | No. Level 3-5 Encounters | 'Kicking' Encounters | | No. Exptls. | Exptls. 'Kicking' | |
		N	%		N	%
2	315	10	3.2%	18	7	38.9%
3	1093	32	2.9%	61	12	19.7%
4	254	54	21.2%	13	12	92.3%
5/6	469	6	1.3%	16	2	12.5%

Table 20.   Frequency with which dominant and subordinate male
G. integer attempted to climb glass sides of jar (ACG)
during experimental-intruder interactions (Levels 3-5)
in Experiments 2-6.

| Expt. | No. Level 3-5 Encounters | Interactions with ACG after Aggressive Bout | | | |
		Dominant	%	Subordinate	%
2	315	3	1.0%	60	19.0%
3	1093	31	2.8%	476	43.5%
4	254	4	1.6%	97	38.2%
5/6	469	14	3.0%	182	38.8%
Total	2131	52	2.4%	815	38.2%

Interspecific Encounters

Laboratory-raised or wild caught G. integer males were exclu-
sively used as intruders in all experiments except Experiment 3; in
this experiment, because of the relatively large number of experi-
mentals involved, it was difficult to have sufficient numbers of
integer intruders available to replace other intruders that died.
Consequently, on several occasions, involving nine of the F_3
experimentals, it became necessary to use males of a different species
as intruders. These males have been tentatively identified as Gryllus
alogus. G. alogus adults are morphologically distinct from G. integer.
Males, and especially females, are micropterous and incapable of flight.
Male alogus are blacker in color and their chirping is distinctive from
integer, having a more bell-like quality. Adult alogus females have
proportionally longer ovipositors than integer females.

G. alogus males are first heard calling in the fall and apparently
appear much later in the year than integer. Numerous collections and
observations of integer congregating around the lights on the University
of Oklahoma campus at night never revealed the presence of alogus
individuals. Although integer is the dominant large field cricket on
the O.U. campus and the only field cricket ever observed there, G.
alogus males were heard chirping on several occasions, and the habitats
of the two species apparently overlap. The eight alogus males used as
intruders in Experiment 3 were collected as adults or late instar nymphs
in unmown lawn grass next to the foundation of a house adjacent to a
large field 1½ miles east of the O.U. campus. Adults of both species
have been captured in the field and entering nearby houses.

Grouping two G. alogus males together in the laboratory results in high level aggressive encounters with aggressive calling and open mandibles, just as usually occurs during integer male encounters. However, interactions between males of the two different species were noticeably non-aggressive in nature (Table 21). Of 176 observed interactions, most (71.6%) were Level 1 encounters of uncertain dominance where, after initial contact, both males usually spent the remainder of the grouping period in different sections of the jar. Occasionally they rested near or, less often, in contact with one another.

The average level of aggression in interspecific encounters was significantly lower than for aggressive encounters of the other F_3 experimentals exposed exclusively to conspecific intruders (refer to Table 23), and significantly lower than the aggressive encounters between the F_3 G. integer experimentals and the conspecific intruders to which they were exposed before and/or after their run of interactions with the heterospecific intruders (Table 22).

With but one exception interspecific aggressive encounters never exceeded a Level 3 aggression, and interactions occurring at this level were infrequent and of low intensity, consisting of only antennal contact, occasional jerking and chirping, and brief charges by either male. Prolonged antennal-fencing and open mandibles occurred infrequently. Extended chasing, commonly observed in interactions between G. integer and conspecific intruders, was observed only once in 176 interactions.

The exception concerned two interactions between experimental integer #224 and heterospecific alogus intruder F_3I-52. During their

Table 21. Number of encounters, levels of aggression, and dominance data for 176 interactions staged between nine F_3 Gryllus integer experimental males and G. alogus heterospecific intruders. (T.N.I. = total no. of interactions for integer experimental; I.W.H. = interactions in which integer experimental was exposed to an alogus intruder; E = experimental G. integer dominant; I = intruder G. alogus dominant).

No. alogus Intruder	No. integer Exptl.	T.N.I.	I.W.H. No's	I.W.H. Total	Level of Encounter 0	1	2	3	4	5	Dominance E	I	?
F_3I-53	211	25	#5-25	21	0	11	7	3	0	0	0	10	11
F_3I-52	224	24	#1-12	12	1	7	1	1	1	1	1	2	9
F_3I-10	231	20	#1-20	20	1	15	3	1	0	0	4	0	16
F_3I-54	232	37	#9-22	14	0	14	0	0	0	0	0	0	14
F_3I-13	233	44	#1-20	20	1	16	2	1	0	0	2	1	17
F_3I-16	239	52	#1-7	7	1	4	1	1	0	0	0	2	5
"	238	41	#8-37	30	0	26	3	1	0	0	0	4	26
F_3I-18	244	52	#1-32	32	0	20	5	7	0	0	12	0	20
F_3I-30	175	21	#2-21	20	0	13	6	1	0	0	6	0	14
Total Observations				176	4	126	28	16	1	1	25	19	132
Total Percent					2.3	71.6	16.0	9.1	0.5	0.5	14.2	10.8	75.0

Table 22. Mean level of aggressive encounters for nine F₃ generation Gryllus integer experimental males exposed to both conspecific and heterospecific (G. alogus) intruders. Significance of difference between mean levels of aggression during conspecific interactions compared with heterospecific interactions analyzed by Mann-Whitney U test (one-tailed).

integer Exptl.	Total Interactions	No. with G. alogus	Ave. Level of Aggression	No. with G. integer	Ave. Level of Aggression	
175	21	20 (#2-21)	1.40	1 (#1)	3.00	*
211	25	21 (#5-25)	1.62	4 (#1-4)	2.50	
224	24	12 (#1-12)	1.75	12 (#13-24)	4.00	***
231	20	20 (#1-20)	1.15	0	-	
232	37	14 (#9-22)	1.00	23 (#1-8,23-37)	2.57	***
233	44	20 (#1-20)	1.15	24 (#21-44)	3.38	***
238	41	30 (#8-37)	1.17	11 (#1-7,38-41)	4.00	***
239	52	7 (#1-7)	1.29	45 (#8-52)	3.98	***
244	52	32 (#1-32)	1.59	20 (#33-52)	3.00	***

Significant   *P < 0.05   ***P < 0.001

fifth interaction both males faced-off and called aggressively without opening mandibles in a Level 4 encounter lasting several seconds; then #224 turned and moved away. F₃I-52 approached and briefly charged, then chirped. Both males remained apart and inactive for the remainder of the grouping period. During the seventh interaction #224 approached after 15 minutes and antennal contact occurred. Immediately, and too rapidly for details to be observed accurately, a face-off with a rapid opening and apparently brief locking of mandibles occurred, after which #224 turned away and chirped. Dominance was uncertain, neither male retreated, and both remained inactive less than one inch apart for the remaining several minutes of the grouping period.

In interspecific interactions both species dominated the other on occasion (Table 21) but most interactions (75%) involved encounters where aggression was reduced or non-evident, contact avoidance was the rule, and dominance by one male was not evident.

Brief courtship calling by three different _integer_ males occurred during five of the 176 interspecific interactions. Courting by _alogus_ intruders never occurred. During one encounter the _integer_ male switched to the courtship call after brief aggressive chirping which occurred immediately after initial antennal contact.

Alexander (1961) mentions the interlocking of mandibles occurring during interspecific aggressive encounters between male field crickets and notes that chemoreceptors on the palpi and mouthparts probably discriminate species-specific chemical stimuli, thereby explaining the phenomenon of males of different species failing to exhibit and engage in sustained combat. In the 176 encounters between G. _integer_ and G.

alogus the existence of contact chemoreceptors on the mouthparts cannot be used to satisfactorily explain the avoidance behavior and fighting reluctance of heterospecific males, as the animals rarely came close enough to palpate one another and locked mandibles on only one occasion. Also, avoidance responses were usually exhibited immediately after initial antennal contact and occasionally before any contact of body parts occurred. Visual discrimination at short range cannot be ruled out, but seems unlikely. Chirping by either male appeared to enhance avoidance behavior, but calling did not occur frequently enough to satisfactorily explain the consistent failure of the two species to engage in combat.

At close range a cricket's antennae are probably its most important sensory apparatus and mutual antennation is one of the most predictable responses observed when two conspecific crickets of either sex initially contact one another (Alexander, 1961). Accordingly, interspecific discrimination by antennal receptors seems the most likely, but probably not the only, explanation for the mutual avoidance of contact and fighting exhibited by males of these two species.

Levels of Aggression

Evaluation of each G. _integer's_ history of interaction (summarized in Table 23, Appendix I) shows that the average aggression level experienced by each experimental male during its adult life ranged from a low of 1.20 (F_3 #231) to a high of 4.43 (F_3 #207) on a scale where 5.0 represents maximal aggression.

For all 3287 observed interactions between experimentals and conspecific intruders most (36.5%) involved bouts of Level 3 aggression,

and Level 5 encounters occurred much more frequently (17.8%) than previous reports (Alexander, 1961) of field cricket aggressive behavior suggest (Table 24). The reasons for these differences will be discussed.

Level 5 Encounters

Of the 116 experimental $\underline{G}$. integer in all experiments, 103 (88.8%) engaged in at least one Level 5 encounter during aggressive bouts with intruders. The highest incidence was noted for F_3 #207 where 20 out of 28 total interactions (71.4%) included Level 5 confrontations (Table 23).

Level 5 aggression data for all experimentals are summarized in Table 25, Appendix I. For each animal the number of Level 5 interactions, the most intense Level 5 encounter (no. discrete mandible engagements/ face-off duration in seconds), and the average for all Level 5 encounters are listed. From the table it is apparent that most Level 5 encounters between experimentals and intruders (1) were of relatively short duration (less than 30 seconds from initial contact to termination of contact), and (2) involved only a few mandible-lockings (1 to 4) between combatants before one male retreated and dominance was determined.

A typical Level 5 behavioral sequence between two $\underline{G}$. integer males characterized by antennal-lashing, jerking, fore leg sparring, and aggressive calling during a face-off with open mandibles leading to mandible-locking is shown in Figs. 6-13.

Intense or protracted Level 5 encounters occasionally occurred, several of which are described below.

F_2 #128 vs. F_2 intruder V - Interaction 25 - 8-11-69

> Experimental #128 on vertical screen - V moving about jar -
> at antennal contact V opens mandibles and climbs opposite side
> of screen - #128 chirps, then both males aggressive call and

Table 24. A comparison of kinds of encounters between (1) experimental G. integer and intruders in all interactions, (2) experimental G. integer and conspecific intruders in interactions involving a contact encounter, and (3) five F$_1$ generation males from a G. firmus X G. sp. cross housed in a small terrarium and for which 1042 encounters were observed during the first four days of a study on hierarchical behavior (from Alexander, 1961).

Level of Aggressive Encounter	(1) All Interactions		(2) Discounting the 176 Heterospecific Intruder Interactions and the No Encounter Interactions		(3) 1042 Encounters seen in 4 days for a 5-male Field Cricket Hierarchy (after Alexander, 1961)
No Encounter	64	1.8%			
Level 1	650	18.5%	524	15.9%	7%
Level 2	523	14.8%	495	15.1%	26%
Level 3	1216	34.5%	1200	36.5%	56%
Level 4	485	13.8%	484	14.7%	7%
Level 5	585	16.6%	584	17.8%	4%
Total	3523	100.0%	3287	100.0%	1042 100.0%

Figs. 6-13. Figure 6 shows an experimental male G. integer
immediately before initial antennal contact with
intruder. The next seven Figures illustrate se-
quential stages in a typical Level 5 aggressive
encounter between conspecific experimental and
intruder male field crickets, terminating in a
locking of mandibles (Fig. 13) (Photographs by
F. J. Sonleitner).
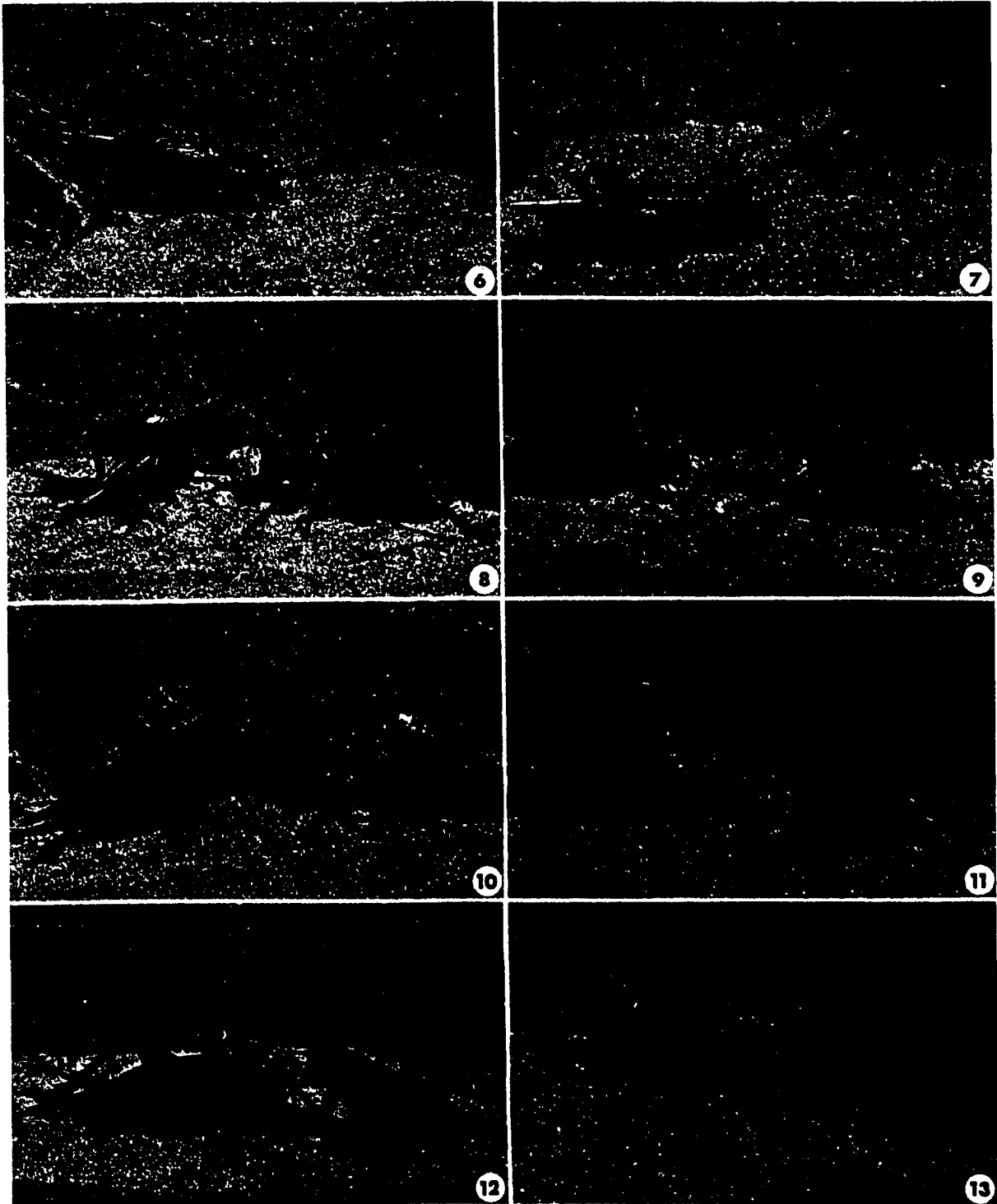
face-off with open mandibles. For $5\frac{1}{2}$ minutes both males antennal fence near top and on opposite sides of screen, frequently aggressive calling, and vigorously jerking their bodies. Eventually V descends screen, comes round to opposite side, and immediately charges up toward #128. Male #128 turns to face-off - 2 LM's - #128 retreats and calls aggressively, then follows and chases.

Aggressive bouts between males frequently occurred on opposite sides of the screening. These encounters were generally long, with relatively few LM's and account for the long average duration of encounter recorded for some males (Table 25, Appendix I). The screening seemed to function as a device for promoting lengthy confrontations by acting as a barrier reducing the probability of mandible-locking and increasing the tactical advantage of both combatants. The males antennal-fenced, jerked, and often brought open mandibles into close proximity at the top of the screen, but when one male advanced upward and moved its head across in an apparent attempt to engage mandibles, the other frequently moved back and down, putting the attacking male at a disadvantage if it attempted to continue its advance across the top.

Protracted dueling and chirping thus continued until one male (1) abruptly retreated or (2) descended the screen and came round to the other side and attacked. Whenever the latter occurred, the male taking the aggressive initiative by coming round the screen to continue the encounter nearly always won and assumed dominance.

Occasionally males did cross over the top of the screen, or males on opposite sides locked mandibles.

Mandible-locking occurs rapidly and mandibles usually remain engaged for only a fraction of a second. Occasionally males may wrestle with locked mouthparts for "several seconds" (Alexander,

1961: 135), and during intense encounters longer as reported below.

F_3 #405 vs. F_3 intruder 85 - Interaction 4 - 10-28-69

> During a face-off with open mandibles and aggressive calling
> that #405 eventually won, 6 LM's occurred, three of which lasted
> over four seconds each. The retreat of the intruder was followed
> by several seconds of vigorous jerking by #405, then several
> minutes of active chasing with frequent stops to chirp. After
> five minutes #405 began courtship calling and backing into the
> intruder, attempting to mate.

Vigorous jerking of the body is especially evident during lengthy

encounters, and is expressed by either or both combatants before, but

only by the winner after, the determination of dominance.

F_3 #165 vs. F_3 intruder 1 - Interaction 8 - 9-23-69

> During this intense highly contested Level 5 encounter last-
> ing over two minutes 8 LM's occurred, three of which lasted
> over 10 seconds, including one LM in which the males wrestled
> with continually locked mandibles for approximately 21 seconds,
> the longest mandible-locking ever witnessed!!
> During the encounter #165 took the initiative and appeared
> stronger by continually pushing forward, gradually forcing the
> intruder to give ground. However, after the last LM which lasted
> 14 seconds, #165 turned and retreated; the intruder called
> aggressively and briefly gave chase.

An excellent example of consistently hard-fought aggressive

interactions is illustrated by the experimental-intruder pair below.

F_4 #454 vs. F_4 intruder 6 (a sibling) - Interactions 3-20

> Thirteen of the 18 successive interactions included lengthy
> highly-contested Level 5 encounters with numerous mandible-
> lockings (Table 26). Both males seemed equally matched and
> equally aggressive.
> Interaction 6 particularly was intense and hard-fought,
> possibly because of experiential effects and the fact that both
> males had dominated in recent past encounters. During one LM,
> mouthparts remained locked for 9 seconds. The encounter in
> interaction 6 occurred at the base of, and adjacent to the edge
> of, the screening, and during the continual orienting movements
> accompanying repeated face-offs both males were observed to
> bite the screen for several seconds duration at different times.

Whether the nearby screening was mistaken for the opponent, or

Table 26. A summary of Interactions 3 to 20 for F_4 experimental #454 (E) and F_4 intruder 6 (I) (a sibling of the experimental) illustrating a series of highly-contested aggressive encounters occurring during successive interactions. See text for other details.

| Interaction | | | If a Level 5 | | |
No.	Date	Level	No. IM's	Duration of Encounter (Sec.)	Dominant
3	3-28-70	5	5	53	I
4	3-29-70	5	9	80	I
5	3-31-70	5	7	35	E
6	4- 2-70	5	10	90	I
7	4- 4-70	5	1	20	I
8	4- 7-70	3			I
9	4- 9-70	5	6	54	I
10	4-11-70	3			I
11	4-12-70	5	3	15	E
12	4-14-70	4			I
13	4-16-70	5	4	22	I
14	4-18-70	5	8	38	I
15	4-19-70	3			I
16	4-21-70	3			I
17	4-23-70	5	6	70	E
18	4-25-70	5	9	65	E
19	4-28-70	3			E
20	4-30-70	5	4	15	I

whether redirected aggression was involved is not known, but screen

biting was observed during intense Level 4 and 5 encounters on several

other occasions.

The two most hard-fought aggressive encounters ever witnessed

among male G. integer were recorded for the same experimental-intruder

pair and are discussed below. Both encounters are unusual in that no

other fighting bouts observed even closely approached these in terms

of intensity and aggressive persistence of combatants.

F_1.#545 vs. F_1 intruder 16 (wild caught 5-17-70; missing l. hind leg)

Interaction 10 - 6-11-70

This Level 5 encounter, the most intense ever witnessed,
involved a face-off with open mandibles lasting over five
minutes during which both males called aggressively and locked
mandibles 54 times!!! All mandible-lockings were brief, except
for the last which exceeded 4 seconds, after which #545 re-
treated and the intruder actively chased.

Interaction 13 - 6-16-70 (intruder lost r. hind leg 3 days ago)

In spite of the physical handicap of both hind legs missing,
the intruder again won this encounter and actively chased #545
after a face-off with reciprocal aggressive calling lasting
over three minutes with 50 mandible-lockings!!

As will be discussed, it is not always possible to predict the

outcome of fighting from the physical condition of the combatants,

and in many instances males with obvious physical handicaps (e.g.,

smaller size, missing legs, etc.) assumed dominance. In the case of

the experimental-intruder pair just described the intruder missing both

hind legs dominated Interaction 14 (a Level 3 with much chasing), but

during Interaction 15 after a two-minute fight with four LM's, it was

thrown off balance during the fifth LM; #545 immediately jerked and

chirped, then followed and chased. The remainder of the encounter

consisted of #545 alternately chasing and courting.

Male #545 lived through 29 interactions, nine of which included Level 5 encounters involving a total of 124 mandible-lockings; most of these occurred during the two hard-fought fights described previously.

Age Effects

The earliest at which an experimental adult G. *integer* assumed aggressive initiative was Day 1 for experimental #514; it dominated after a Level 3 encounter with a sibling intruder. The earliest Level 5 encounter occurred on Day 5 for F_3 #445, and involved a face-off with one mandible-locking; fighting lasted nearly two minutes and ended in uncertain dominance.

Intense fighting bouts involving old experimentals were common. One instance involved Interactions 36-48 for F_3 #239; all included hard-fought Level 5 encounters except Interaction 45 (a Level 4). Interactions 38-48, involving 1 to 15 mandible-lockings, were all won by the experimental which aged from 78 to 98 days during the period.

Generally, young adult males (less than two weeks after final molt) exhibited reduced aggression levels or avoided contact and appeared disinclined to engage in face-offs and Level 4 or 5 fighting bouts with intruders. A noteworthy exception was F_3 #238 exposed to its first interaction at nine days of age. This initial interaction and the succeeding five all involved active Level 5 encounters with one to three LM's. The intruder dominated Interaction 1 after a bout exceeding 50 seconds, and won in the next three interactions after face-offs lasting 10-30 seconds. Interaction 5 included a face-off with two LM's lasting over two minutes, won by #238. In Interaction

6, however, #238 lost and re-assumed subordinate rank.

It is interesting and perhaps significant to note that during one of the six interactions #238 initially responded to antennal contact by courting, resulting in mounting by the intruder. This interaction, the only one in which #238 courtship-called, was Interaction 5, the only interaction where #238 assumed dominant status after fighting.

Changing Aggression Levels Over Time

To ascertain whether levels of aggression for any given intruder-experimental pair varied over time in any consistent manner, two sets of data were considered: (1) experimental males always exposed to the same intruder for at least 15 interactions until their death were considered as one group, and (2) experimental males exposed to more than one intruder, but which were exposed to the first intruder for at least 24 consecutive interactions until the intruder's death were considered as a second group.

The data for experimental-intruder pairs exposed to one another from Interaction 1 until the experimental's death are shown graphically in Figures 14-1 to 14-21.

As is evident from graphic analysis, variability exists between the 21 different experimental-intruder pairs considered. Five pairs showed a fairly consistent decrease in aggression from relatively high levels during initial encounters. For most other pairs the opposite was true, with aggression levels (1) gradually increasing and generally continuing to increase until the experimental's death, or (2) reaching a plateau, then tending to decrease.

In about half of the cases reduced aggressiveness is characteristic

of the last interactions, perhaps due to the experimental's gradual weakening prior to death, or the effects of aging on either intruder or experimental. A noticeable and sustained decline in aggression level during several successive interactions generally, though not always, signaled the impending death of one, and sometimes both, of the animals.

Data for the encounters between experimental #231 and a G. alogus intruder (Fig. 14-16) are included to show graphically the reduced aggression levels characteristic of encounters between heterospecific males, compared to conspecifics.

For the second group, considering experimentals exposed to intruders for at least 24 interactions until the intruder's death, the graphs (Figs. 15-1 to 15-17) illustrate a more consistent pattern. For 14 of the 17 experimental-intruder pairings, aggression levels generally increased, leveled off, and then decreased, in this case probably largely due to aging or general weakening and debilitation of the intruder. An experimental (#244) exposed to a heterospecific intruder is included for purposes of comparison (Fig. 15-6).

In spite of these general trends in changing aggression levels over time, considerable variability exists among different intruder-experimental pairings which, in Experiments 2-4, may be due in part to unconstant laboratory environmental conditions. Animals in Experiments 5 & 6 (No's. #510 or larger), however, were under controlled conditions and the troughs and peaks in their curves may largely reflect a manifestation of variability in behavioral response — a phenomenon exhibited by all animals with well-developed nervous systems.

Figs. 14-1 to 14-21. Graphic analyses of changing aggression
    levels for experimental G. integer males exposed to the
    same intruder male for a minimum of 15 consecutive inter-
    actions until their death.
        Each point on the horizontal axis represents the
    average aggression level for five consecutive interactions
    (i.e., point 1 = Interactions 1-5; point 2 = Interactions
    6-10, etc.). The number in the lower right hand corner of
    each graph denotes the total number of interactions involved.

Fig. 14-1. No. 121 vs.
            Intruder IV

Fig. 14-2. No. 128 vs.
            Intruder V

Fig. 14-3. No. 133 vs.
            Intruder VII

Fig. 14-4. No. 142 vs.
            Intruder IX

Fig. 14-5. No. 167 vs.
            F_3 Intruder 2

Fig. 14-6. No. 170 vs.
            F_3 Intruder 3

LEVEL OF AGGRESSION
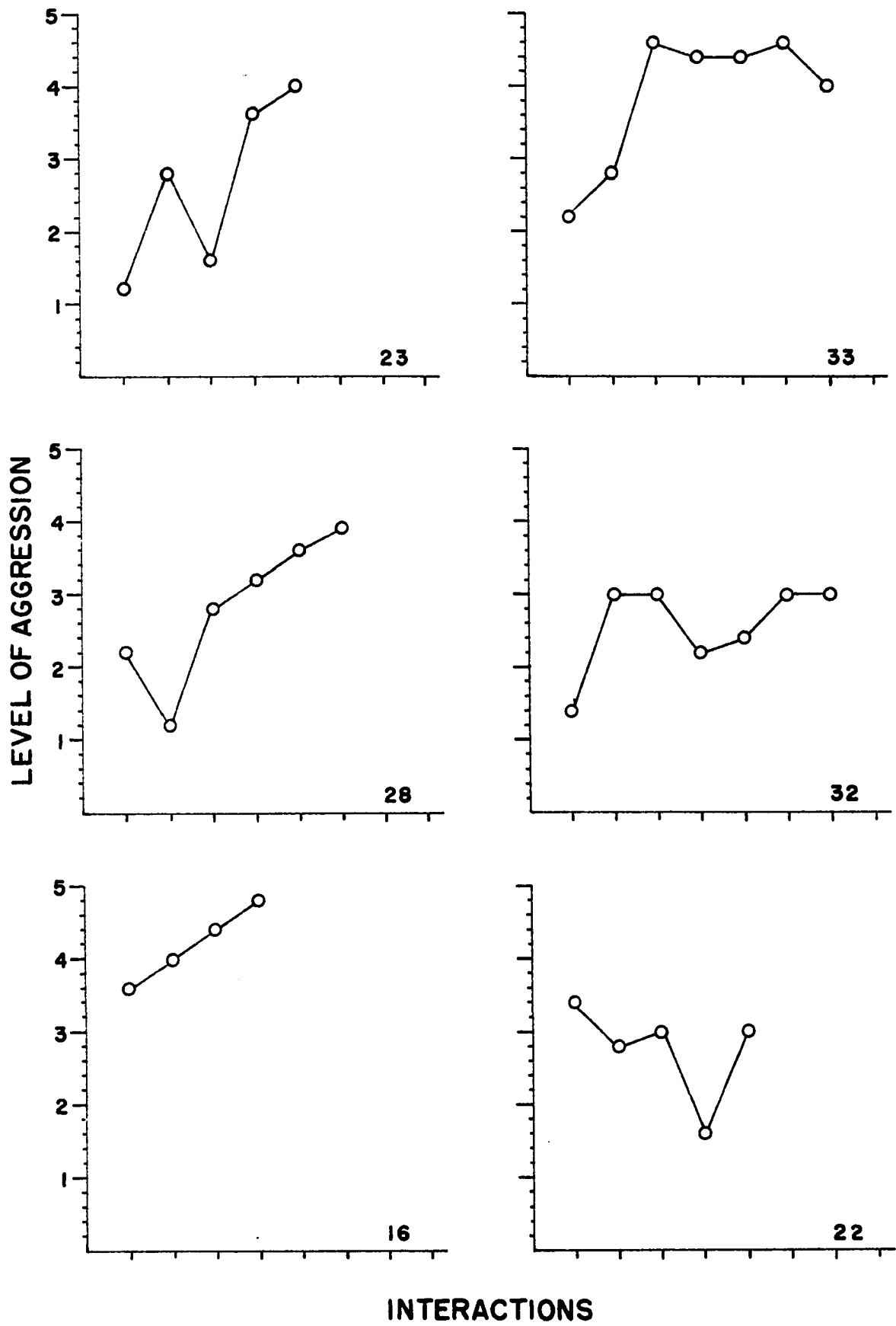
INTERACTIONS

Fig. 14-7.   No. 171 vs.
             F_3 Intruder 19

Fig. 14-8.   No. 192 vs.
             F_3 Intruder 33

Fig. 14-9.   No. 202 vs.
             F_3 Intruder 36

Fig. 14-10.   No. 204 vs.
              F_3 Intruder 37

Fig. 14-11.   No. 205 vs.
              F_3 Intruder 38

Fig. 14-12.   No. 214 vs.
              F_3 Intruder 43

LEVEL OF AGGRESSION

INTERACTIONS

104.
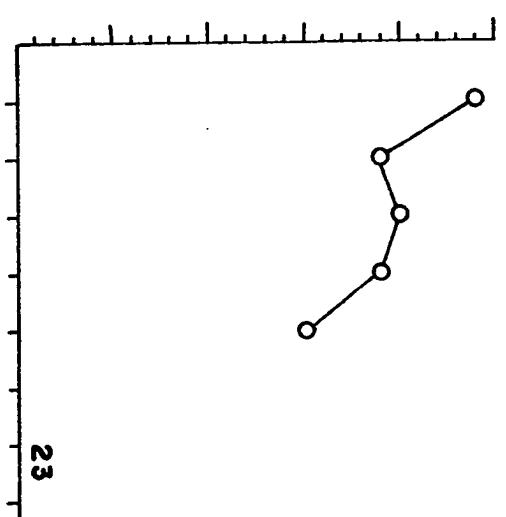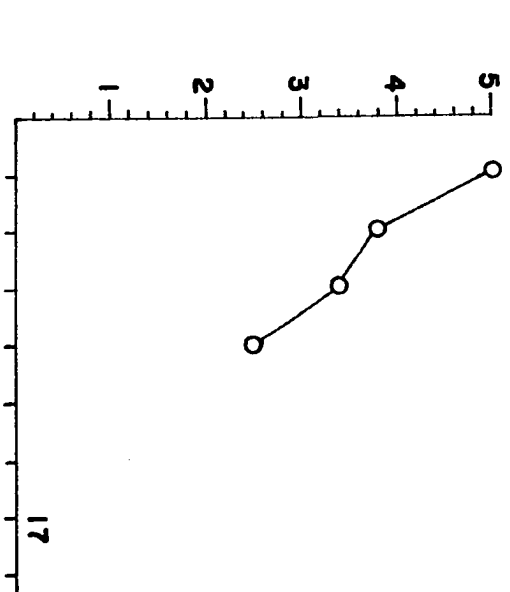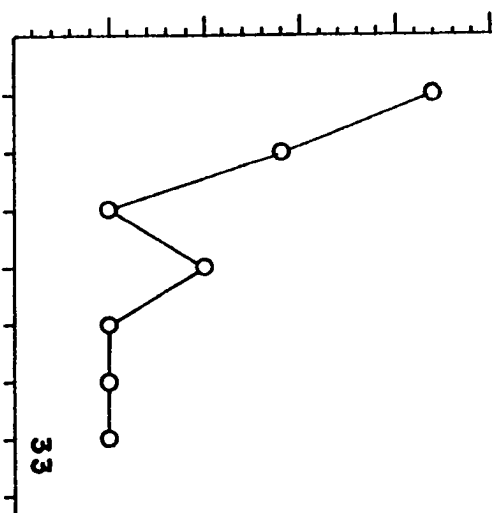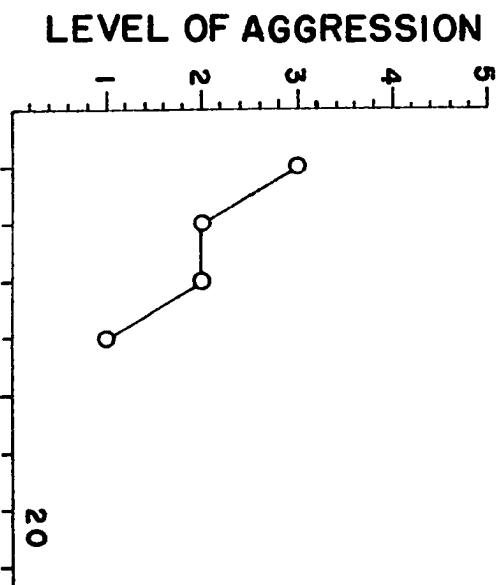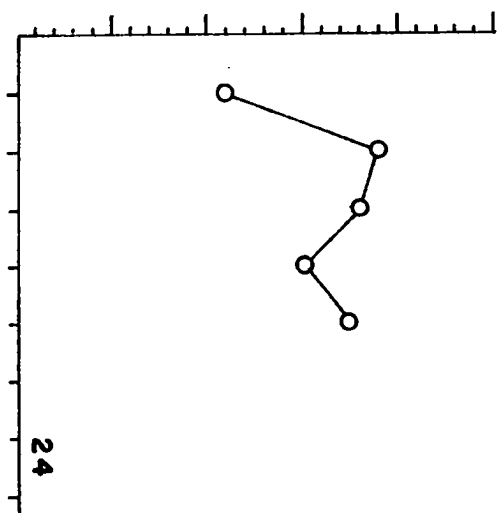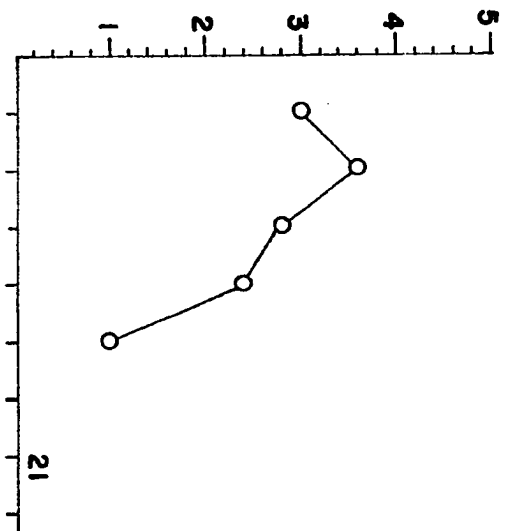
Fig. 14-13. No. 217 vs.
F_3 Intruder 45

Fig. 14-14. No. 226 vs.
F_3 Intruder 50

Fig. 14-15. No. 228 vs.
F_3 Intruder 51

Fig. 14-16. No. 231 vs.
F_3 Intruder 10

Heterospecific Intruder
(G. alogus)

Fig. 14-17. No. 408 vs.
F_3 Intruder 89

Fig. 14-18. No. 469 vs.
F_4 Intruder 5
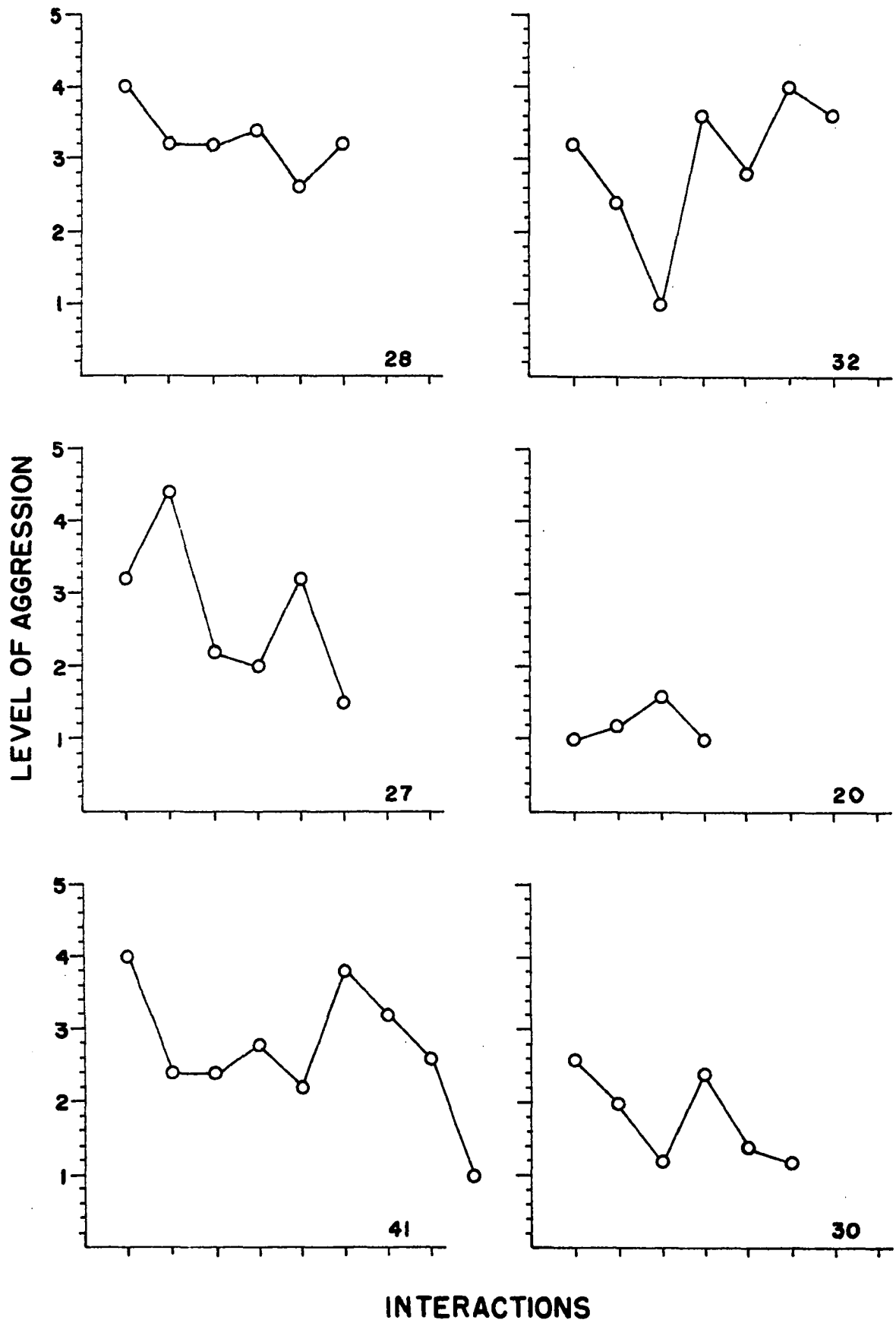
Fig. 14-19. No. 503 vs. F_4 Intruder 20

Fig. 14-20. No. 511 vs. F_1 Intruder 3

Fig. 14-21. No. 528 vs. F_1 Intruder 8
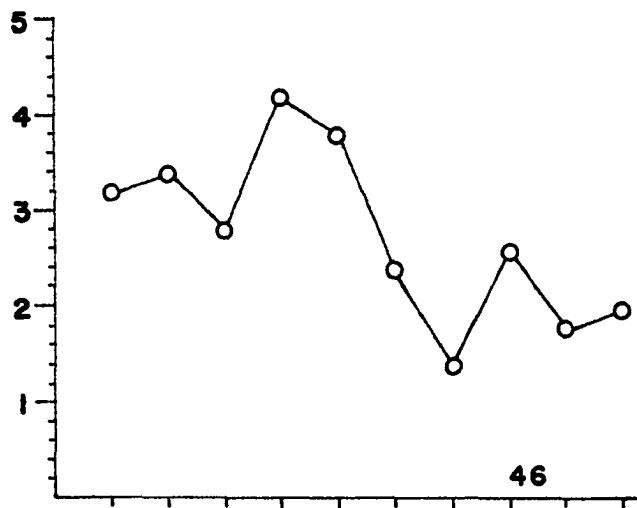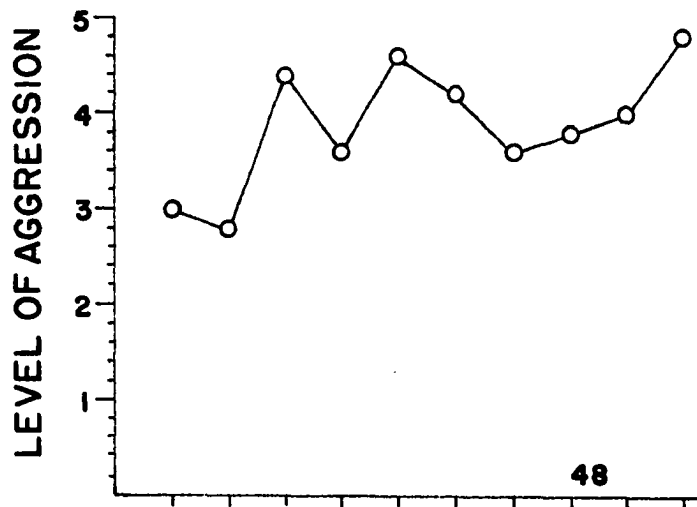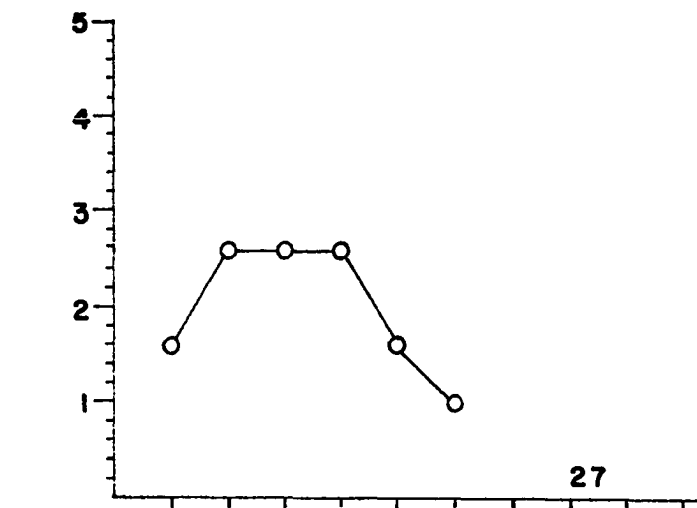
Figs. 15-1 to 15-17. Graphic analyses of changing aggression
levels for experimental <u>G</u>. <u>integer</u> males exposed to the
same intruder for at least 24 consecutive interactions
until the intruder's death.

Each point on the horizontal axis represents the
average aggression level for five consecutive interactions
(i.e., point 1 - Interactions 1-5; point 2 = Interactions
6-10, etc.). The number in the lower right hand corner of
each graph denotes the total number of interactions involved.

Fig. 15-1. No. 129 vs.
            Intruder VI

Fig. 15-2. No. 139 vs.
            Intruder VIII

Fig. 15-3. No. 186 vs.
            F_3 Intruder 23

Fig. 15-4. No. 220 vs.
            F_3 Intruder 46

Fig. 15-5. No. 241 vs.
            F_3 Intruder 17

Fig. 15-6. No. 244 vs.
            F_3 Intruder 18

Heterospecific Intruder
(G. alogus)

LEVEL OF AGGRESSION
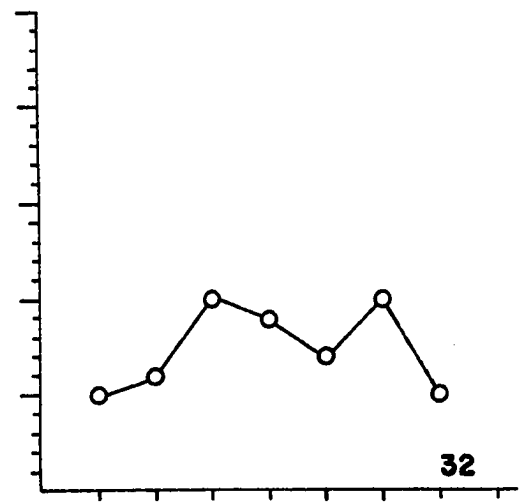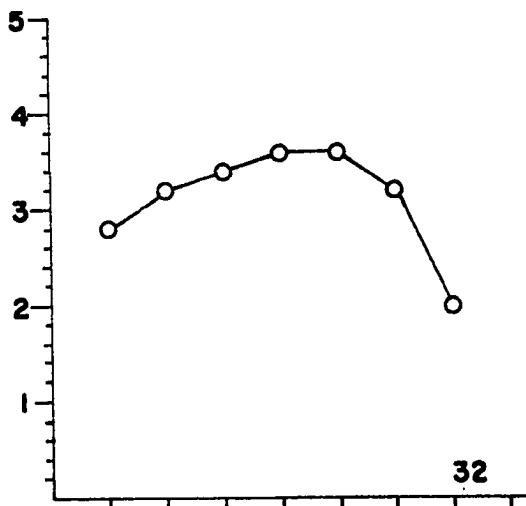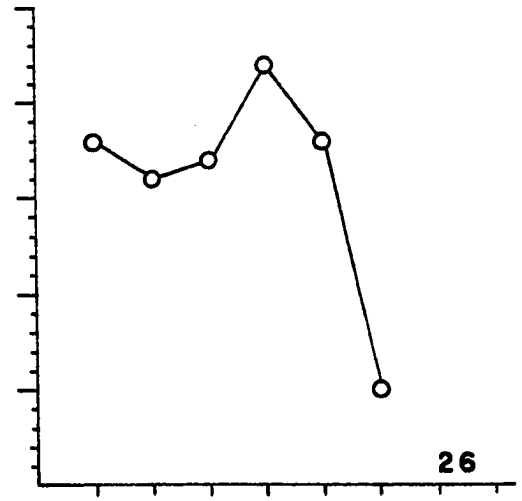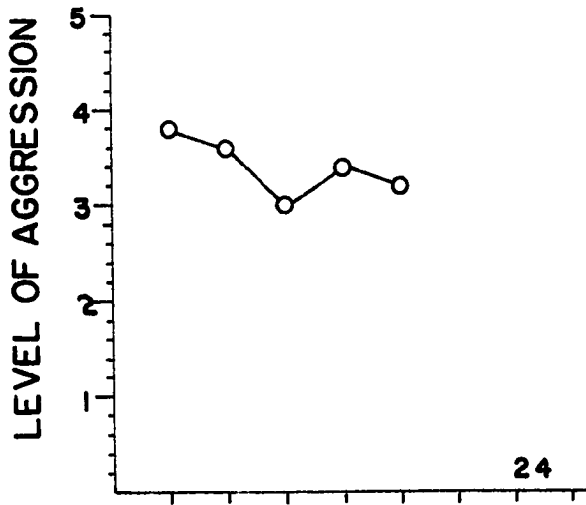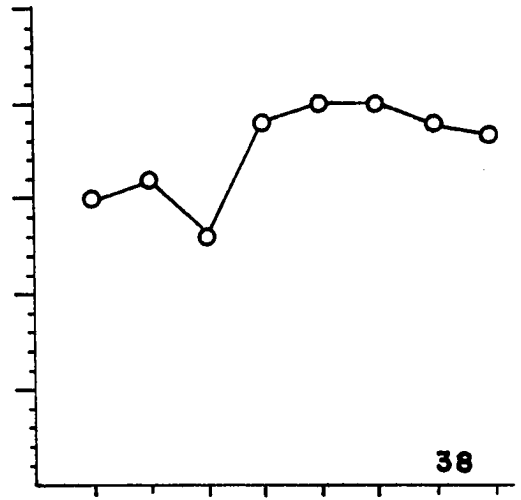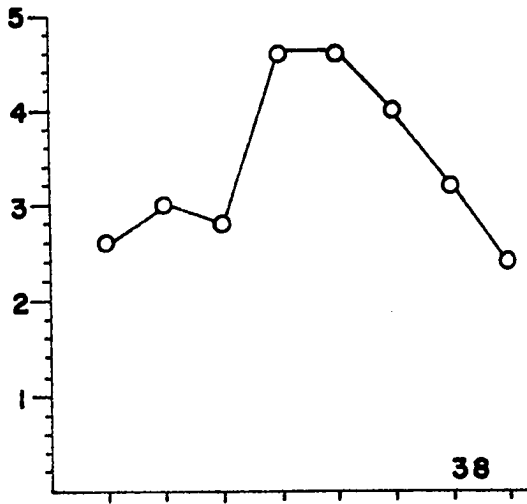
INTERACTIONS

Fig. 15-7. No. 389 vs.
            F_3 Intruder 72

Fig. 15-8. No. 453 vs.
            F_4 Intruder 3

Fig. 15-9. No. 470 vs.
            F_4 Intruder 2

Fig. 15-10. No. 510 vs.
             F_1 Intruder 2

Fig. 15-11. No. 518 vs.
             F_1 Intruder 5

Fig. 15-12. No. 522 vs.
             F_1 Intruder 6
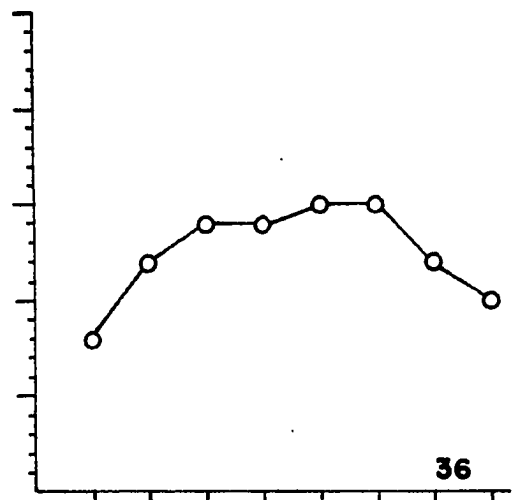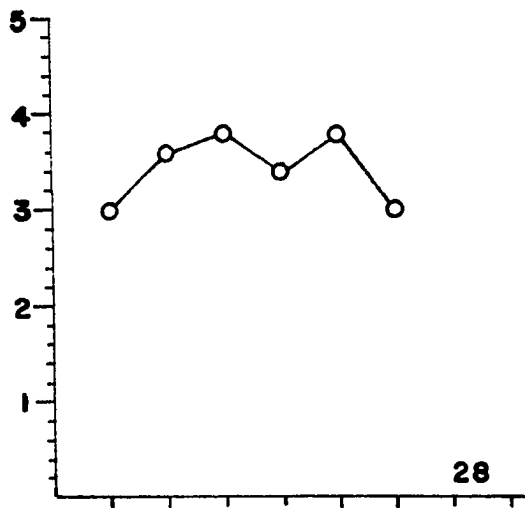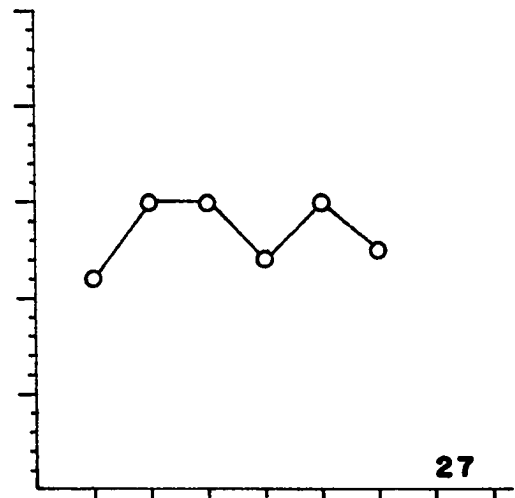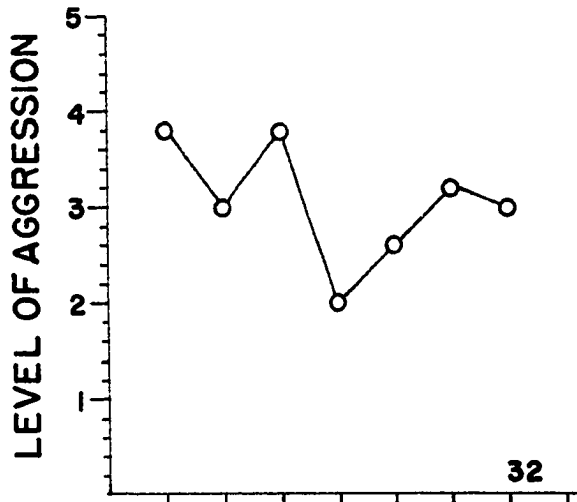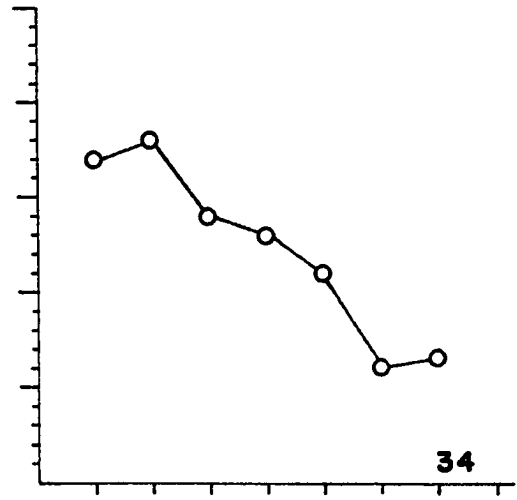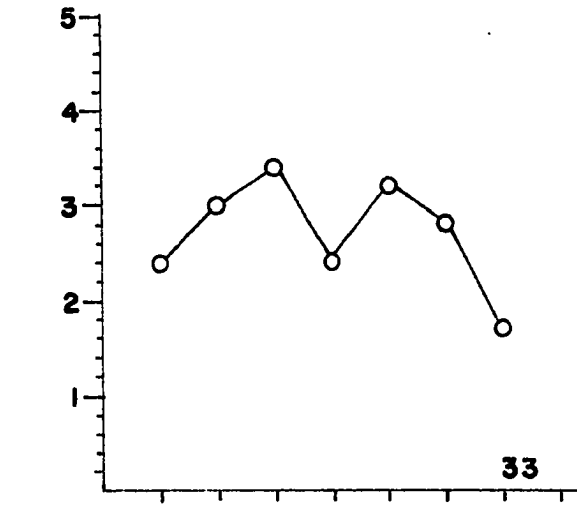
Fig. 15-13.   No. 524 vs.
              F_1 Intruder 7

Fig. 15-14.   No. 537 vs.
              F_1 Intruder 12

Fig. 15-15.   No. 539 vs.
              F_1 Intruder 13

Fig. 15-16.   No. 541 vs.
              F_1 Intruder 15

Fig. 15-17.   No. 549 vs.
              F_1 Intruder 18

LEVEL OF AGGRESSION
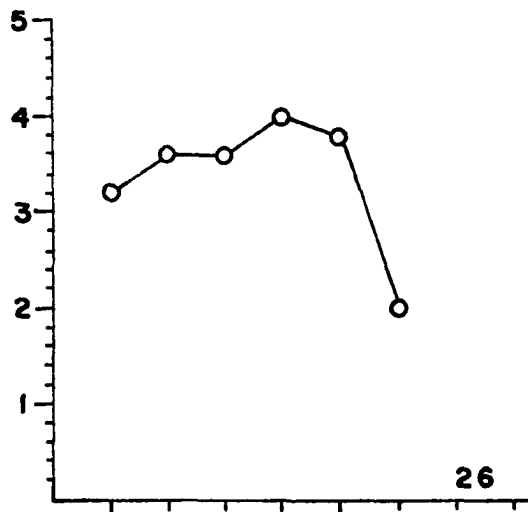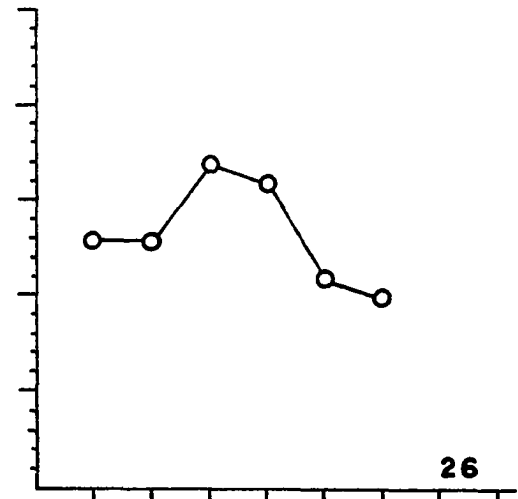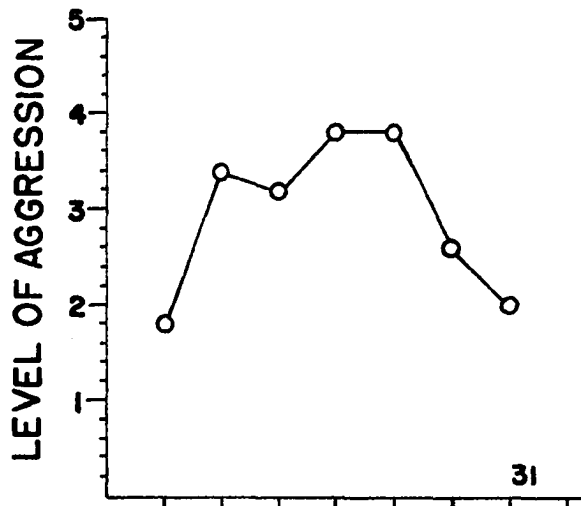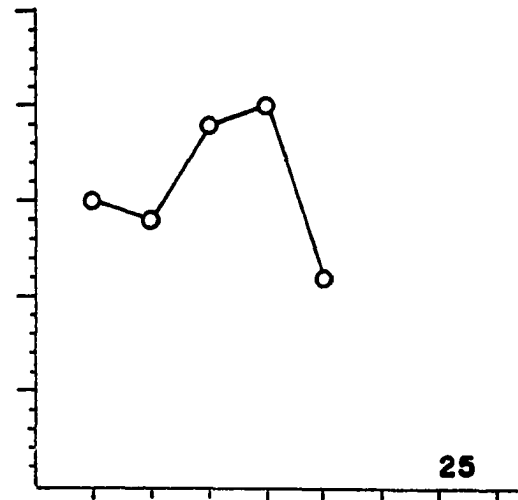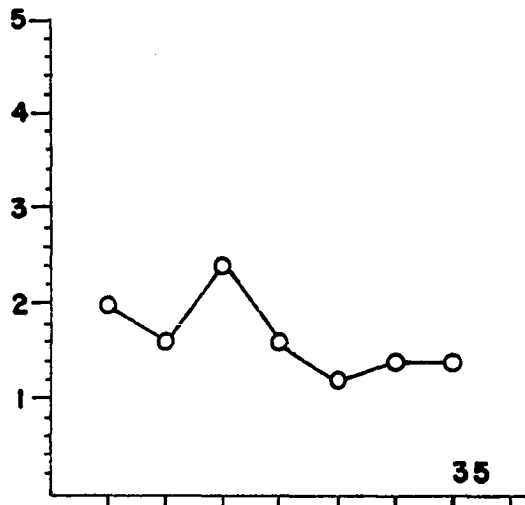
INTERACTIONS

Biting and Wounding

With the exception of mandible-locking, a natural behavioral response between male field crickets during Level 5 aggressive encounters, actual biting rarely occurred, and was observed for only 8 (0.2%) in the total of 3523 experimental-intruder interactions. All eight instances occurred following aggressive encounters where the dominant bit the hind leg(s) (rarely abdomen) of a retreating subordinate during active chasing bouts. Since in all cases the submissive cricket was bitten only after several minutes of protracted, almost continuous, chasing around the periphery of the jar, it can be speculated that biting rarely, if ever, occurs in natural populations where defeated males could escape from further attacks by aggressive dominants. In three of the eight instances, biting appeared definitely linked to wounding and the loss of a hind appendage (Table 27). However, of the two experimental males (#179 and #528) seemingly wounded as a direct result of biting, wounding and appendage loss had no apparent effects on longevity.

Male #179 dropped its right hind leg during active chasing in Interaction 6, and lost the remainder of its left hind leg four days after the intruder wounded the femoro-tibial joint during Interaction 7. Though missing both hind legs, it survived 20 more interactions, frequently defeating the intruders it encountered.

Male #528 was exposed to F_1 intruder 8 for a total of 46 successive interactions until its death at 91 days adult age. During Interactions 1-17 the intruder always dominated, but in Interaction 18 a dominance switch occurred. Initially the intruder dominated,

Table 27. A summary of the eight interactions in which biting occurred out of 3523 interactions observed between experimental and intruder field crickets ($\underline{Gryllus}$ $\underline{integer}$). All biting was elicited during extended bouts of active chasing.

No. Exptl.	No. Interaction	Level	Action	Body Part Bitten	Effects
F_3 #167	4	3	#167 bites F_3I-2	R. tibia & abdomen (several times)	none observable
F_3 #179	7	4	F_3I-9 bites #179	L. femoro-tibial joint	tibia loose and nearly off
F_3 #183	5 6	3 4	F_3I-21 bites #183 "	Abdomen Femur	none observable "
F_3 #199	1	3	#199 bites F_3I-34	Hind legs (several times)	R. hind leg falls off during chase. Due to biting?
F_3 #405	1	5	#405 bites F_3I-81	R. tibia	Immediately afterwards, intruder "rattles" leg and it falls off.
F_4 #472	23	5	F_4I-11 bites #472	L. hind leg (several times)	none observable
F_1 #528	14	4	F_1I-8 bites #528	L. hind leg	L. hind leg immediately falls off.

actively charging and chasing, but after 30 seconds of a Level 5

encounter with three mandible-lockings, #528 assumed dominance and

although missing a left hind leg (Table 27) it dominated all 28

succeeding interactions until its death.

This example of male #528 well illustrates (1) the absence of

any consistent relationship between loss of hind appendages due to

wounding or chasing, and longevity or fighting success, and (2) the

stability of the dominant-subordinate relationship which characterized

the majority of experimental-intruder pairings in all six experiments.

Maintenance of dominant social rank and success in fighting by

handicapped males was often striking. Approximately 12 of the 116

experimentals lost one hind leg as a result of biting, chasing bouts,

or unknown causes, and some of these lost both hind legs. F_3 males

#165, #167, and #179 are examples of the latter, yet they lived

through numerous interactions in their condition, frequently defeat-

ing intruders larger than themselves in Level 5 aggressive encounters.

Determination of Dominance

In most Level 2 and in nearly all Level 3-5 encounters a dominant-

subordinate relationship was clear-cut and easily determined. After

an aggressive encounter in which retreat by the defeated animal was

usually obvious, the subordinate male characteristically (1) avoided

the dominant, (2) ran or moved quickly away whenever the dominant

approached, (3) frequently attempted to climb the glass sides of the

jar, and (4) failed to aggressive call. The dominant in turn (1) often

approached, charged or chased the subordinate and/or (2) exhibited

jerking movements as it locomoted, and (3) often called aggressively.

Rarely, however, in Level 3-5 encounters dominance could not be determined with certainty as, for example, in the case of Interaction 42 between F_4 #480 and F_4 intruder 10 in which both males suddenly turned away during a Level 4 encounter and moved to opposite sides of the jar where the intruder commenced courting.

Stability of the Dominant-Subordinate Relationship

The social status of most experimental males, exposed to one or more different intruders, tended to remain constant over time. Table 28, Appendix I, summarizes the total hierarchical data for experimental males in all six experiments. It is evident that social rank was often completely stable, with each experimental either winning or losing all aggressive encounters, regardless of the number of different intruders to which it was exposed (Table 29a). The number of experimentals showing completely stable, unchanging social rank in all interactions during their adult life varied from 6% in Experiments 5/6 to 31% in Experiment 4. Of the total of 116 experimentals in all experiments, 29 (25%) showed completely stable social rank data (Table 29a).

Other experimentals frequently changed social rank. This was true for both males exposed to the same intruder or to several different intruders. Of the 116 experimentals, however, only 17 (14.7%) failed to show significant social rank stability using a nonparametric one-sample runs test (Table 29a).

The experimentals exhibiting the greatest social rank instability and one of the lowest incidences of complete stability were the F_1's in Experiment 1 (Tables 28, 29a). This is conceivably because these males, unlike animals in the other experiments, were exposed to 7-14

Table 29a. Percentage of experimental male G. **integer** in Experiments 1-6 showing a perfectly stable or non-significantly stable social rank relationship for all interactions with intruder male(s).

Expt.	No. Experimentals	No. Completely Stable Rank Relationship	%	No. Non-sig. Stability	%
1	8	1	12.5%	3	37.5%
2	18	5	27.8%	3	16.7%
3	61	18	29.5%	9	14.8%
4	13	4	30.8%	1	7.6%
5/6	16	1	6.2%	1	6.2%
Total	116	29	25.0%	17	14.7%

Table 29b. Percentage of experimental-intruder pairings in Experiments 2-6 in which experimental G. **integer** were exposed to the same intruder for nine or more consecutive interactions showing a perfectly stable or non-significantly stable social rank relationship.

Expt.	No. Exptl.-Intruder Pairings	No. Completely Stable Rank Relationship	%	No. Non-sig. Stability	%
2	18	7	38.9%	4	22.2%
3	74	42	56.8%	12	16.2%
4	19	9	47.4%	3	15.8%
5/6	27	12	44.4%	5	18.5%
Total	138	70	50.7%	24	17.4%

different intruders, with exposure to a different intruder during each consecutive interaction. By thus continually rotating the intruders confronting each of these experimentals, establishment and maintenance of a stable rank relationship was somehow discouraged. In spite of the experimental design of Experiment 1, however, half of the animals exhibited a rank relationship with their intruders that significantly departed from random expectations (Table 28), i.e., a significant tendency existed for experimentals that had won or lost aggressive encounters during an interaction to do likewise in subsequent interactions, regardless of the fact that the intruder differed each time.

For the majority of $\underline{G}$. integer experimentals, 70 out of 116 (60%), exposure to the same or different intruders during successive interactions produced a social rank relationship that, although not completely stable, approached complete stability and was significantly non-random using the one-sample runs test (Table 28); in most cases the data were highly significant.

To illustrate the procedure for evaluating social rank relationships, the data recorded for the 28 interactions between F_2 experimental #133 and F_2 intruder VII are shown in Fig. 16. Each run represents and includes the total number of successive interactions during which the same male won all aggressive encounters or, in the case of Level's 0 and 1 where activity was minimal and aggression non-evident, or other interactions where certain dominance was indeterminable, there was no change in dominance from previous interactions. For some experimental-intruder pairings the first one to several interactions were of uncertain dominance. This explains why in Table 28 the number of inter-

INTERACTIONS

| 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 |

? I I ? ? I ? I I I ? I I I I I E ? I I I I I I I I I I

RUN 1   **RUN 2**   **RUN 3**

E = Experimental dominant
I = Intruder dominant
? = Dominance uncertain

Fig. 16. Evaluation of the dominant-subordinate relationship during the 28 consecutive interactions between F$_2$ experimental $\underline{G}$. integer #133 and intruder VII (6-24-69 to 8-17-69).

actions (column 2) is occasionally larger than the total number of

interactions for which dominance was ascertained (columns 5 and 6).

Table 30 (Appendix I) summarizes social rank data for each experi-

mental male in Experiments 2-6 and all intruders exposed to it for

nine or more consecutive interactions. Again, nearly all experimental-

intruder pairings exhibit perfect or highly significant stability re-

garding the dominant-subordinate relationship. However, a considerable

increase (51%) in the number of pairings showing complete stability

(Table 29b) as compared with the previous data (Table 29a) suggests a

correlation between a change in intruder and changing social rank of

experimental males. This possibility is considered in the next section.

Although only experimentals with nine or more successive inter-

actions with the same intruder were considered (Table 30) a stable

social rank relationship was evident for nearly all shorter sequences

as well, but these were not reported as numbers were too small to

justify use of the runs test.

A good example of a $\underline{G}$. $\underline{integer}$ experimental consistently assuming

the same social status in all agonistic encounters is F_3 #413 exposed

successively to five different intruders over an experimental period

lasting 52 interactions (see Table 28). In not a single interaction

did #413 assume the dominant role. Two other examples illustrating

nearly stable social rank relationships are briefly described below.

F_3 experimental #326 - Interactions 1-22

> After an initial interaction of uncertain dominance, #326
> was defeated in Level 3 and 5 encounters during Interactions
> 2 & 3 by F_3 intruder 31. After Interaction 3, the intruder,
> now weakening, was replaced by F_3 intruder 71. During Inter-
> action 4 with this new intruder #326 assumed dominant rank
> during a Level 5 encounter, and for the remaining 19 inter-

actions with this same intruder #326 maintained dominant sta-
tus in spite of frequent challenges and Level 5 encounters
until its death after Interaction 22.

The only near threat to the stability of the alpha-omega
relationship between the two males occurred during Interaction
15. During a Level 5 encounter with one LM, #326 suddenly
turned away; the intruder immediately jerked and chirped.
Within seconds #326 turned, approached and re-engaged the
intruder. Another Level 5 encounter lasting 20 seconds ensued
and at the second mandible-locking the intruder quickly
retreated and #326 gave active chase as usual.

F₃ experimental #417 - Interactions 16-25

For the first four interactions with F3 intruder 92, #417
was subordinate. During Interaction 20, #417 turned and
quickly retreated after mandible-locking in a Level 5 encoun-
ter lasting 20 seconds. The intruder followed and chased,
but #417 occasionally chirped while retreating (Chirping by
a defeated male occurs rarely and usually signals further
impending aggressive bouts). For several minutes dominance
was indeterminable as each male briefly charged and oriented
towards the other. Eventually re-confrontation occurred and
after a face-off with open mandibles lasting 24 seconds during
which only #417 called aggressively, the males locked mandibles
and the intruder retreated. In the remaining five interactions
between these two males #417 won each aggressive encounter.

The preceding examples illustrate the two circumstances account-

ing for changing social rank relationships: (1) a change in intruder,

and (2) a dominance switch occurring during an encounter between

an experimental and intruder which had met and/or fought in previous

interactions.

Effects of a Change in Intruder

Substituting a new intruder frequently preceded a change in

social rank of the experimental male, even though the experimental's

rank had been stable, or nearly so, during all interactions prior to

the substitution. Data for changing dominance and intruder changes

are summarized in Table 31. Approximately 8% of the interactions in

Experiments 2-6 involved dominance switches, and 16-41% of the dominance

switches occurred during interactions in which experimental males were exposed to new intruders.

Table 31. Data on dominance changes and intruder changes during interactions between experimental and intruder field crickets, G. integer, in Experiments 2-6.

Expt.	Total No. of Interactions	Total No. of Changes in Dominance		Total No. of Changes in Intruder	No. of Dom. Changes during 1st Interac. with New Intruder	
2	483	45	9.3%	25	4	16%
3	1755	130	7.4%	87	34	39%
4	427	36	8.4%	23	9	39%
5/6	659	53	8.0%	27	11	41%
Total	3324	264	7.9%	162	58	36%

Chi-square tests of these data show that, except for Experiment 2, a highly significant ($P < .001$) relationship exists between a change in intruder and changing social rank of experimental males (Table 32).

Concerning effects associated with a change in intruder, the data for three males are particularly interesting.

Case 1 - F_3 experimental #186

The interactions and aggressive data for this male are summarized in Fig. 17a. During Interactions 1-24 with intruder 23, #186 consistently lost each agonistic encounter, all but one, of Levels 3-5 aggression. Beginning Interaction 25 a new intruder was substituted. Soon after initial antennal contact, #186 commenced courting, a response it had never made during encounters with the previous intruder, perhaps because of differences in behavioral response; i.e., intruder 86 was inactive whereas intruder 23 responded aggressively soon after initial contact in all its encounters.

Table 32. Chi-square tests of independence examining the degree of relationship between changing intruders and dominance changes during interactions between experimental G. *integer* and intruder males in Experiments 2 to 6.

Expt. 2 (N=18)	No Change in Dominance	Change in Dominance	
No Change in Intruder	417	41	458
Change in Intruder	21	4	25
	438	45	483 $x^2 = 1.39$

Expt. 3 (N=61)	No Change in Dominance	Change in Dominance	
No Change in Intruder	1572	96	1668
Change in Intruder	53	34	87
	1625	130	1755 $x^2 = 134.03$ ***

Expt. 4 (N=13)	No Change in Dominance	Change in Dominance	
No Change in Intruder	377	27	404
Change in Intruder	14	9	23
	391	36	427 $x^2 = 29.25$ ***

Expts. 5/6 (N=16)	No Change in Dominance	Change in Dominance	
No Change in Intruder	590	42	632
Change in Intruder	16	11	27
	606	53	659 $x^2 = 40.73$ ***

*** Significant (P < 0.001; 1 df)

Fig. 17. a. — Synopsis of social rank data for $\underline{G}$. $\underline{integer}$
experimental No. 186 exposed to intruders
F₃I-23 (Interactions 1-24) and F₃I-86
(Interactions 25-26).

b. — Determination of dominance and synopsis of
social rank data for $\underline{G}$. $\underline{integer}$ experimental
No. 405 exposed to intruders F₃I-81 (#1-2),
F₃I-85 (#3-4), F₃I-33 (#5-9), F₃I-70 (#10-
14), and F₃I-37 (#15-24).

E = Experimental dominant
I = Intruder dominant
? = Dominance uncertain
+ = Level 5 encounter
↑ = New intruder substituted

INTERACTIONS

```
     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

     I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I  I   E  ?
     +           +        +                    +                         ↑  +
A. └─────────────────────────────────────────────────────────────────────┘  └──┘

                                  RUN                                         RUN
                                   1                                           2
```

```
     1  2  3  4  5  6  7  8  9  10 11 12 13 14 15 16 17 18 19 20 21 22 23 24

     E  E  ?  E  I  I  I  I  I  E  ?  E  ?  E  I  ?  ?  I  I  I  ?  I  ?  I
     +  +  ↑  +  ↑  +              +  ↑  +        +  ↑  +
B. └──────┘ └─────────────┘ └───────────────┘ └──────────────────────────┘

         RUN          RUN          RUN                 RUN
          1            2            3                   4
```

128
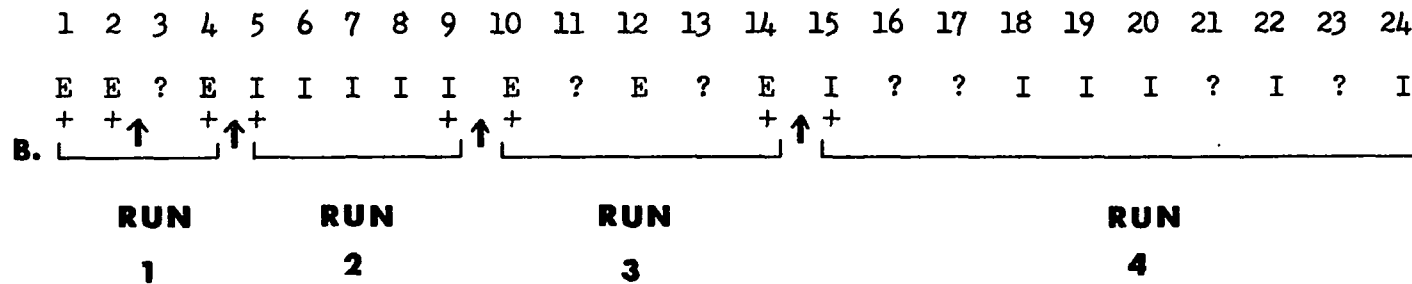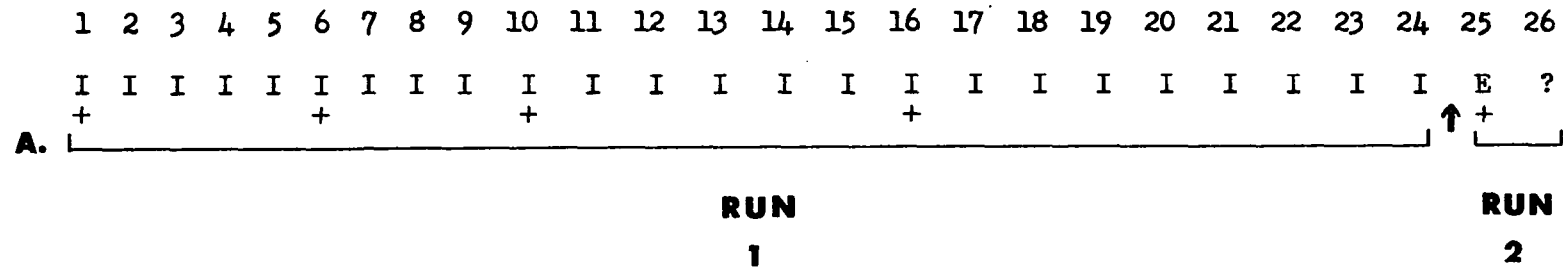
After several seconds of mutual antennation and no aggressive response by either male, #186 suddenly pushed forward with open mandibles and after a brief LM the intruder retreated. For the remainder of the interaction #186 dominated with sudden charging bursts, and brief chasing bouts interspersed with chirping.

Case 2 - F_3 experimental #405

Over the course of 24 interactions #405 was successively exposed to five different intruders (Fig. 17b). The fact that each of the three dominance changes experienced by #405 followed a change in intruder, emphasizes the importance of intruder identity as a significant factor influencing the stability of the experimental male's rank.

What are the factors involved when substitution of a new intruder brings a change in an experimental's social rank? Differences in size and strength of intruders may be important factors at times. However, most initial encounters with new intruders did not reach a Level 5 confrontation, as was true for experimental #405 (Fig. 17b). What determines switching dominance with new intruders, or the relative stability of successive encounters with the same intruder in the major- ity of interactions where no fighting and little physical contact other than initial antennal contact is involved? Do the animals detect variabilities in behavioral response?, differing aggressive states?, etc. in a new opponent.

The variety of factors involved in dominance determination will be discussed later. Another case might be considered at this time, however, as an example illustrating the possible effects of aging or past experience.

Case 3 - F_4 experimental #480

Male #480 was exposed to F_4 intruder 10 during its first 12 interactions and dominated each encounter. At Interaction 13 F_4 intruder 12 was substituted and #480 became subordinate after losing a Level 5 encounter with two LM's. Male #480 remained submissive in all but four of the following encounters with

intruder 12 and one other. Then at Interaction 34, F_4 intruder 10 was reintroduced and this time it won, and continued to win the next nine interactions, nearly all involving intense Level 4-5 aggressive bouts, until the death of #480 following Inter- action 43 (see Table 30).

Effects of Dominance Change on Level of Aggression

Interactions involving encounters preceding a change in the pre-existing social rank relationship were characterized by increased fighting. Of the 80 males in Experiments 2-6 for which interactions involving changing dominance occurred, for 72 (90%) the interactions involving changes in social status were accompanied by noticeably higher aggression levels. Data for the 24 experimental males in Experiments 4-6 (Table 23) were analyzed according to the Mann-Whitney U-test and for 7 (29%), aggression levels occurring during interactions involving changing dominance were significantly higher ($P < 0.05$).

Summarization of the aggressive behavior occurring during all first interactions between experimentals and a new intruder in Experiments 2-6 (Table 33), and comparison with interactions not in- volving a change in intruder (Table 34) show that for all experiments, except Experiment 2, aggression levels were higher during those inter- actions involving the exposure of G. integer experimentals to new intruder males. For the 159 interactions observed where integer experimentals were initially exposed to a different intruder male, nearly 28% included a Level 5 aggressive encounter (Table 33), notice- ably more than Level 5 encounters usually occurred (see Table 24).

See-sawing Dominance

Although the rank relationship between most experimentals and

Table 33. A summary of the level of aggressive encounter for all interactions which represent the first interaction of G. integer experimental males with a new and different intruder out of the total number of 3324 experimental-intruder interactions observed in Experiments 2 to 6. (F.D.I. = no. of first interactions with a different intruder male from previous interactions)

| Expt. | F.D.I. | Level of Encounter | | | | | | Average Level of Aggression |
		0	1	2	3	4	5	
2	24	5	5	1	7	1	5	2.38
3	85	1	18	10	21	12	23	3.11
4	23	0	2	1	11	0	9	3.57
5/6	27	0	3	4	10	3	7	3.26
Total	159	6	28	16	49	16	44	
Percentage		3.7	17.6	10.1	30.8	10.1	27.7	

Table 34. A comparison of level of aggressive encounters in those interactions in which experimental G. integer males were exposed to a different intruder male for the first time and those in which no change in intruder was involved.

| Expt. | No Change in Intruder | | Change in Intruder | |
	N	Average Level of Aggression	N	Average Level of Aggression
2	459	2.89	24	2.38
3	1670	2.82	85	3.11
4	404	2.75	23	3.57
5/6	632	3.04	27	3.26
Total	3165	2.86	159	3.09

intruders stabilized to greater or less degree, there were several

exceptions, the best example being F_3 experimental #207 and the four

intruders exposed to it for a total of 28 interactions.

Many of #207's interactions were characterized by highly-
contested Level 5 encounters involving protracted dueling with
numerous IM's, interspersed with bouts of chirping and active
chasing. Reciprocal chasing occurred frequently and definite
dominance was often indeterminable. Occasionally G. integer
males separate during aggressive encounters, exhibit mild
agonistic behavior (e.g., chirping, jerking, brief charges
forward, etc.) then re-engage again in Level 4 or 5 face-offs
with open mandibles. Male #207, however, was the only male
ever observed to suddenly stop retreating during an active
chasing bout and re-engage the pursuing intruder in a Level
5 confrontation after it had been defeated in an intense Level
5 fight minutes earlier; and it responded in this manner on
several occasions.

In several ways the data for G. integer experimental #207 and

its intruders are unique, claiming both the most unstable social

dominance relationship (see Table 28) and the most aggressive inter-

actions (see Table 25) observed during $2\frac{1}{2}$ years of experimentation.

Dominance Switch Interactions

Thirty (1.4%) out of 2131 observed Level 3-5 interactions between

experimentals and intruders involved a dominance switch. In the 28

single switch interactions, the male initially dominant was subordi-

nate at the end of the 15-20 minute grouping period. Only two double

switch interactions were observed; one is described below.

F_1 experimental #511 vs. F_1 intruder 3 - Interaction 41 - 7-12-70

Initial antennal contact led directly to a face-off with
open mandibles; only the intruder called aggressively. At
the first IM the intruder retreated and #511 immediately
chirped (Level 5 - #511 dominant). At antennal contact sever-
al minutes later, however, the intruder quickly charged and
chirped, then commenced chasing the retreating #511, frequent-
ly stopping to aggressive call (Level 3 - intruder dominant).
After several minutes #511 suddenly turned about to face its

pursuer. Another Level 5 encounter lasting 30 seconds occurred during which both males called aggressively and locked mandibles five times. Suddenly the intruder turned and moved away; #511 immediately jerked its body and chirped (Level 5 - #511 dominant). During all subsequent antennal contacts in this interaction, the intruder retreated and #511 called aggressively.

Table 35. Incidence of dominance switches during 2131 observed interactions (Levels 3-5) between experimental and intruder male field crickets.

No. Exptl.	No. Interactions with a Dominance Switch	Aggression Level of Interaction
133	1	5
156	1	5
163	1	3
167	2	5
		5
207	1	5
216	1	5
220	2	3
		4
221	1	4
226	1	5
231	1	3
233	1	5
238	1	5
239	1	5
244	2	3
		3
246	1	3
389	1	3 *
412	1	5
417	1	5
445	1	5
480	1	5
511	2	5
		5 *
518	2	3
		3
528	1	5
539	1	3
545	1	5
Total	30	128 $\bar{Y} = 4.27$

* denotes interaction with a double dominance switch

Aggression levels of interactions with encounters comprising

dominance switches were high, with a mean aggression level of 4.27

for the 30 interactions involved (see Table 35).

Aggressive Calling

Data on the incidence of aggressive calling by dominants and

subordinates before and after aggressive encounters (Levels 3-5)

are tabulated in Table 36 (Appendix I).

For Level 3 aggressive bouts most aggressive calling before and

during each encounter was by the dominant male (Table 37), whereas

in Level 4 & 5 encounters lasting from several seconds to several

minutes or more, aggressive calling by both combatants was common

and occurred approximately 50% of the time (Table 38).

In all experiments, males that eventually assumed dominance

showed an increased tendency to call aggressively, whereas aggressive

calling by subordinates was significantly and drastically reduced

(Tables 37, 38).

Chi-square tests demonstrate a very significant relationship

between subordinate social rank and reduced chirping, and dominant

rank and increased chirping, following Level 3-5 aggressive encoun-

ters between experimentals and intruders in Experiments 2-6 (Tables

39, 40).

Some instances where the subordinate animal was credited with

aggressive calling after an aggressive encounter occurred during

dominance switch interactions in which the subordinate won an en-

counter early in the grouping period and called aggressively after-

ward, but was defeated in a later encounter. Of the 18 Level 3

Table 37. Incidence of aggressive calling (ACa) (1) before or during and (2) after Level 3 aggressive encounters for dominants (Dom.) and subordinates (Sub.) during experimental-intruder interactions between adult male G. integer in Experiments 2-6 (E.D.S. = excluding dominance switch interactions).

| Expt. | No. of Level 3 Interactions | Level 3 Interactions with ACa | | | | ACa After by Sub. (E.D.S.) |
| | | ACa Before | | ACa After | | |
		Dom.	Sub.	Dom.	Sub.	
2	153	33.3%	5.9%	73.2%	0%	0%
3	576	32.5%	11.5%	61.6%	2.1%	1.4%
4	154	38.3%	14.3%	71.4%	1.3%	1.3%
5/6	270	35.2%	11.5%	77.8%	1.5%	0.7%
Total	1153	34.0%	11.1%	68.3%	1.6%	1.0%

Table 38. Incidence of aggressive calling (ACa) (1) before or during and (2) after Level 4-5 aggressive encounters for dominants (Dom.) and subordinates (Sub.) during experimental-intruder interactions between adult male G. integer in Experiments 2-6 (E.D.S. = excluding dominance switch interactions).

| Expt. | No. of Level 4-5 Interactions | Level 4-5 Interactions with ACa | | | | ACa After by Sub. (E.D.S.) |
| | | ACa Before | | ACa After | | |
		Dom.	Sub.	Dom.	Sub.	
2	162	45.7%	38.9%	73.5%	1.2%	0.6%
3	517	48.4%	46.0%	65.2%	3.3%	1.4%
4	100	52.0%	45.0%	73.0%	4.0%	3.0%
5/6	199	58.8%	51.8%	85.4%	2.0%	1.0%
Total	978	50.4%	45.9%	71.5%	2.8%	1.3%

Table 39. Chi-square tests of independence for aggressive calling (ACa) (1) before or during and (2) after aggressive encounters in Level 3 interactions by dominant (Dom.) and subordinate (Sub.) male G. integer in Experiments 2-6.

		No. Level 3 Interactions with ACa				
	No. of Level 3	ACa Before		ACa After		Chi-Square
Expt.	Interactions	Dom.	Sub.	Dom.	Sub.	Value
2	153	51	9	112	0	17.72 ***
3	576	187	66	355	12	70.89 ***
4	154	59	22	110	2	27.81 ***
5/6	270	95	31	210	4	44.39 ***
Total	1153	392	128	787	18	161.36 ***

*** Significant (P < 0.001; 1 df)

Table 40. Chi-square tests of independence for aggressive calling (ACa) (1) before or during and (2) after aggressive encounters in Level 4-5 interactions by dominant (Dom.) and subordinate (Sub.) male G. integer in Experiments 2-6.

		No. Level 4-5 Interactions with ACa				
	No. of Level 4-5	ACa Before		ACa After		Chi-Square
Expt.	Interactions	Dom.	Sub.	Dom.	Sub.	Value
2	162	74	63	119	2	66.98 ***
3	517	250	238	337	17	187.86 ***
4	100	52	45	73	4	36.00 ***
5/6	199	117	103	170	4	97.33 ***
Total	978	493	449	699	27	388.27 ***

*** Significant (P < 0.001; 1 df)

interactions with aggressive calling afterward by the submissive cricket (Table 39), six involved dominance switches where the eventual subordinate called aggressively after winning the initial encounter, but did not call after it was subsequently defeated during a later encounter of the same interaction.

Likewise 14 of the 27 Level 4 and 5 interactions with aggressive calling afterward by subordinates involved dominance switches; two of these were double switches where several distinct encounters occurred during the interaction and one male, initially dominant, was defeated and became subordinate, then reassumed dominance (or vice versa).

When dominance switch interactions are excluded it is evident that following an aggressive encounter subordinate field crickets rarely call. Of 2131 observed Level 3-5 interactions with aggressive calling, in only 25 (1.2%) (19 different males involved) did the defeated animal call aggressively.

Longevity

Longevity data were analyzed in three different ways: (1) analysis of variance of mean adult longevity (Table 41), (2) analysis of variance of mean total longevity from the day of hatching (Table 42), and (3) paired t-tests for experimentals and their appropriate controls (Table 43). In the analysis of variance, significance of difference between means in Experiments 2-6 was determined by the Student-Newman-Keuls (SNK) test.

In all experiments, control animals showed increased mean total longevity and adult longevity (Fig. 18) compared to experimentals and permanently paired males.

Experiment 1:

Controls showed an increased mean adult longevity compared to experimentals that was nearly significant. Analysis of data according to total longevity and paired t-tests (Tables 42, 43) showed significant differences ($P < 0.05$).

Experiment 2:

A paired t-test showed that controls lived significantly longer than experimentals and paired males ($P < 0.05$). Controls significantly outlived only paired males ($P < 0.05$) using the SNK test.

During the latter stages of Experiment 1 and during Experiment 2, laboratory temperatures were often high and varied considerably (see Fig. 5). The highest laboratory temperature ever recorded was 98° F at 3 p.m. on 7-10-69. High temperatures undoubtedly shortened longevity during these two experiments, but during Experiment 2 it is assumed that animals in all three treatments (i.e., experimentals, controls and pairs) were equally affected, and that the higher temperatures constituted an additional factor of physical stress affecting the physiology of all animals equally.

However, this was not the case in Experiment 1; in this experiment by 6-30-69 all eight experimentals had died, but seven of the eight controls were still alive. Therefore, the effects of increasing July temperatures, and especially a heat wave from 7-9 to 7-13-69 during which laboratory temperatures remained 90° F or over from 8 a.m. to midnight, influenced only controls, and shortened their longevity to an unknown degree. Were it not for these temperature effects the results of Experiment 1 would undoubtedly show greater significance.

Fig. 18.　Mean adult longevity (in days) of G. integer
males (all treatments) in all experiments.
(vertical bars = range)
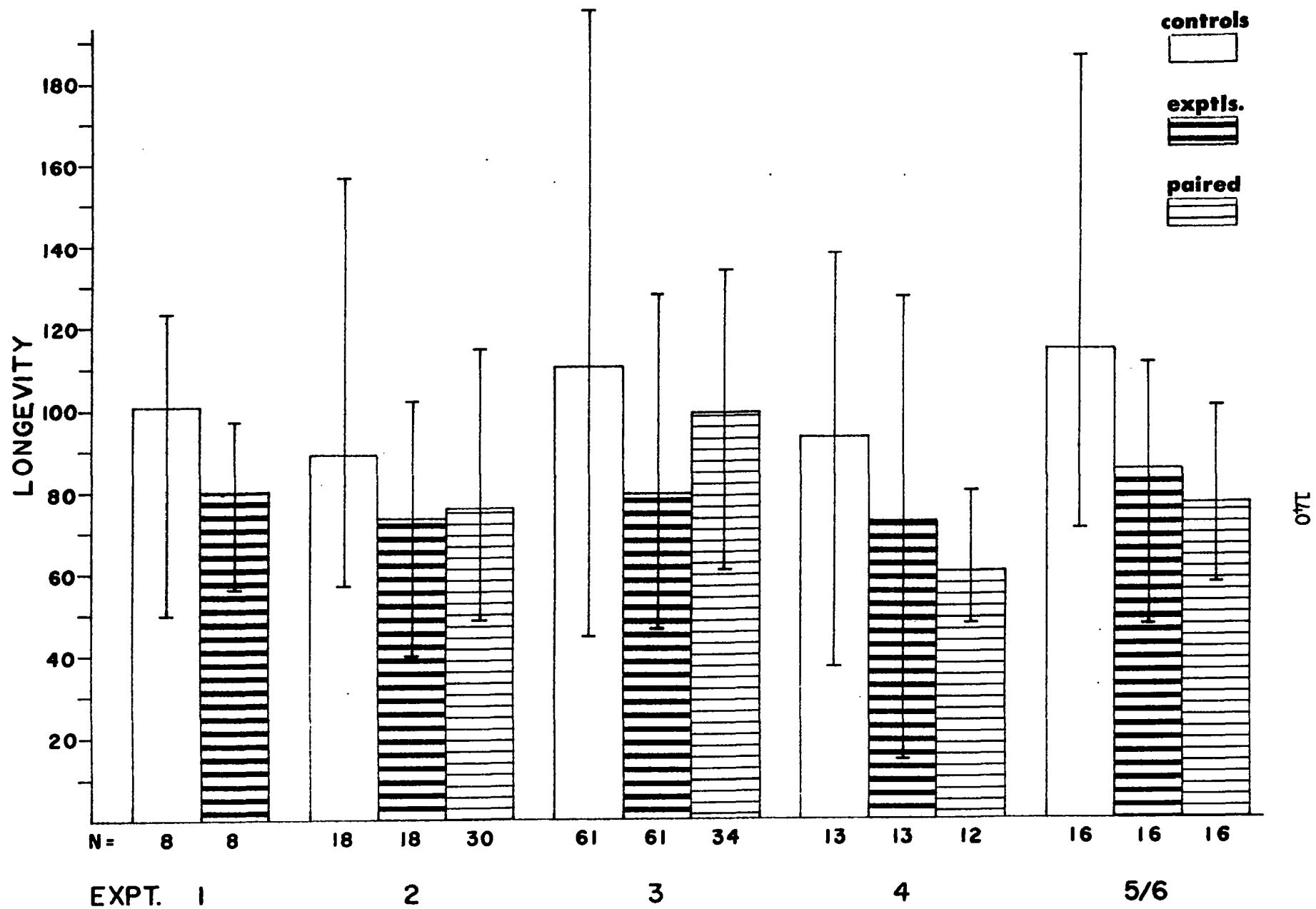
Table 41. Analysis of variance of mean adult longevity (in days) from day of adult molt for controls (C), experimentals (E), and permanently paired (P) male G. integer in Experiments 1-6. Significance of difference between means determined by an a posteriori Student-Newman-Keuls (SNK) test.

Expt.	Treatment	N	Mean	SE	MS error	F-value	
1	Controls	8	100.50	8.40	369.68	4.44	NS
	Exptls.	8	80.25	4.67			
2	Controls	18	88.33	5.88			
	Exptls.	18	73.75	3.61	349.52	3.52	*
	Pairs	30	75.43	2.93			

SNK test:
C vs. E NS
C vs. P * (LSR = 11.15)
E vs. P NS

	Controls	61	110.05	3.75			
3	Exptls.	61	78.75	2.33	523.71	28.88	***
	Pairs	34	98.18	2.80			

SNK test:
C vs. E *** (LSR = 14.83)
C vs. P * (LSR = 9.60)
E vs. P *** (LSR = 16.12)

	Controls	13	92.46	9.60			
4	Exptls.	13	71.77	7.92	731.90	4.66	*
	Pairs	12	59.92	3.32			

SNK test:
C vs. E NS
C vs. P * (LSR = 26.53)
E vs. P NS

	Controls	16	113.25	7.59			
5/6	Exptls.	16	84.62	4.31	457.28	13.44	***
	Pairs	16	75.75	3.09			

SNK test:
C vs. E *** (LSR = 26.62)
C vs. P *** (LSR = 29.34)
E vs. P NS

Significant *$P < 0.05$ ***$P < 0.001$ NS = not significant
LSR = Least Significant Range

Table 42. Analysis of variance of mean total longevity (in days) from day of hatching for controls (C), experimentals (E), and permanently paired (P) male G. integer in Experiments 1-6. Significance of difference between means determined by an a posteriori Student-Newman-Keuls (SNK) test.

Expt.	Treatment	N	Mean	SE	MS error	F-value	
1	Controls	8	240.12	6.17	211.03	7.87	*
	Exptls.	8	219.75	3.84			
	Controls	18	220.56	7.71			
2	Exptls.	18	206.00	3.45	483.45	3.83	*
	Pairs	30	202.80	3.15			

SNK test:

C vs. E	NS	
C vs. P	*	(LSR = 15.75)
E vs. P	NS	

Expt.	Treatment	N	Mean	SE	MS error	F-value	
	Controls	61	173.48	5.53			
3	Exptls.	61	142.39	4.74	1350.28	10.93	***
	Pairs	34	156.50	3.31			

SNK test:

C vs. E	***	(LSR = 23.82)
C vs. P	*	(LSR = 15.41)
E vs. P	NS	

Expt.	Treatment	N	Mean	SE	MS error	F-value	
	Controls	13	287.38	10.99			
4	Exptls.	13	267.00	7.18	875.25	1.97	NS
	Pairs	12	267.67	5.33			

SNK test:

C vs. E	NS
C vs. P	NS
E vs. P	NS

Expt.	Treatment	N	Mean	SE	MS error	F-value	
	Controls	16	209.88	7.59			
5/6	Exptls.	16	181.50	5.08	533.23	10.04	***
	Pairs	16	175.69	4.07			

SNK test:

C vs. E	**	(LSR = 22.00)
C vs. P	***	(LSR = 31.68)
E vs. P	NS	

Significant *P < 0.05   **P < 0.01   ***P < 0.001

Table 43. Paired t-tests for significant difference between adult
longevity (in days) of experimental G. integer and their
appropriate controls in Experiments 1-6. The appropri-
ate control for each experimental often represented a
male sibling that (i) hatched on the same day and developed
in the same rearing jar and/or (ii) final molted on the
same day and was approximately of equal adult age. In
most instances, however, experimentals and sibling con-
trols only closely approximated each other (e.g., never
differing by more than 1-2 days) in either of these two
respects.

Expt.	Treatment	No. Pairs	Mean Deviation	Std. Error	df	t-statistic	
1	Controls Exptls.	8	20.25	7.72	7	2.62	*
2	Controls Exptls.	18	14.78	6.95	17	2.13	*
3	Controls Exptls.	61	31.30	4.25	60	7.37	***
4	Controls Exptls.	13	20.69	12.24	12	1.68	
5/6	Controls Exptls.	16	28.62	9.41	15	3.04	**

Significant $*P < 0.05$ $**P < 0.01$ $***P < 0.001$

Experiment 3:

Regardless of the method of data analysis, controls lived significantly longer than experimentals (P < 0.001) and longer than paired males (P < 0.05). Paired males showed increased adult longevity (P < 0.001) compared to experimentals.

Experiment 4:

The only significant difference found was the increased adult longevity of controls compared to paired males (P < 0.05).

Experiments 5/6:

By all three analytic methods controls exhibited significantly increased longevity compared to experimentals (P < 0.01 to < 0.001) and paired males (P < 0.001).

It is significant to note that the mean adult longevity of paired males exceeded that of experimentals in Experiments 2 & 3, but that the reverse was true for Experiments 4 & 5/6, and that only in Experiment 3 were the differences significant.

Adult longevity frequency distributions for males in Experiments 2, 3, and 5/6 (Figs. 19-21) illustrate that only controls commonly survived beyond 110 days. For each experiment the longevity of controls was more variable; much of this variability is due to the fact that in each experiment, especially Experiments 2, 3, and 5/6, one or two control males exhibited extended adult longevity (i.e., five or six months); such long-lived adults never occurred among experimentals and pairs.

Fig. 19. Frequency distribution of adult longevity (days)
of F_2 generation male G. integer (all treatments)
in Experiment 2.

PAIRED   (N=30)

EXPTLS.   (N=18)

CONTROLS (N=18)

NO. OF ANIMALS

31-40 41-50 51-60 61-70 71-80 81-90 91-100 101-110 111-120 121-130 131-140 141-150 151-160

ADULT   LONGEVITY   (DAYS)
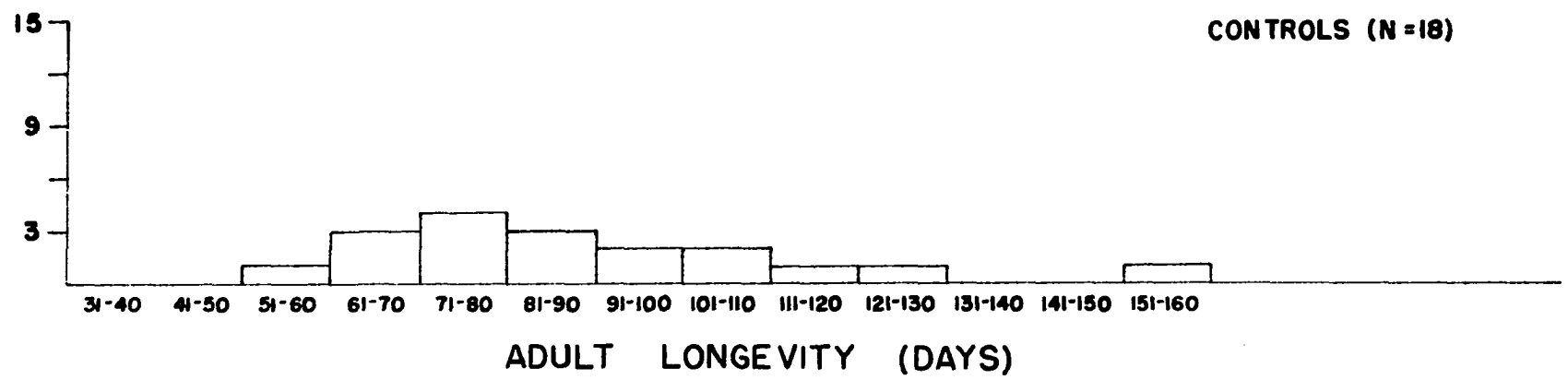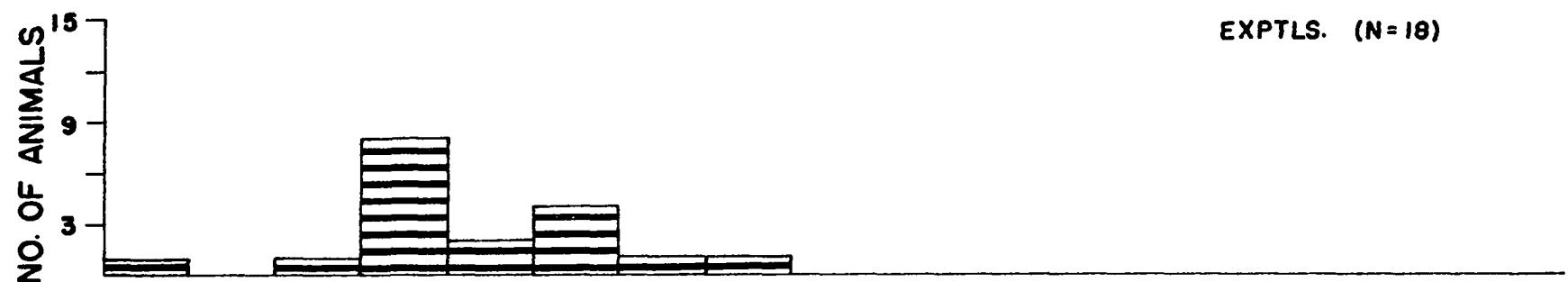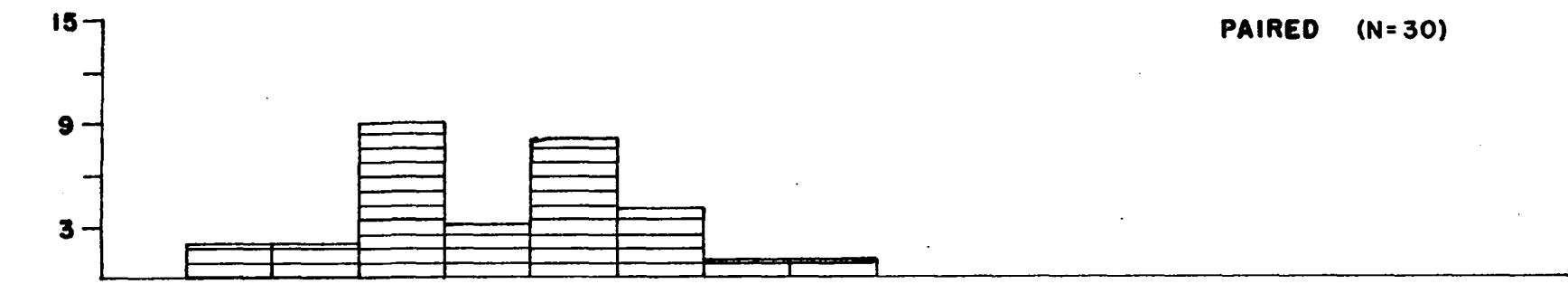
Fig. 20. Frequency distribution of adult longevity (days) of F3 generation male G. integer (all treatments) in Experiment 3.

PAIRED   (N=34)

EXPTLS. (N=61)

CONTROLS (N=61)

NO. OF ANIMALS

ADULT   LONGEVITY   (DAYS)
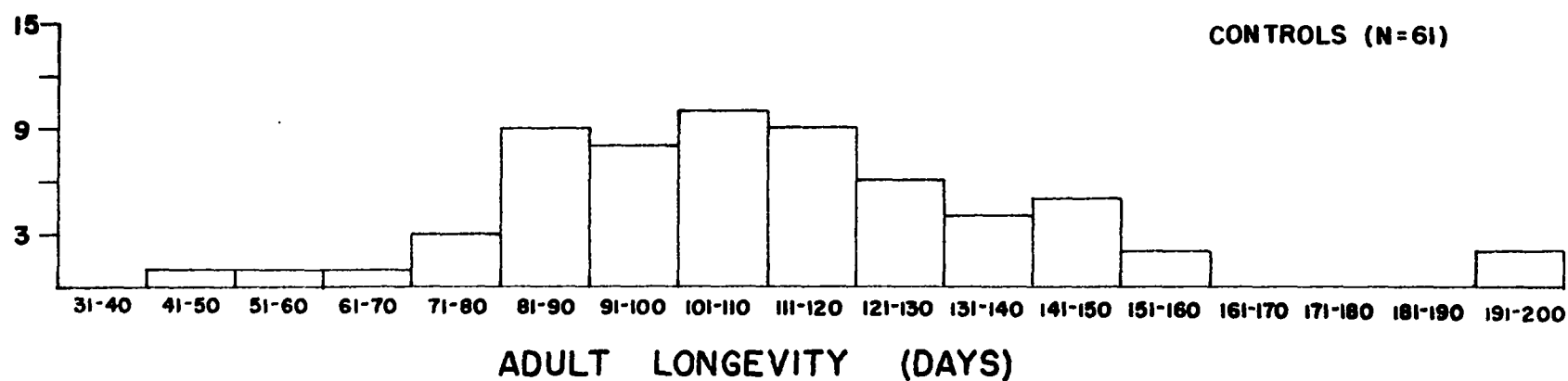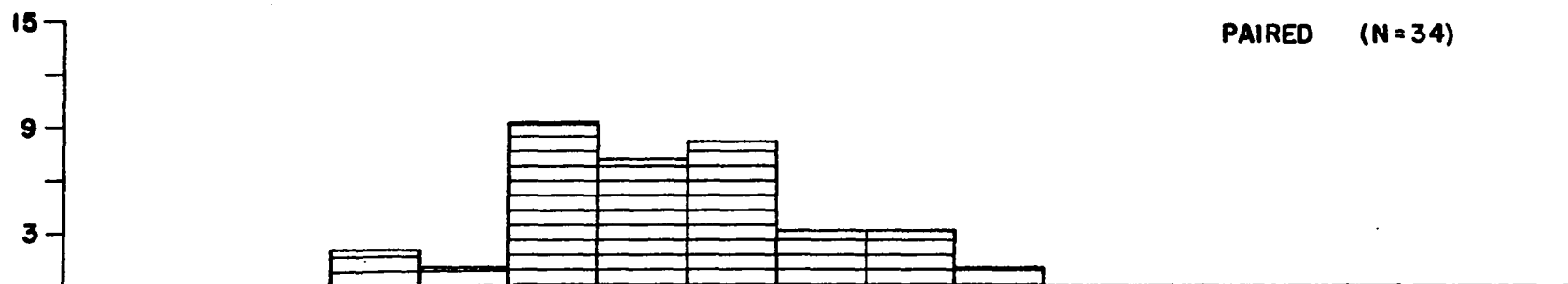
Fig. 21. Frequency distribution of adult longevity (days)
          of F_1 generation male G. integer (all treatments)
          in Experiments 5 & 6.

ADULT LONGEVITY (DAYS)
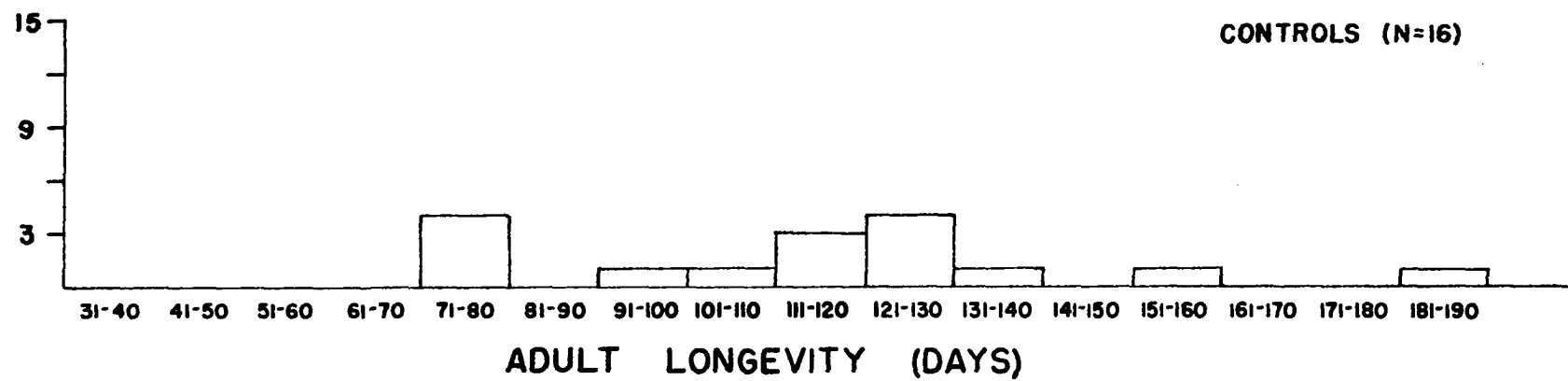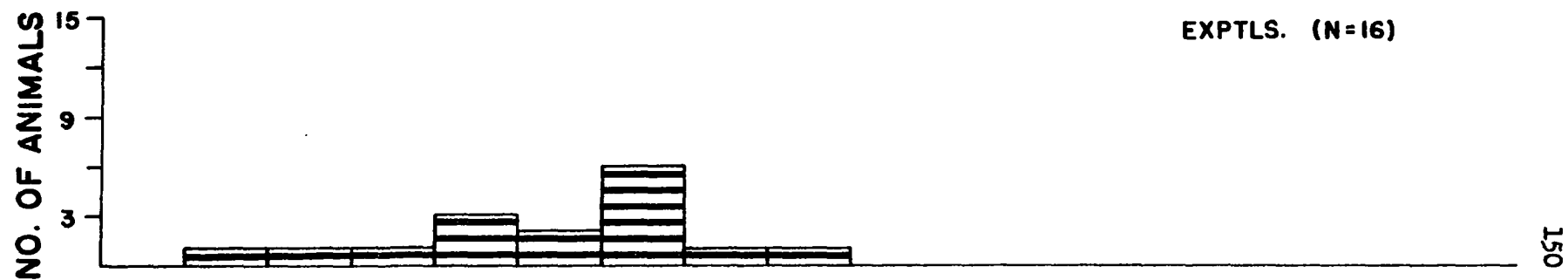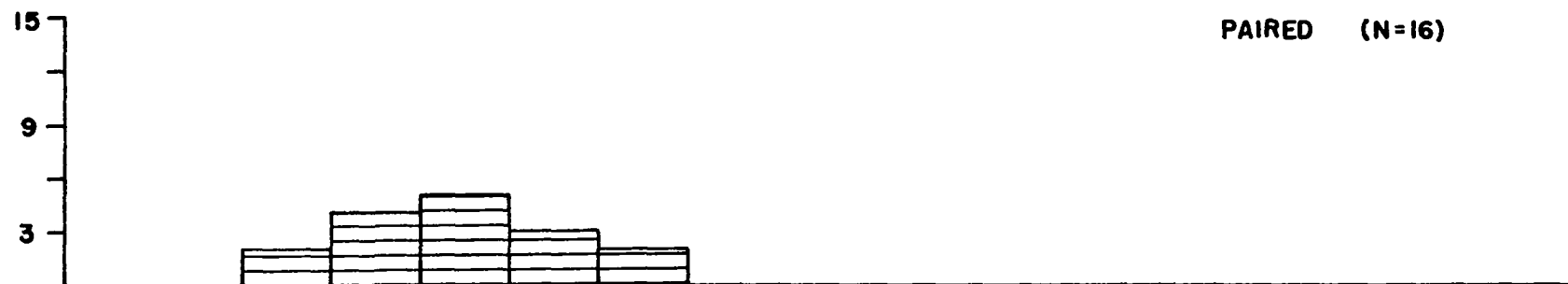
Correlation Studies

There was no correlation of adult longevity data with (1) average level of aggression, (2) percentage of interactions where the experimental male was definitely subordinate, or (3) percentage of interactions involving Level 5 aggressive encounters (Fig. 22), for experimental males in all experiments. Correlation coefficients obtained were +0.07, -0.03, and -0.05, respectively.

Longevity appeared unrelated to hierarchical status, and the oldest experimentals at death (F_3 #413, F_4 #453) were animals that had never achieved dominant social rank (see Table 25).

If, in Fig. 22, the data from Experiments 1 & 2 (animals exposed to high laboratory temperatures), and the males in Experiments 3-6 that engaged in no Level 5 encounters (perhaps because of overall weakness or poor health that would have caused these males to die relatively early, regardless of circumstances) are excluded, thereby considering only 78 of the 116 experimentals, then a correlation coefficient of -0.31 is obtained, indicating a significant relationship ($P < 0.01$) between fighting intensity and reduced longevity.

Failure to achieve significant correlations with the total data suggests, as might be expected, that the reduced longevity of experimental males is a complex phenomenon involving several to many factors, some of which were not considered or controlled for, and others of which may be inter-related in ways not discernible by employment of standard statistical testing methods.

Fig. 22. Correlation of adult longevity (days) with the percentage of total interactions that involved Level 5 aggressive encounters for all experimental G. integer (N = 116) in all six experiments.

r = -0.05
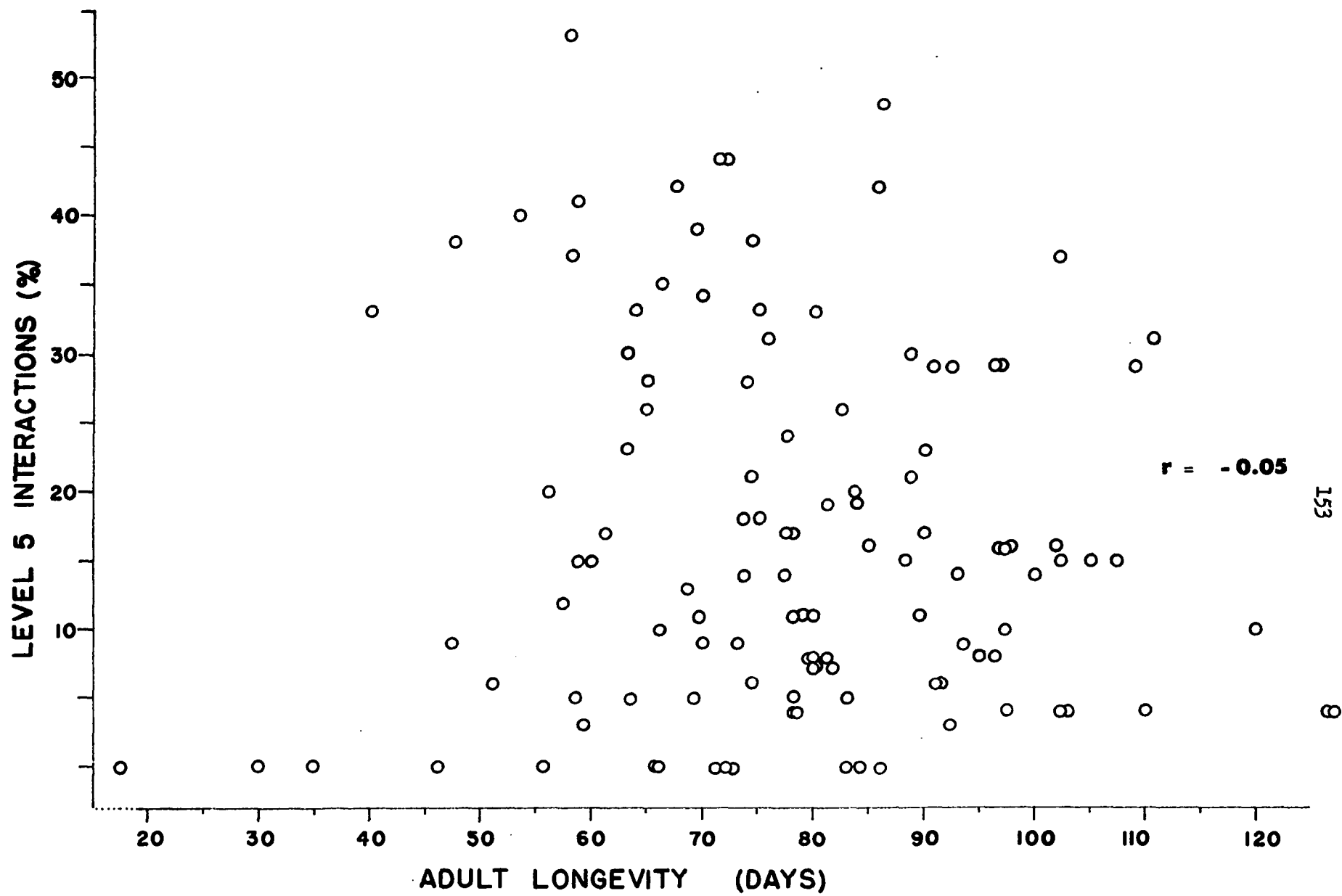
Death Postures and Death Symptoms

During Experiment 1, I noted that several experimental males assumed distinctive death postures, the most obvious being one in which the hind legs were extended stiffly and frequently held off the substrate. Because of the small numbers of animals involved, no particular importance was assigned to these observations. Midway through Experiment 2, however, this phenomenon was again noted for experimental males, but not for controls, and beginning with Experiment 3 particular attention was given to postures assumed at death, and close observations were made of dying cricket behavior patterns whenever possible.

It soon became evident that most control animals at death exhibited symptoms and assumed a posture designated as "non-paralysis" (Figs. 23, 25, 27), for which the following conditions were evident:

1. Hind legs not held stiffly. Carcass conveyed an overall appearance and impression of 'looseness'. Loose hind legs bent at the femoro-tibial joint were easily flexed and manipulated by the experimenter after death.
2. Animals were characteristically collapsed 'heap-like' on the substrate, legs usually tucked up against body rather than extended.
3. Antennae usually lying flat on substrate, uncurled and flexible; easily bent and manipulated with a probe without breaking.
4. Body not noticeably desiccated; abdomen soft and compressible, and frequently sunken on the ventral surface in region of segments 1-3.

Animals designated as in "paralysis" exhibited several consistent symptoms as follows (Figs. 24, 26, 28, 29):

1. Hind legs becoming stiff and extended and not loose and flexible at death; frequently held high off substrate and at an angle from the body, prior to or after death.
2. Body often noticeably desiccated. This was especially evident

Fig. 23. Death posture of non-paralyzed control male #462.
Side view.

Fig. 24. Death posture of paralyzed F_1 intruder 8. Side view.

Fig. 25. Death posture of non-paralyzed control male #462.
Angle view.

Fig. 26. Death posture of paralyzed F_1 intruder 8. Angle view.

Fig. 27. Death posture of non-paralyzed control male #462.
Top view.

Fig. 28. Death posture of paralyzed F_1 intruder 8. Top view.
(Photographs by F. J. Sonleitner).
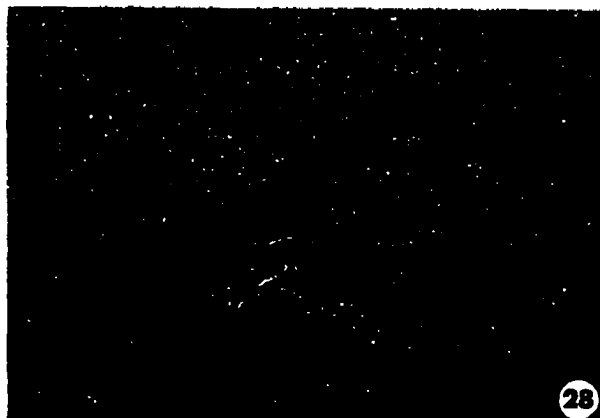
for the abdomen which became hard and unyielding, or for the antennae, frequently curled and held off the substrate.

3. There was a sequential order of paralytic symptoms. The first signs were a stiffness of the hind limbs and difficulty in loco-motion. The hind legs, stiffened and frequently held off the sub-strate, became non-functional in locomotion and the cricket moved by dragging itself with the fore appendages. Paralysis proceeded anteriorly with fore limb movement last to disappear before immo-bility and only antennal and especially palp movements to suggest the presence of life.

4. Stiffening hind legs, held off the substrate, frequently went from a bent position to a total extension and straightening in later paralysis stages.

5. Usually, once stiffness and the first signs of difficulty in locomotion were noted, death occurred rapidly -- within 12 hours and usually less. However, instances were observed where only the hind legs were affected by a local stiffness which did not spread anteriorly; some crickets thus affected survived for weeks thereafter, some engaging in aggressive encounters and winning.

6. Infrequently slight spasms or tremors of the appendages, especi-ally hind legs, were observed in crickets dying in paralysis, and a few exaggerated tremors were witnessed. Whenever observed, such tremors of the hind legs were always few in number and of short duration -- unlike the continual violent tremors of DDT-poisoned insects.

To be designated as "paralyzed" or "non-paralyzed", dying crickets or recently-fresh carcasses had to exhibit nearly all of the previously described symptoms. Most control animals consistently exhibited loose, relaxed postures at death, and were easily distinguished as unparalyzed; and many experimentals showed the sequential progression of paralysis from the hind legs anteriorly and assumed characteristic death postures, the most notable and dramatic symptom being the stiffly extended hind legs held high off the substrate (Fig. 29).

However, numerous gradations occurred between the two extremes, and some crickets were assigned to categories of "probably paralyzed," "questionable," and "probably unparalyzed," depending largely on the position of appendages and degree of stiffness, etc. at death (Table 44). Many crickets placed in these categories were animals dying at
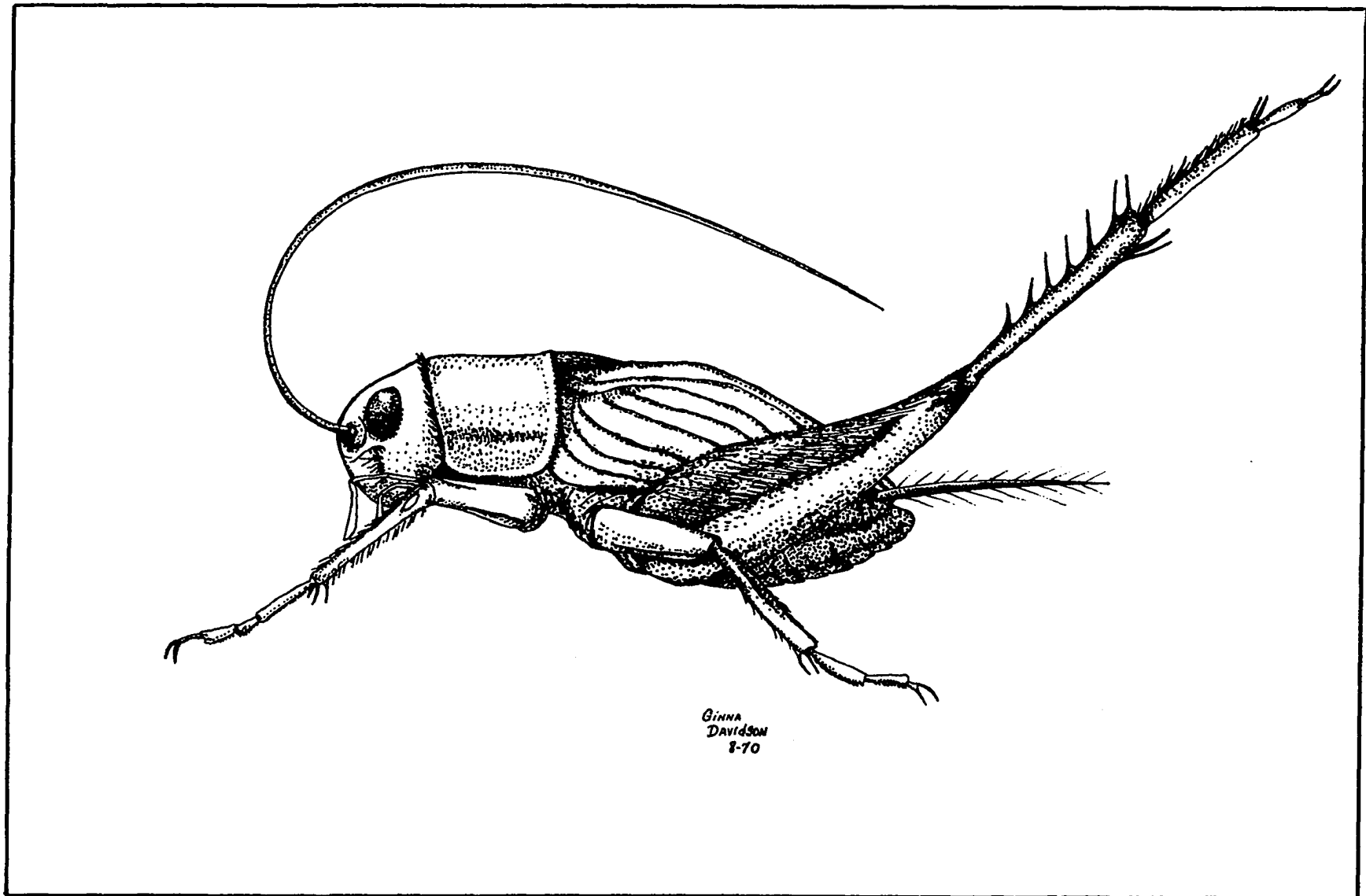
Fig. 29. Death posture of F_4 experimental #469

Table 44. Incidence of paralytic symptoms at death for controls, experimentals, and permanently paired male G. integer in Experiments 1 to 6 and for intruder integer males in Experiments 4 to 6.

Expt.	Males	N	Definite Paralysis	Probable Paralysis	?	Probable Non-paralysis	Definite Non-paralysis
1	Controls	8	0	0	6	1	1
	Exptls.	8	2	3	2	1	0
	Controls	18	0	0	11	0	7
2	Exptls.	18	6	5	5	1	1
	Pairs	30			Not Recorded		
	Controls	61	3	3	2	2	51
3	Exptls.	61	31	7	16	1	6
	Pairs	34	2	4	19	1	8
	Controls	13	1	2	0	0	10
4	Exptls.	13	8	0	0	0	5
	Pairs	12	7	1	1	0	3
	Controls	16	3	3	0	1	9
5/6	Exptls.	16	12	2	1	1	0
	Pairs	16	9	6	0	0	1
	Intruders:						
4	F4's	8	4	1	2	0	1
	Wild Caught	12	7	0	3	1	1
	Intruders:						
5/6	F4's	8	3	1	1	0	3
	Wild Caught	21	14	1	4	0	2

night and discovered hours later, so that behavioral observations before death were not possible.

Incidence of Paralysis

From data for Experiments 3-6 during which special attention was given to death postures, condition of carcasses, and/or behavior of dying crickets, it is evident that most controls (56-84%) died in a state of non-paralysis, with relatively few (5-19%) instances of definite paralysis (Table 45).

Among experimentals and permanently paired males, however, definite well-authenticated paralysis was frequent (experimentals 5-75%; pairs 6-58%) and non-paralysis was less commonly observed (experimentals 0-38%; pairs 6-25%) (Table 45).

Table 45. Incidence of well-authenticated cases of paralysis (P) and non-paralysis (NP) at death among control, experimental, and permanently paired $\underline{G}$. integer in Experiments 1-6, and among $\underline{G}$. integer intruders in Experiments 4-6.

Expt.	Controls		Experimentals		Pairs		Intruders	
	P	NP	P	NP	P	NP	P	NP
1	0%	0%	25%	0%	-		-	
2	0%	38.9%	33.3%	5.6%	Not Recorded		-	
3	4.9%	83.6%	50.8%	9.8%	5.9%	23.5%	-	
4	7.7%	76.9%	61.5%	38.5%	58.3%	25.0%	55.0%	10.0%
5/6	18.8%	56.2%	75.0%	0%	56.2%	6.2%	58.6%	17.2%

Many crickets in the "probably paralyzed" and "questionable" categories exhibited stiffened appendages, but did not assume the

dramatic posture of paralyzed crickets with pronounced hind leg
extension, nor was the body loose and flexible as in non-paralysis.
Many more experimentals and paired males, than controls, were placed
in these categories (Table 44).

For Experiments 3-6 an average of approximately 57% of the
experimentals, 29% of the paired males, and only 8% of the controls
showed definite paralysis at death (Fig. 30a), whereas carcasses
exhibiting limp appendages and undesiccated bodies symptomatic of
non-paralysis characterized approximately 12% of the experimentals,
19% of the paired males, and 78% of the controls (Fig. 30b).

Well-pronounced paralysis also accompanied intruder male
mortality (Figs. 24, 26, 28). Complete records were kept for in-
truders used in Experiments 4-6, representing both laboratory-raised
F_4 generation males (siblings of males used in Experiment 4) and
wild caught animals; 55-59% exhibited definite paralysis at death
(Table 45).

Onset of Paralysis

Several representative cases illustrating the usual gradual
sequential appearance of paralytic symptoms are given in Appendix IV.

Rapidly occurring death was observed on only a few occasions.
F_3 experimental #389, observed locomoting with difficulty, was stimu-
lated by being carefully picked up with forceps for a few seconds,
then replaced on the sand. Immediately its hind legs were fully ex-
tended backward and trembled slightly, as the fore legs slowly extended
forward, conveying the impression of a slow, sustained tetanic convul-
sion. After one minute the hind legs quivered several times, all move-

Fig. 30. a. — Incidence (expressed as %) of well-authenticated
paralysis at death for G. integer males (all
treatments) in Experiments 3-6

        b. — Incidence (expressed as %) of well-authenticated
non-paralysis at death for G. integer males
(all treatments) in Experiments 3-6.

%

70 —
60 —
50 —
40 —
30 —
20 —
10 —

controls

exptls.

paired

N= 90   90   62

A.   PARALYSIS

N= 90   90   62
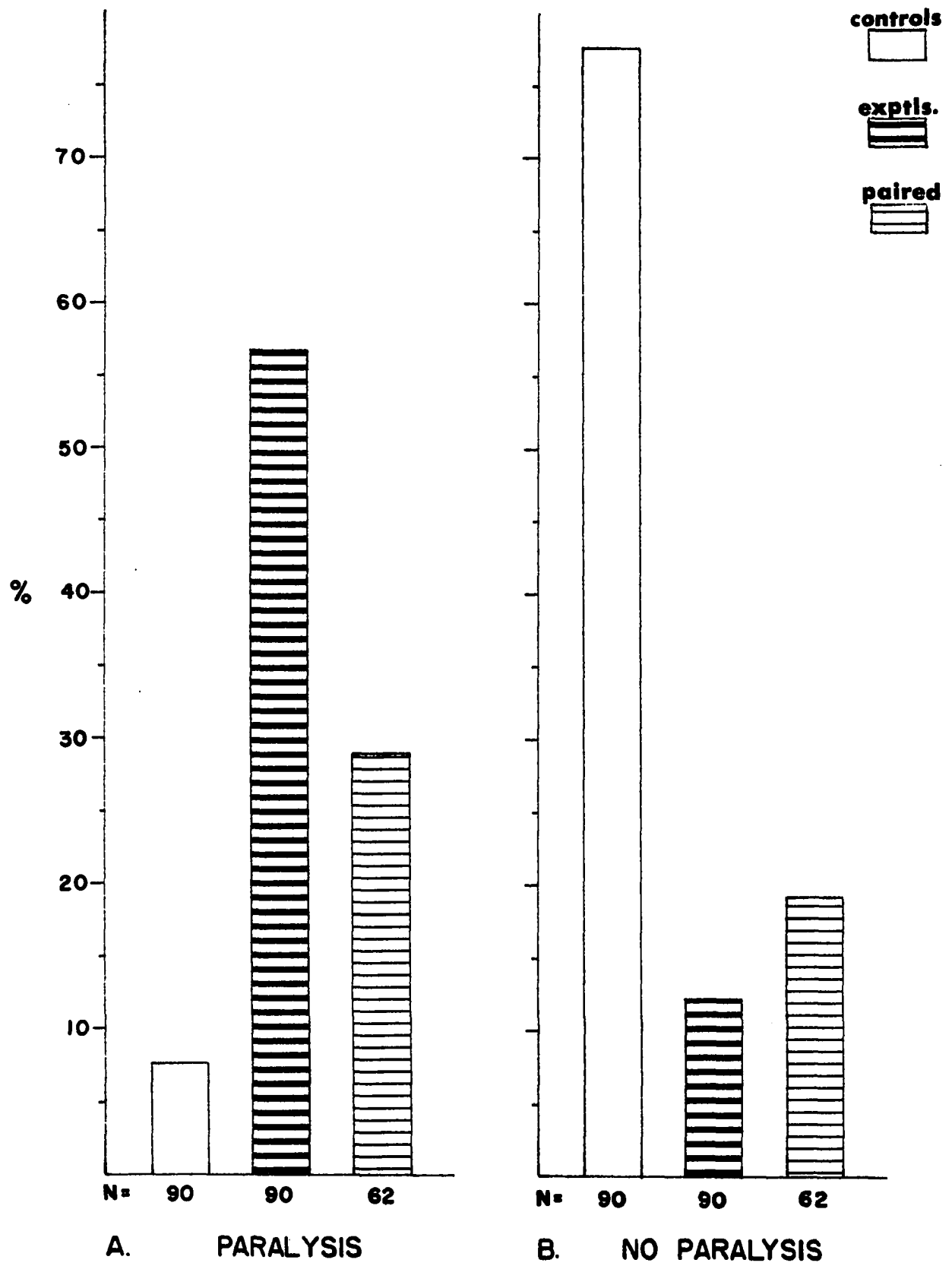
B.   NO PARALYSIS

ments ceased, and the cricket died in this extended position. Data for F_4 pair #493-494 (Appendix IV) also illustrate the rapidity with which paralysis can develop and death occur. Such observations might be explained by supposing that stimulation can induce the release of a sufficiently large and fatal quantity of some neurotoxin.

Several observations (see F_4 pair #493-494, Appendix IV) along with the occurrence of hind leg stiffening in subordinate animals pursued during chasing bouts suggest that (1) temporary stiffening of appendages, or (2) permanent and irreversible paralysis, may be associated, in part, with excessive muscular activity.

In paralysis, then, a sequential progression of symptoms, first significantly affecting the hind legs and moving anteriorly, usually occurred. The animal gradually weakened, finally becoming immobile with hind legs usually fully extended or nearly so, held out from the body, and thrust aloft. Palp movements continued for several hours after immobility, becoming less obvious until finally all evidences of life ceased.

Variability of the Paralytic Response

Although most evident for experimentals (Fig. 30a), paralysis was observed under several different circumstances, including behaviorally, though not acoustically, isolated controls, paired males, and a large wing bud male. This F_3 male was reared in a gallon jar under crowded conditions at 68° F before isolation as a small wing bud instar. After molting the cricket survived for 91 days before dying in paralysis. The symptoms shown by this late instar nymph and by paralyzed controls did not differ from paralysis exhibited by experimentals and paired males.

There is no strong evidence to suggest that paralysis at death is (1) influenced by exposure to fighting, or (2) a manifestation of subordinance either in all or in the most recent aggressive encounters, since of the 26 experimentals in Experiments 1-6 that survived less than 80 adult days and/or 25 interactions, and that showed definite paralysis at death, seven dominated their last several interactions before death, eight were subordinate, and for 11 dominance was undeterminable.

In one known instance a cricket exhibiting some paralysis-associated symptoms (i.e., tremors) before death, did not show paralysis at death hours later (see #416, Appendix IV).

Temporary Stiffening and Immobility of Hind Legs

Signs of difficulty in locomotion accompanied by noticeable hind leg stiffening usually foreshadowed the subsequent occurrence of the 'paralysis wave' moving anteriorly, effects on the fore appendages, immobility, and eventual death. Once symptoms progressed beyond the early stages of hind leg involvement, paralysis was irreversible, and death occurred within hours.

However, on a number of occasions among both controls and pairs, but especially among experimentals, a localized paralysis occurred affecting one and rarely both hind legs in which the leg perceptibly stiffened, and was held off the substrate, generally bent, becoming non-functional in locomotion; stiffening was limited to the hind legs and was usually temporary, persisting for varying time periods. Crickets exhibiting this local paralysis did not necessarily exhibit paralysis when they eventually died at a later date.

With several exceptions, most stiffening appendages among experi-
mentals occurred in actively chased subordinate males after Level 3-5
aggressive encounters during the 20-minute interactions. The associ-
ation between stiffening hind legs and chasing again suggests that the
phenomenon is directly or indirectly related to excessive muscular
activity.

An example illustrating localized hind leg stiffening in a
subordinate exposed to chasing bouts is F_1 experimental #533 discussed
below; this male is also the best example of the few cases observed
in which localized stiffening remained permanent.

> During its first three interactions #533 was defeated and
> frequently chased by the intruder. During active chases in
> Interaction 4, and again in 5, #533's left hind leg stiffened,
> eventually becoming fully extended and useless as #533 continu-
> ally retreated from the intruder's charges. Stiffening of the
> same hind leg again appeared during a less intense chase in
> Interaction 8, but this time the leg was held bent, not extended.
> In Interactions 9-15, #533 frequently fought the intruder in
> intense Level 5 encounters. One face-off with open mandibles
> in which both males chirped and jerked on opposite sides of the
> screen lasted a record $8\frac{1}{2}$ minutes. In each interaction #533
> eventually retreated and was chased. In Interaction 16, during
> chasing, the left hind leg again stiffened and remained held
> off the substrate for the remainder of the grouping period.
> Stiffening was temporary and disappeared soon after the intru-
> der was removed.
>   Beginning with Interaction 22 and up to Interaction 27,
> #533 assumed and maintained dominance after very intense Level
> 5 encounters, one involving over 20 successive LM's. Each
> interaction involved numerous chasing bouts by #533, but no
> stiffening symptoms appeared.
>   Beginning Interaction 28 a new intruder was used, and #533
> became subordinate again. Interactions 29-42 were generally
> highly aggressive, with many Level 5 encounters; in each case
> #533 retreated and was chased. During Interactions 30 and
> 32-34 the left hind leg fully extended, and in Interactions
> 35 and 37-40 both hind legs stiffened and became temporarily
> non-functional.
>   Before Interaction 42 was staged it was noted that #533 lost
> its right hind leg; loss of a hind leg that had previously been
> noted stiffening was noted for several other male field crickets.
> From Interactions 43-48, the left hind leg remained permanently
> stiff and extended, and at death #533 exhibited total paralysis
> with curled antennae and desiccation.

Interestingly, temporary hind leg stiffening noted in chased subordinate males was never observed for any of the chasing dominants.

In contrast to temporary hind leg stiffening, male crickets exhibiting the first stages of permanent irreversible paralysis locomoted in a characteristic manner. The hind legs were initially most affected, but locomotion was unsteady and the animal conveyed an impression of a tightening over the entire body; it became possible to reliably predict the approaching death of males showing these early symptoms.

Hind leg stiffening noted for experimental males during the interaction periods, expecially during chasing bouts, was different. Effects were localized, usually temporary (i.e., lasting only during the interaction periods and shortly thereafter), and locomotion was not seriously impaired; the animal continued to move and run with its remaining legs. It is possible that the two conditions are indicative of physiological changes differing in magnitude or detail.

Temporary hind leg stiffening can be experimentally induced by mechanical stimulation. On 10-21-70, 14 F_1 males (76-83 day old sibling adults) and a wild caught adult male 70 days old, maintained in behavioral isolation in quart jars since adult molt, were stimulated by contacting the cerci with forceps. Six of the males responded by excitedly jumping for 10-15 seconds, then running around the jar; when they stopped running the cerci were re-stimulated. Five of these males exhibited stiffening within 15-20 seconds after they ceased jumping and commenced running, and in two, the wild caught and one F_1, the hind legs fully extended and were held off the substrate when the animal came to

rest. In the other three animals the hind limbs remained bent at the femoro-tibial joint, but were held stiffly, slightly off the substrate or dragged through the sand when the animals moved. All four F_1's were locomoting normally within 15 minutes after the cessation of stimulation. The hind legs of the wild male remained off the substrate for nearly two hours, and all symptoms of stiffness did not disappear until at least six hours later.

The other eight males which initially responded with running rather than excited jumping were stimulated continually for 2-3 minutes but did not exhibit stiffness, only fatigue. After repeated stimulation five of these males raised their body high off the sand, and with head downward, held their body axis nearly perpendicular to the sand surface. Further cercal stimulation did not induce further running, only frequent kicking backward with the hind legs. Running could only be induced by picking up the cricket with forceps, then dropping it and restimulating the cerci.

Although both excessive muscular activity and individual differences in response seem to be involved, generalizations regarding temporary hind leg paralysis are risky in view of the apparently complex nature of the phenomenon.

CHAPTER IV

DISCUSSION

Social Dominance

What accounts for the social rank stability observed for most
experimental-intruder interactions? Alexander (1961) discussed seven
factors that can influence shifts in dominance order among male field
crickets: (1) territoriality, (2) size, (3) age, (4) general fighting
ability, and the effects of (5) isolation, (6) copulation and (7)
previous wins and losses.

Copulation Effects

Subordinate males that have recently copulated become hyper-
aggressive and can maintain dominant hierarchical status for a short
time after mating (Alexander, 1961). Since no male $\underline{G}$. $\underline{integer}$ in
the present study had encountered adult females, this factor can be
disregarded.

Territoriality

Alexander (1961) noted that the expression of territorial behavior
among male field crickets was necessarily associated with the occupancy
of a crevice or burrow, that burrow occupancy increased aggressiveness,
and that fighting success was correlated with a male's proximity to its

burrow. Males inhabiting burrows or crevices and acting territorially
exhibited distinctive behavior, including periodic "patrols" during
which the crickets stalked in quick, positive and offensive fashion
before returning directly to its burrow.

Male G. integer did not exhibit this territorial behavior, and
crevice construction or occupation did not occur in their jar envi-
ronments. In fact, as is evident from the data (Table 25, Appendix I),
although all social encounters were staged in the home jar of the
resident experimental, this seemed to confer no fighting advantage,
and actually most (67%) encounters with determined dominance were won
by intruder males. Consequently, territoriality can be ruled out as
a factor explaining social rank stability during successive inter-
actions between experimentals and intruders in this study.

Effects of Isolation

Among male field crickets isolation induces increased aggressive-
ness. For natural cricket populations this phenomenon helps promote
spacing and localization and enhances the ability of males to defend
and maintain possession of their burrows. The effects of isolation
in increasing aggressiveness for many animals, including field crickets
(Alexander, 1961) and many mammalian species (Krsiak and Janku, 1969;
Valzelli, 1969), are potent and well-authenticated. In the present
experiments, however, isolation can be discounted as an important
influencing factor since, in almost every instance, experimentals and
their intruders were isolated for identical time periods between
interactions.

Age

Alexander (1961) stated that male field crickets achieve peak dominance at 10-14 days adulthood and that increasing age does not affect their social status until shortly before death, which occurs in 2-3 months.

G. integer shows peak aggressiveness generally after two weeks and adults commonly live beyond three months. The data suggest that age is a possibly significant factor in fighting ability and social rank stability only for some young adults, and old males exceeding three months of age.

Size

Alexander's (1961) observation that social rank rarely correlates directly with body size was confirmed in the present study. Size is certainly an influential factor during fighting bouts and was obviously significant in the outcome of many experimental-intruder Level 4-5 encounters where a much larger animal either intimidated a smaller opponent during a Level 4 face-off, or physically overwhelmed it during Level 5 mandible-lockings.

However, the reverse situation of a noticeably smaller animal defeating a larger male was noted for many experimental-intruder pairings.

In most cases, experimentals and intruders were of equal or nearly equal size, and the importance of size, though significant in a few instances, is minimized as a general explanation. In this regard, it is noteworthy to consider the fighting success of several males exhibiting handicaps (e.g., missing appendages) other than small size.

Effects of Previous Experience

Alexander (1961) discovered that the dominance status of two
males could be reversed by repeatedly 'defeating' the dominant with
the aid of an artificial antennal lashing device and playbacks of
aggressive calling. Although difficult to explain because of the
probable interaction of many factors, Alexander believed that some
type of conditioning is involved in cricket hierarchies, that several
successive defeats or wins enhance subordinance and dominance respec-
tively, and that aggressive calling by dominant animals during and
after fighting bouts reinforces subordinance and helps maintain
hierarchical stability. Alexander noted that after several intense
aggressive encounters among males continually maintained together in
a terrarium, subordinate animals tended to avoid and retreat from
future encounters.

A similar phenomenon was evident for $\underline{G}$. $\underline{integer}$, but to a lesser
degree. Once defeated in an encounter during any given interaction,
a submissive $\underline{integer}$ male nearly always remained subordinate, retreating
from contact with the dominant, until the end of the grouping period;
only rarely did dominance switches occur. Also, for some experimental-
intruder pairings it was common for a male defeated during a series
of previous interactions to exhibit less aggressiveness and quickly
retreat from contact with intruders during subsequent interactions,
suggesting that learning did occur among consistently defeated males.

However, in many other cases, males continually losing a series
of previous encounters showed little or no decrease in aggressiveness,
suggesting that if experiential factors influence social rank stability

of consistently defeated animals, these learning effects can be masked
or supplanted by the hyperaggressiveness associated with the 48-72
hour isolation periods between interactions.

General Fighting Ability

Alexander (1961) included this category to explain undetermined
causes of dominance; he speculated that individual differences expressed
during fighting bouts (e.g., unique tactics, ability to move faster,
etc.), or factors less directly related or unrelated to fighting ability
might be involved.

Individual peculiarities in behavior among conspecific male
field crickets observed and described by Alexander were noted for
male G. integer. Some males frequently turned around and kicked back
with hind legs during face-offs; others never kicked. One experimental
male rarely locked mandibles, and instead achieved dominance during
face-offs by suddenly charging forward into its opponent, continuing
to charge as the intruder moved backward and eventually retreated.

Individual males did show differences in aggressiveness and this
may have contributed largely to continual success or failure in
fighting. Differing aggressive states between combatants was particu-
larly evident in fights between males of unequal size. Some small
males, distinctly inferior in size and strength, frequently pushed or
thrown backward by a larger opponent during mandible-lockings, consis-
tently returned to re-engage and by so doing often achieved and main-
tained dominant rank. After witnessing several such encounters one
wonders whether the descriptive human term "guts" is not appropriate
for some fighting male crickets as well.

In view of the probable fact that crickets do not exhibit individual recognition or "retain information from encounters which causes them to respond differently in subsequent encounters with the same individual" (Alexander, 1961: 162) it would appear that the two main factors explaining the social rank stability between experimental and intruder G. integer in these experiments were (1) experiential effects associated with previous wins or losses, and (2) general fighting ability, including individual differences in aggressiveness.

The aggressive 'state' of male crickets can vary over time and although crickets probably do not exhibit individual recognition on a physical basis, they may 'recognize' and respond to other males by discriminating behavioral differences associated with differing aggressive 'states' (Alexander, 1961).

Fluctuation in aggressive state and tactical advantages during fighting between two equally matched males probably account for many of the experimental-intruder interactions involving see-sawing dominance where the social rank relationship failed to stabilize.

In spite of Huber's (1955) suggestion that the physiological priming mechanism for courtship differs from priming for aggression, an unusually large number of dominance switches or changes in relatively stable rank relationships occurred during interactions involving courtship.

Longevity

Increased longevity of controls as compared with experimentals and paired males, and the usual lack of significant differences between

animals in the two latter groups, is noteworthy.

Permanently paired males exhibited increased courtship, much
of which was not recorded, and reduced or nonevident aggression.
Grouping male field crickets is known to lead to reduced aggression,
and for males isolated from females, continued experience with reduced
or no aggression promotes courtship. Whether increased incidence of
courtship behavior among male field crickets housed together is due
to the depression of aggression levels, to physiological changes re-
sulting from failure to mate, or to some other factor is not known
(Alexander, 1961). Ewing (1967) observed less fighting among perma-
nently paired male lobster cockroaches, Nauphoeta, and suggested the
possible involvement of a passive inhibition mechanism.

One explanation for greater longevity among controls is that
grouping male Gryllus either permanently or for short interactions
on alternate days may constitute a social stress situation which
produces physiological changes influencing mortality rates. The
relatively high incidence of paralysis among dying experimentals
and paired males supports such a hypothesis, and suggests direct
nervous system involvement.

The results for experimentals and paired males in Experiments
2 & 3 suggest that short-term periodic interactions resulting in
increased levels of aggression (largely due to effects of previous
isolation) are as effective or more so in reducing longevity than is
permanent housing in pairs. However, although permanent pairing
appeared to reduce the intensity of aggressive encounters, it was
as effective a treatment as short intermittent exposures in reducing

longevity in Experiments 4-6.

No information is available concerning the frequency of nocturnal aggressive displays between paired males. If the incidence of aggression did not differ appreciably from that of diurnal observation, and if the reduced longevity of experimentals and paired males is due to a social stress mechanism as hypothesized, then it would seem that the stress mechanism involved is complex and generalized, and not merely a result of fighting and aggression. The lack of correlation between longevity and (1) percentage of Level 5 interactions, and (2) average level of aggression for experimental males, supports this idea. Nowosielski and Patton (1965) make no mention of specific types of behavior, such as aggression, when describing the effects of grouping on reduced longevity patterns of adult house crickets, Acheta domestica. Chauvin (1958) was the first to show that group-reared house crickets develop more rapidly than those reared individually, and Alexander (1968a) cited other cricket studies corroborating the acceleration of growth associated with tactile stimulation. In the present experiments it might be legitimate to question whether tactile stimulation, independent of aggression, can also reduce longevity.

Just as Pence et al. (1963) decided that continuous motor activity alone was not responsible for the prostration and eventual death of honey bees subjected to forced confinement, the high activity levels of paired males, especially in the morning, suggest that reduced longevity of experimentals is not solely due to increased metabolic rates or energy expenditure occurring during 15-20 minute interactions on alternate days. Activity directly or indirectly

resulting from social contacts was much greater for permanently paired males than for experimentals.

A number of possible explanations, then, exist for the reduced longevity of paired males in the observed absence or reduced frequency of aggression:

1. Increased activity and energy expenditure from continual tactile stimulation.

2. Unobserved and perhaps more frequent or intense aggressive contests occurring at night.

3. Courtship behavior acting as a significant socially stressful stimulus.

4. Frequent exposure and infrequent low level aggressive encounters occurring continually over time producing the same effect as several short intense encounters occurring at periodic intervals.

In all likelihood several interacting factors are involved, and agonistic behavior and fighting, although probably influential, are but one piece of the total picture. For example, the F_4 paired males exhibiting the lowest aggression levels also exhibited the shortest longevity, and it is quite possible that the data for Experiment 4, in part, reflect the fact that all the F_4 generation males were communally reared in a terrarium prior to isolation as late instars.

Although some experimental males survived only relatively few interactions following exposure to frequent intense fighting bouts, other such males survived much longer times. No correlation existed between longevity and social dominance, and, interestingly, the two longest-lived experimentals in all experiments were males that failed

to assume dominance in any of their encounters.

Paired males, as opposed to experimentals: (1) were grouped together continuously from at least the last nymphal stage until death, (2) were often tactually stimulated and frequently acoustically stimulated by each other, (3) were exposed to twice the density and twice the concentration of waste products per unit area, and (4) characteristically exhibited few to many low level aggressive encounters, few or no Level 3-5 encounters, and frequent courtship encounters. Yet, they showed either no significant difference in longevity or increased longevity compared to experimentals.

These facts suggest that short periodic bouts of social contact with other males, including but not necessarily involving fighting, contribute significantly to reduced longevity, possibly by acting more effectively in triggering a neuroendocrine-mediated social stress response that affects normal physiological functions, chronically disturbs homeostasis, and induces death.

Paralysis

Aside from increased survival times for controls, the only relatively consistent finding regarding longevity and survival was the large number of experimentals and paired males paralyzed at death, and the infrequent occurrence of paralysis among controls.

Paralytic symptoms in field crickets, including desiccated shortened abdomen and curled antennae, are identical with those observed in paralyzed roaches following exposure to chemical (i.e., DDT), mechanical, or electrical stress (Beament, 1958; Heslop and

Ray, 1959; Colhoun, 1960). Beament's (1958: 201) description of the posture of paralyzed roaches with legs projected out from the body, femurs raised dorsally "like a spider" so that the animal could be rocked on its ventral surface without the legs touching ground, describes the postures of "definitely paralyzed" G. integer in the present study. Beament, however, found that although paralysis was irreversible, paralytic symptoms in Periplaneta persisted as long as 3 to 29 days before eventual death.

For subordinate male lobster cockroaches exposed to fighting and attacks from dominants, Ewing (1967) noted a relatively rapid onset of irreversible paralysis on Days 3 and 4 after initial exposure. No G. integer males died in paralysis this early. However, Ewing exposed Nauphoeta to daily confrontations and although interaction times are unstated, she does mention fighting contests lasting up to 30 minutes.

In discussing stress paralysis among adult Periplaneta, Cook et al.(1969: 965) reported that after 4 hours of rough tumbling in rotating jars 30-40% of the animals were paralyzed, but that some recovered rapidly and appeared normal within an hour. However, according to their description the roaches "were unable to right themselves once ... placed on their backs" and during cercal stimulation "their legs moved in a slow, uncoordinated fashion or not at all." These findings described by Cook et al. appear quite different from the irreversible paralysis and appendage rigidity observed in Beament's (1958) Periplaneta and the Gryllus in this study.

Ewing (1967) noted most mortality and paralysis disproportion-

ately affecting subordinate roaches. Among $\underline{G}$. integer there was no such tendency, and paralysis was noted for experimentals that had always held dominant rank as well as those that were always, or nearly always, subordinate.

This is not to imply that dominant and subordinate animals are equally affected by aggressive encounters. As was mentioned, only subordinates showed pronounced abdominal pumping following chasing bouts, although presumably pursueing dominants expended as much energy as retreating subordinates. Aside from sensitivity to increasing CO_2 or decreasing O_2 concentrations, respiratory centers in each abdominal ganglion and a respiratory pacemaker in the suboesophageal ganglion of Gryllus are sensitive to nervous stimuli from elsewhere in the system (Wigglesworth, 1965). It is possible that the pronounced post-fighting respiratory movements of subordinate crickets are linked with their increased sensitivity to stressful stimuli (e.g., chasing, aggressive chirping) associated with and accompanying defeat.

During most experimental-intruder interactions only one or two minutes at most of the 15-20 minute grouping period were spent in actual combat or chasing. After initial antennal contact, fighting or chasing, most of the remaining period usually involved the dominant male calling or chirping aggressively while the subordinate remained inactive or moved about the jar attempting to climb the glass sides. Aggressive calling is a significant social behavior among male field crickets and is rarely heard in defeated animals following aggressive encounters. In many jars where body contact or chasing was minimal, frequent chirping by dominant males was common. If exposure to the

calling of a nearby male does constitute socially stressful stimu-
lation, subordinate males are undoubtedly most affected.

Paralysis in field crickets may be a natural outcome of social
stress resulting from social interactions including, but not necessarily
exclusively involving, aggression, but in all probability it represents
a generalized response to any number of stressful situations as
suggested by Beament (1958), Heslop and Ray (1959), Hodgson and
Geldiay (1959), Sternberg (1963), and Clarke (1966).

Aside from the fact that paralysis can result from a multiplicity
of causal factors, one of which may be social stress induced by
social contact and fighting, it appears that considerable variability
in susceptibility to, or incidence of, paralysis exists among
different species and among individuals of the same species.

The control animals in any given experiment were presumably
exposed to identical conditions of stress resulting from confine-
ment, acoustic stimulation, and changing temperature and humidity.
If paralysis does represent a stress response, then those few controls
exhibiting paralysis may have represented individuals with genetic or
behavioral characteristics making them most susceptible to stressors.
Results of identical experiments, using male Acheta domestica in this
laboratory, indicate that this species, provided it is exposed to
isolation periods between social encounters, is as aggressive as
Gryllus integer, but that paralysis is an infrequent phenomenon.

Among rodents it is known that some species (e.g., Peromyscus
maniculatus) do not exhibit the physiological responses to social
stress characteristic of other mice (Bronson and Eleftheriou, 1963;

Christian, 1970) and that noticeable behavioral and hormonal differ-
ences, even among different inbred strains, demonstrate a need for
exercising caution in generalizing results (Thiessen and Nealey,
1962). There is no reason to doubt that this caution should also
apply to studies of stress in roaches and other Orthoptera.

Stress paralysis may result from a number of physiological
changes involving the release of chemical substances from sites within
the nervous system. Studies suggest the probable involvement of
several secretions released from different cells in the C.N.S.
(Hodgson and Geldiay, 1959; Milburn et al., 1960; Sternberg et al.,
1959; Chapman, 1969). The corpora cardiaca are a likely source for
the neurohormones, active principles, neurotoxins, autocatalytic sub-
stances, etc., and have been suspected as such in most studies to date.

Desiccation

Desiccation accompanying paralysis (Beament, 1958; Lewis et al.,
1960) suggests disturbed fluid metabolism. Beament (1958) suggested
that dehydration through hemolymph depletion may have been the real
cause of eventual mortality in paralyzed Periplaneta, and Ewing
(personal communication) has evidence to suggest that water loss is
involved in long term stress effects on submissive roaches.

Desiccated abdomens, curling antennae, and continual mouthpart
movements in crickets in late stages of paralysis show dehydration
and suggest disturbance of salivary function. In this regard, it is
interesting to note the recent finding by Wright et al. (1970) of
neurosecretory materials in axonal processes in the roach midgut,

which they postulate act in neurosecretory control of diuresis.

Insect corpora cardiaca are known to contain a diuretic hormone which originates in neurosecretory cells of the cerebrum (Highnam and Hill, 1969). Desiccation accompanying paralysis in Gryllus integer is probably due to derangement of the homeostatic mechanism of fluid metabolism, in which diuretic hormone may be intimately involved. The corpora cardiaca are known to release stored neurosecretions and 'empty' under stress situations (Hodgson and Geldiay, 1959; Highnam, 1961; Clarke, 1966). It is possible that in socially-stressed Gryllus, diuretic hormone from the corpora cardiaca induces water loss by (1) increasing water movement through the malpighian tubules, or (2) inhibiting reabsorbtion by the rectum, both of which are known to occur in locusts (Highnam and Hill, 1969).

Significance of Findings

The significance of these findings to natural field cricket populations is not immediately obvious. Although studies showing the effects of density on insect, and specifically orthopteran, growth, behavior, or longevity are easily found (e.g., Highnam and Haskell, 1964; Wharton et al., 1968; Ebeling and Reierson, 1970), with the exception of Wynne-Edwards (1962), the relevance of behavior in natural studies of insect population dynamics has been largely neglected (Wilson, 1968).

Stress resulting from fighting among territorial, burrow-inhabiting male field crickets could conceivably influence natural populations in one of two ways: (1) increasing emigration and dispersal

rates, or (2) increasing mortality.

In nature, increasing densities would result in increasing overlap of male territories, increased frequency of aggressive encounter, and dispersal from the population of weaker or less-aggressive subordinate males. Escape behavior expressed by attempts to climb the glass sides of the jars represent but a simplistic behavioral manifestation of dispersal behavior which would occur on a much larger scale in natural populations undergoing increases in numbers. Increasing emigration rates are a natural result of increasing density in cricket populations (Alexander, 1968), especially for macropterous species like G. integer. Unfortunately, Johnson (1969) totally neglected a discussion of crickets in his otherwise thorough treatment of insect migration and dispersal by flight.

Concerning mortality effects, it is suggested that under certain conditions within field cricket populations, usually associated with increasing numbers, increasing social encounters between males involving chirping, fighting, and chasing would not only increase emigration of subordinates but would also increase mortality via endocrine or nervous changes constituting a social stress response. This stress-related mortality, often accompanied by paralysis, would affect males differentially according to a number of factors, and not merely social rank and fighting success.

Considering other regulatory factors — predation, weather, available food supply — such stress-related mortality is probably not a consistent or significant factor to be considered in evaluating the dynamics of natural cricket populations. However, among insects

such as field crickets with well-ordered populations stabilized by a spacing mechanism maintained by territoriality, acoustical repellance, and innate aggressiveness, stress-related mortality could conceivably influence population density and for this reason the phenomenon is significant, both to field cricket biology and human understanding.

CHAPTER V

SUMMARY

In an experiment designed to test for the possible existence
of a social stress response in a selected invertebrate, laboratory-
reared adult male field crickets (<u>Gryllus</u> <u>integer</u>) of known ages
were exposed to one of three treatments: (1) controls, (2) experi-
mentals, and (3) permanent pairs

Isolated experimentals and controls were maintained in behavioral
isolation from late nymphal stages. Beginning at 0 to 47 days adulthood
each experimental male was exposed to 15-20 minutes of social inter-
action with an intruder male placed in its jar. Interactions were
staged on alternate days, generally between 9 a.m. and noon, and
behavior, especially agonistic displays, was observed and recorded.
Intruders represented laboratory-reared siblings of experimentals, or
wild caught males. Whenever possible, experimentals were exposed to
the same intruders during successive interactions until the death of
one or the other. Each interaction was ascribed a certain aggression
level (1-5) dependent on the amount and intensity of aggression ex-
hibited by both combatants; social rank was determined from outcome of
encounters, and the stability of the dominant-subordinate relationship
for each experimental-intruder pairing over time was determined.

Control males were left undisturbed. Paired males remained permanently housed together from late instar stages, and were observed daily or more often.

All animals were housed in quart Mason jars with several inches of sand, water vial with paper wick, vertical climbing screen, and Gaines dog meal supplied ad libitum.

Six replicate experiments were conducted involving a total of 116 controls, 116 experimentals, and 92 paired males. Animals among treatments in each experiment were siblings; animals between experiments were of different parentage and represented F_1 to F_4 generations. Experiments 1-4 were performed under varying conditions of temperature and humidity in a laboratory; Experiments 5-6 were conducted in an insectary under more controlled conditions of temperature (67°-73° F) and relative humidity (61-65%).

General Biology

Data on courtship, mating, oviposition, hatching, growth of instars, molting (number of instars, molting time) and nymphal mortality for Gryllus integer are discussed.

Permanently Paired Males

From observations of permanently paired integer males several points were evident.

1. Sexual/Aggressive ambivalent behavior occurred frequently:

   (a). An aggressive encounter involving antennal fencing, jerking, and aggressive calling was often terminated when one male turned away and commenced courtship calling.

(b). A male approaching a courting male from behind, prior to
mounting, frequently did so in a distinctly aggressive manner,
usually with jerking and rarely with open mandibles.

(c). While mounted, the male on top, temporarily assuming the
female role, continued to lash antennae with the male below,
and often stridulated aggressively.

(d). Dismounting males jerked, called aggressively, or opened
mandibles, often remounting the other male and repeating the
process up to 3-4 times in quick succession.

2. As was true for experimental males given short periodic exposures
to intruders, a dominant-subordinate relationship for paired males,
once established, tended to remain quite stable over time.

3. For some pairs, possibly involving males closely matched as
regards aggressiveness or fighting ability, dominance switches
occurred often; up to six and undoubtedly more times for any given
pair. Dominance switches sometimes followed courtship bouts, when
a previously submissive male responded to courtship behavior by the
dominant with aggressive calling and chasing.

4. Alexander's (1961: 136) statement that courtship between two
males is rarely initiated after head-on encounters unless one animal
displays the passivity characteristic of females was substantiated
by observations of courtship sequences during experimental-intruder
interactions, but less well explains the courting observed between
permanently paired males.

5. Aggression was observed as early as the second day after adult
molt. Agonistic displays also occurred, although less frequently,

among paired males in late nymphal stages.

6. Fighting during intense reciprocal encounters (Levels 4-5) between adult paired males was infrequently observed; most agonistic bouts involved interactions of Level 2-3 intensity. For some pairs aggressive behavior was not evident.

7. One-sided or mutual courtship among paired males, in contrast to fighting, was frequently observed, occurring as early as 24 hours after the final molt. For only three out of 46 pairs were no courting sequences observed. Many courtship displays terminated in mounts lasting up to 40 seconds in duration, and for 26 pairs from one to ten attempted spermatophore transfers were witnessed. In most cases, the same male was responsible for all, or nearly all, the mounting.

8. Pairs exhibiting much courtship were also characterized by more than average aggression; the data are insufficient to allow more than conjecture.

Experimental-Intruder Interactions

1. Of 3523 observed experimental-intruder interactions in all six experiments, 608 (17.5%) involved courtship sequences, and of these, 37 terminated with mounting by the courted male. Courtship calling before and after aggressive encounters was not independent of social rank and was usually expressed by the actual or eventual dominant animal (Chi-square value = 7.27; $P < 0.01$).

2. For the 3287 interactions involving encounters between experimentals and conspecific intruders, approximately 16% were Level 1, 15% were Level 2, the majority (36%) were Level 3, 15% were Level 4, and 18% were intense Level 5's involving reciprocal fighting and

mandible-locking.

3. For 176 interactions in Experiment 3 staged between G. integer experimentals and heterospecific intruders (G. alogus) aggression levels were significantly reduced.

4. For many Level 2 encounters and for most Level 3-5 encounters a clear-cut dominant-subordinate relationship was easily determined. Behavior associated with different levels of aggression and character-istic of dominants and defeated subordinates is described.

5. Of the 116 experimentals, 103 (88.8%) engaged in at least one Level 5 encounter during its grouping periods with intruders. Most Level 4-5 contests did not exceed 30 seconds; the most intense fighting bout witnessed lasted over five minutes and involved 54 mandible-lockings before dominance was determined.

6. Most mandible-lockings were brief; the longest continuous unbroken engagement of mandibles between fighting males lasted approximately 20 seconds.

7. For most experimental-intruder pairings aggression levels tended to increase during initial encounters, level off, then decrease during later interactions. Many factors were conceivably involved (e.g., aging, experiential effects, behavioral variability, etc.), and considerable variability existed regarding changing aggression levels over time.

8. Biting and wounding were rare and occurred in only eight (0.2%) of 3523 interactions; appendage loss resulting from wounding or active chasing had no observable effects on longevity.

9. Dominant-subordinate relationships were stable over time. This was least true for Experiment 1 in which experimentals were exposed

to many (7-14) different intruders, and never the same intruder for two or more successive interactions.

10. Of the 116 experimentals in all experiments, 29 (25%) exhibited completely stable social rank relations (i.e., either dominated or lost all of their aggressive encounters), and 70 (60%) showed social dominance data that closely approached complete stability or were significantly non-random; in most cases the data were highly significant (P<0.001).

Social dominance stability is explained to a small degree by size and age of combatants, although many instances were observed where males handicapped by smaller size or missing legs successfully maintained dominant status. Staging of bouts in the resident experimental's jar conferred no apparent territorial advantage and most encounters (67%) were won by intruders.

It is suggested that the main factors explaining maintenance of stable social rank were (1) differences in aggressive 'state' and general fighting ability, and (2) experiential effects associated with previous wins and losses.

11. Experimental-intruder pairings showing unstable social rank relationships over time (17, or 15%) are discussed, as are the two main explanations for social rank instability -- (1) dominance switches, especially in interactions involving encounters between equally aggressive, evenly-matched combatants, and (2) effects associated with a change in intruder male.

12. Most (90%) interactions involving a change in dominance from previous encounters were characterized by increased levels of aggression.

13. Chi-square tests demonstrated the existence of a very significant relationship ($P < 0.001$) between subordinate social rank and reduced aggressive calling, and dominant rank and increased aggressive calling following Level 3-5 aggressive encounters in all experiments. In only 25 (1.2%) of 2131 observed Level 3-5 interactions did a defeated male call aggressively after an aggressive encounter.

Longevity

Longevity data were analyzed in three ways: (1) analysis of variance of mean adult longevity, (2) analysis of variance of mean total longevity since hatching, and (3) paired t-tests of adult longevity for experimentals and their appropriate paired controls.

Consistent results occurred for all six replicate experiments conducted with adult male G. integer of different genetic backgrounds under both controlled conditions and uncontrolled temperatures and humidities at different times of the year.

In all experiments controls lived longer than experimentals or paired males; in most cases, differences were significant ($P = < 0.05$ to < 0.001). Paired males lived longer than experimentals in Experiments 2-3; the reverse was true in Experiments 4-6. Only in Experiment 3 were the differences significant ($P < 0.001$).

The total data for all 116 experimentals showed no correlation between adult longevity and (1) average level of aggression, (2) percentage of interactions in which experimental was subordinate, or (3) percentage of interactions involving Level 5 encounters. Data for 76 experimentals did, however, show a significant ($P < 0.01$) correlation between incidence of fighting and reduced longevity.

Paralysis

Paralysis, involving a sequential appearance of symptoms first affecting the hind legs and moving anteriorly, accompanied by desiccation, was associated with the reduced longevity of most experimentals (57%) and many paired males (29%). Paralyzed crickets assumed characteristic death postures with extended hind legs rigid and usually held off the substrate. Most controls (78%) exhibited loose, limp, non-desiccated bodies at death.

Incidence of paralysis or reduced longevity could not be related to social rank. A small percentage (8%) of behaviorally isolated controls exhibited paralytic symptoms at death, and it is suggested that the phenomenon represents a generalized stress response, of which social stress resulting from agonistic encounters and fighting is only a single aspect.

Paralysis is discussed, and the corpora cardiaca are implicated. It is suggested that increasing numbers of social encounters between adult male field crickets in natural populations could influence population dynamics by (1) inducing emigration and dispersal of subordinate males, or (2) increasing mortality rates via a social stress mechanism involving paralysis.

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APPENDIX

I

Tables

Table 11. Data on aggression for paired male G. integer in Experiments 2 to 6, including level of first observed aggressive encounter involving open mandibles, chasing, or aggressive calling, and the adult age (in days) of the aggressor or (if a Level 4 or 5) the youngest combatant. Also included are the number of aggressive encounters (Levels 3-5) observed during the entire experiment, and data on dominance stability (i.e., no. of runs observed) and adult longevity (in days).

No. Pair	1st Obs. Aggression		Level of Encounter			No. Runs	Longevity	
	Level	Age	3	4	5			

Experiment 2

No. Pair	Level	Age	3	4	5	No. Runs	Longevity	
83-84	2	17	0	0	0	1	83	91
85-86	3	11	3	0	1	2	82	70
87-88	3	14	9	0	0	3	114	73
89-90	2	9	2	0	0	3	62	101
93-94	3	17	2	0	0	1	88	85
95-96	2	9	0	0	0	1	91	72
97-98	2	8	2	2	4	2	61	96
99-100	2	8	1	0	0	2	74	64
101-102	3	8	17	0	1	5	62	61
106-107	2	12	1	0	1	1	50	51
111-112	2	7	4	10	1	1?	82	65
140-141	2	3	2	0	0	2	91	89
145-146	2	2	1	0	0	1	58	48
147-148	2	2	2	0	0	2	83	66
151-152	2	14	4	0	0	3	81	69

Experiment 3

No. Pair	Level	Age	3	4	5	No. Runs	Longevity	
248-249	3	24	4	1	0	1	86	95
250-251	3	38	2	0	0	1	104	69
252-253	2	24	0	3	0	1?	61	88
254-255	2	20	2	2	0	2	103	84
256-257	2	17	2	0	0	3	126	89
258-259	3	17	4	1	0	1?	102	92
260-261	-	-	0	0	0	-	108	84
262-263	-	-	0	0	0	-	88	110
264-265	2	17	0	1	0	1?	98	101
266-267	2	15	10	5	0	3	85	82
268-269	3	14	3	1	0	5	95	86
270-271	2	5	5	2	0	5	92	116

Table 11. (Continued)

No. Pair	1st Obs. Aggression		Level of Encounter			No. Runs	Longevity	
	Level	Age	3	4	5			
272-273	4	19	7	2	0	3	119	114
274-275	2	3	8	1	0	2	79	121
276-277	2	4	11	2	1	4	133	95
278-279	4	24	0	2	0	1?	125	101
384-385	2	43	0	0	0	1	110	97

Experiment 4

No. Pair	1st Obs. Aggression		Level of Encounter			No. Runs	Longevity	
473-476	3	4	1	0	0	1	47	76
481-483	2	10	0	0	0	1	71	79
487-488	3	27	1	0	0	1?	62	50
486-489	2	10	0	1	0	1?	58	57
493-494	-	-	0	0	0	-	49	48
557-558	2	20	0	0	0	1?	52	70

Experiment 5

No. Pair	1st Obs. Aggression		Level of Encounter			No. Runs	Longevity	
515-516	3	10	27	1	1	7	74	75
519-520	2	4	15	1	0	5	70	68
525-526	2	4	9	0	0	5	72	63
531-532	3	10	15	1	0	6	68	76

Experiment 6

No. Pair	1st Obs. Aggression		Level of Encounter			No. Runs	Longevity	
535-536	2	23	0	0	0	?	60	57
543-544	2	6	2	0	0	1	75	100
547-548	-	-	0	0	0	-	88	96
553-554	5	15	0	0	1	?	89	81

Table 12. Courtship data for paired male G. integer in Experiments
2 to 6, including adult age (in days) of male first ob-
served courting, total number of courtship encounters, and
number of courtship encounters terminating in mounting,
attempted spermatophore transfer (AST), or involving
mutual courtship calling (CoCa) back to back.

No. Pair	1st Obs. Courtship	Courtship Encounters			
		Total	No. Mountings	AST	Mutual CoCa
Experiment 2					
83-84	17	6	3	1	0
85-86	11	10	3	2	0
87-88	9	13	8	6	0
89-90	15	3	0	0	0
93-94	10	13	8	5	2
95-96	16	9	7	3	1
97-98	17	4	3	3	0
99-100	9	3	0	0	1
101-102	13	8	2	1	0
106-107	12	5	5	1	0
111-112	6	18	20	10	2
140-141	53	2	2	1	0
145-146	1	5	2	1	0
147-148	4	5	2	0	0
151-152	3	4	0	0	0
Experiment 3					
248-249	26	2	2	2	0
250-251	-	-	-	-	-
252-253	22	4	4	4	1
254-255	20	6	2	1	3
256-257	22	5	4	2	1
258-259	-	-	-	-	-
260-261	76	2	1	1	0
262-263	22	1	1	1	0
264-265	69	3	0	0	0
266-267	15	5	2	1	2
268-269	21	4	2	0	0
270-271	42	11	5	4	2

Table 12. (Continued)

No. Pair	1st Obs. Courtship	Courtship Encounters			
		Total	No. Mountings	AST	Mutual CoCa
272-273	31	4	2	2	0
274-275	42	2	1	1	0
276-277	70	6	2	2	0
278-279	25	8	1	1	0
384-385	65	1	0	0	0

Experiment 4

No. Pair	1st Obs. Courtship	Total	No. Mountings	AST	Mutual CoCa
473-476	14	6	1	0	0
481-483	56	8	2	1	0
487-488	9	2	0	0	0
486-489	21	5	0	0	0
493-494	42	1	0	0	0
557-558	19	7	0	0	0

Experiment 5

No. Pair	1st Obs. Courtship	Total	No. Mountings	AST	Mutual CoCa
515-516	13	3	0	0	0
519-520	22	5	1	0	0
525-526	10	11	1	0	0
531-532	13	10	3	3	0

Experiment 6

No. Pair	1st Obs. Courtship	Total	No. Mountings	AST	Mutual CoCa
535-536	35	5	1	1	0
543-544	27	5	1	0	0
547-548	27	2	0	0	0
553-554	-	-	-	-	-

Table 16. Incidence of encounters involving courtship calling (CoCa) during experimental-intruder interactions for experimental G. integer in all experiments, including incidence of courting by dominant (Dom.) and subordinate (Sub.) males before and after aggressive encounters in Level 3-5 interactions.

No. Exptl.	No. Inter-actions	No. with CoCa		Level 3-5 Interactions			
		Total	Levels 3-5	CoCa Before Dom.	Sub.	CoCa After Dom.	Sub.
Experiment 1							
43	22	3	2	2	0	2	0
44	18	0	0	-	-	-	-
45	25	1	1	1	0	0	0
48	30	2	1	1	0	0	0
50	15	3	1	1	0	0	0
52	29	5	3	3	0	0	0
54	41	6	3	0	0	3	0
56	19	0	0	-	-	-	-
	199	20	11	8	0	5	0
Experiment 2							
64	24	4	3	1	0	3	0
74	18	1	0	-	-	-	-
76	19	2	1	0	0	1	0
113	17	1	1	0	0	0	1
114	20	6	4	2	2	0	0
115	34	1	1	0	0	1	0
121	23	2	2	0	0	1	0
128	33	3	3	1	1	0	1
129	33	1	1	0	0	1	0
133	28	10	8	6	2	0	2
139	41	2	2	2	0	0	0
142	32	10	8	6	1	1	0
144	25	3	2	0	0	2	0
149	23	4	3	2	3	0	0
154	27	4	2	2	0	1	0
156	29	10	9	4	0	6	0
158	36	6	5	4	1	1	0
163	21	3	2	0	2	0	0
	483	73	57	30	12	18	4

Table 16. (Continued)

No. Exptl.	No. Inter-actions	No. with CoCa		Level 3-5 Interactions			
		Total	Levels 3-5	CoCa Before Dom.	Sub.	CoCa After Dom.	Sub.

Experiment 3

No. Exptl.	No. Inter-actions	Total	Levels 3-5	Dom.	Sub.	Dom.	Sub.
165	16	5	4	1	2	2	1
167	16	4	4	0	1	2	2
170	22	1	1	0	1	0	0
171	21	11	8	3	0	6	0
174	10	2	2	2	0	0	0
175	21	1	0	-	-	-	-
176	23	1	0	-	-	-	-
179	27	4	4	2	0	3	0
180	21	1	0	-	-	-	-
183	8	0	0	-	-	-	-
185	13	0	0	-	-	-	-
186	26	3	3	2	0	1	0
188	15	1	1	0	0	1	0
191	26	1	1	1	0	0	0
192	24	4	4	1	1	1	0
194	20	9	5	2	1	3	1
199	31	4	4	0	4	0	0
201	27	1	1	0	1	0	0
202	20	12	5	1	0	1	3
204	33	2	0	-	-	-	-
205	17	0	0	-	-	-	-
207	28	11	11	6	0	5	1
209	19	2	1	0	1	0	0
211	25	0	0	-	-	-	-
214	23	0	0	-	-	-	-
216	19	0	0	-	-	-	-
217	28	0	0	-	-	-	-
220	49	1	1	0	0	0	1
221	38	2	2	0	1	1	0
224	24	5	5	2	0	3	1
226	32	2	1	0	0	1	0
228	27	1	0	-	-	-	-
231	20	1	0	-	-	-	-
232	37	6	4	1	1	0	2
233	44	7	6	2	0	4	1
235	43	3	1	1	1	0	0
238	41	5	3	1	2	1	0
239	52	10	9	1	2	5	3
241	36	4	2	0	0	1	1
244	52	1	1	1	0	0	0
246	18	6	2	0	0	1	1

Table 16. (Continued)

No. Exptl.	No. Inter- actions	No. with CoCa		Level 3-5 Interactions			
		Total	Levels 3-5	CoCa Before Dom.	Sub.	CoCa After Dom.	Sub.
322	43	3	2	0	0	1	1
324	37	4	2	1	0	0	0
326	22	1	0	-	-	-	-
328	28	4	2	0	1	0	1
387	27	3	3	0	1	2	0
389	38	4	2	2	0	0	0
395	16	2	0	-	-	-	-
397	28	1	1	0	1	0	0
400	26	7	5	5	1	1	0
401	21	4	3	2	0	2	0
404	31	0	0	-	-	-	-
405	24	3	2	1	1	2	0
408	41	12	5	2	0	4	0
409	30	1	0	-	-	-	-
412	45	9	4	2	1	0	1
413	57	11	2	2	0	0	0
416	32	3	3	1	1	0	0
417	41	10	7	3	1	4	0
443	41	8	0	-	-	-	-
445	35	5	3	1	0	2	0
	1755	229	142	52	27	60	21

Experiment 4

No. Exptl.	No. Inter- actions	Total	Levels 3-5	CoCa Before Dom.	Sub.	CoCa After Dom.	Sub.
453	55	14	4	4	0	1	0
454	33	10	5	2	1	2	0
469	30	10	4	3	1	2	0
470	41	6	4	2	0	2	0
472	40	11	8	1	4	4	1
474	32	12	9	3	5	2	1
480	43	13	9	4	1	3	1
490	27	5	3	1	0	2	0
498	3	1	1	1	0	0	0
500	35	12	4	3	1	0	0
503	27	4	1	0	1	0	0
504	13	2	2	0	0	2	0
505	48	15	13	4	5	5	0
	427	115	67	28	19	25	3

Table 16. (Continued)

No. Exptl.	No. Inter- actions	No. with CoCa		Level 3-5 Interactions			
		Total	Levels 3-5	CoCa Before Dom.	Sub.	CoCa After Dom.	Sub.
			Experiments 5 & 6				
508	23	17	10	6	2	5	2
510	50	10	8	3	2	4	0
511	48	1	1	1	0	0	0
514	34	7	2	0	1	1	0
518	34	16	13	4	1	8	0
522	41	9	5	3	0	3	0
524	40	18	1	0	1	0	0
528	46	23	13	9	3	4	0
529	33	7	3	2	0	2	0
533	48	29	22	9	5	10	1
537	52	8	5	3	0	2	0
539	49	5	5	3	1	0	1
541	45	8	7	3	0	4	0
545	29	7	5	1	3	1	1
549	44	5	5	4	0	0	1
551	43	1	1	1	0	0	0
	659	171	106	52	19	44	6
Total	3523	608	383	170	77	152	34
Total Percent		17.3		44.4	20.1	39.7	8.9

Table 23. Data on aggression for experimental male G. __integer__ in Experiments 1-6, including age (in days) at first exposure to intruder (F.E.I.), aggression level for all interactions, and average level of aggression (A.L.A.) for all interactions. Also included are the number of interactions constituting a change in the previous dominant-subordinate relationship (I.C.C.) and the average level of aggression (A.L.A.) exhibited during these interactions.

No. Exptl.	F.E.I.	No. Inter- actions	Level of Encounter						A.L.A.	I.C.C.	
			0	1	2	3	4	5		No.	A.L.A.
Experiment 1											
43	31	22	0	3	3	11	2	3	2.95	Varied Intruders	
44	39	18	0	0	0	8	4	6	3.89		
45	32	25	0	0	1	13	6	5	3.60	"	"
48	38	30	2	1	3	10	11	3	3.20		
50	21	15	0	4	2	1	5	3	3.07	"	"
52	18	29	0	4	2	7	8	8	3.48		
54	8	41	2	11	2	11	5	10	2.88	"	"
56	52	19	0	2	1	4	9	3	3.53		
		199	4	25	14	65	50	41	3.28		
Experiment 2											
64	42	24	2	5	7	5	0	5	2.46	0	–
74	33	18	4	3	6	3	0	2	1.89	0	–
76	32	19	1	12	1	3	1	1	1.68	0	–
113	24	17	0	6	1	6	2	2	2.59	0	–
114	24	20	1	2	4	11	1	1	2.60	1	3.00
115	24	34	4	1	1	21	4	3	2.85	8	3.28
121	23	23	2	4	6	5	3	3	2.52	1	4.00
128	22	33	2	2	1	5	7	16	3.85	1	5.00
129	22	33	0	2	4	10	7	10	3.58	7	4.29

Table 23. (Continued)

No. Exptl.	F.E.I.	No. Inter-actions	Level of Encounter						A.L.A.	I.C.C. No.	I.C.C. A.L.A.
			0	1	2	3	4	5			
133	21	28	2	8	2	5	6	5	2.71	2	3.50
139	20	41	0	0	4	20	11	6	3.46	4	4.25
142	18	32	1	7	2	18	4	0	2.53	3	2.67
144	17	25	0	2	1	10	5	7	3.56	4	4.50
149	16	23	3	6	5	3	2	4	2.30	0	-
154	11	27	3	5	4	5	3	7	2.74	2	5.00
156	9	29	0	1	2	8	8	10	3.83	6	3.33
158	8	36	7	8	1	12	5	3	2.25	1	3.00
163	1	21	4	4	2	3	1	7	2.67	5	3.80
		483	36	78	54	153	70	92	2.87		

Experiment 3

No. Exptl.	F.E.I.	No. Inter-actions	Level of Encounter						A.L.A.	I.C.C. No.	I.C.C. A.L.A.
			0	1	2	3	4	5			
165	39	16	0	1	2	4	2	7	3.75	4	4.25
167	39	16	0	0	0	6	3	7	4.06	3	4.33
170	34	22	0	4	3	11	3	1	2.73	0	-
171	35	21	0	4	2	11	1	3	2.86	2	4.00
174	33	10	0	0	0	6	0	4	3.80	2	4.00
175	33	21	0	13	6	2	0	0	1.48	0	-
176	32	23	0	2	0	14	6	1	3.17	1	5.00
179	28	27	0	1	1	7	11	7	3.81	9	4.11
180	32	21	1	5	4	9	2	0	2.29	1	3.00
183	31	8	1	1	0	1	2	3	3.38	3	5.00
185	32	13	0	1	1	7	2	2	3.23	0	-
186	30	26	0	1	1	16	3	5	3.38	1	5.00
188	28	15	0	0	2	5	0	8	3.93	0	-
191	28	26	0	3	0	16	5	2	3.12	0	-
192	29	24	0	2	1	15	2	4	3.21	1	3.00
194	28	20	1	2	2	11	2	2	2.85	1	3.00

Table 23. (Continued)

No. Exptl.	F.E.I.	No. Inter-actions	Level of Encounter						A.L.A.	I.C.C.	
			0	1	2	3	4	5		No.	A.L.A.
199	29	31	0	1	5	20	4	1	2.97	6	3.33
201	28	27	4	6	5	4	6	2	2.30	3	4.00
202	27	20	0	10	1	8	1	0	2.00	0	-
204	26	33	1	20	1	4	5	2	1.94	0	-
205	28	17	0	1	1	4	4	7	3.88	0	-
207	25	28	0	1	2	1	4	20	4.43	11	4.73
209	23	19	0	1	1	15	1	1	3.00	1	4.00
211	21	25	0	12	8	4	1	0	1.76	0	-
214	21	23	0	0	0	10	4	9	3.96	1	5.00
216	20	19	0	4	0	2	6	7	3.63	1	5.00
217	21	28	0	2	0	17	6	3	3.29	0	-
220	19	49	0	7	6	21	10	5	3.00	4	3.25
221	21	38	0	1	1	26	7	3	3.26	0	-
224	34	24	1	10	1	1	1	10	2.88	4	4.75
226	21	32	1	8	4	6	7	6	2.88	5	3.80
228	16	27	2	5	3	6	6	5	2.89	1	2.00
231	8	20	1	15	3	1	0	0	1.20	0	-
232	7	37	0	19	6	9	0	3	1.97	1	5.00
233	15	44	1	18	4	13	1	7	2.36	7	3.57
235	7	43	0	11	2	18	6	6	2.86	0	-
238	9	41	0	28	3	2	1	7	1.93	3	5.00
239	3	52	1	5	2	12	17	15	3.62	3	4.67
241	7	36	0	5	5	18	2	6	2.97	2	3.00
244	5	52	0	22	12	9	7	2	2.13	2	3.50
246	16	18	0	6	4	4	3	1	2.39	4	3.25
322	9	43	4	7	4	17	4	7	2.72	1	3.00
324	8	37	0	11	6	8	8	4	2.68	1	3.00
326	21	22	0	2	2	12	1	5	3.23	1	5.00
328	23	28	0	5	0	17	3	3	2.96	0	-
387	12	27	0	0	3	15	0	9	3.56	1	5.00

Table 23. (Continued)

No. Exptl.	F.E.I.	No. Inter-actions	Level of Encounter						A.L.A.	I.C.C.	
			0	1	2	3	4	5		No.	A.L.A.
389	15	38	1	4	9	16	5	3	2.76	2	3.00
395	4	16	0	8	5	3	0	0	1.69	0	-
397	47	28	0	5	3	16	3	1	2.71	0	-
+ 400	36	26	0	1	3	11	8	3	3.46	0	-
+ 401	33	21	0	1	1	6	5	8	3.86	2	4.00
+ 404	28	31	0	2	7	12	5	5	3.13	1	4.00
+ 405	26	24	0	7	4	2	3	8	3.04	3	5.00
+ 408	26	41	0	4	15	10	6	6	2.88	2	2.50
+ 409	18	30	0	7	11	8	4	0	2.30	3	3.33
+ 412	14	45	0	6	16	4	12	7	2.96	3	4.00
+ 413	15	57	0	27	16	8	4	2	1.91	0	-
+ 416	5	32	0	0	1	15	5	11	3.81	3	4.67
+ 417	13	41	0	21	5	0	3	12	2.51	3	5.00
+ 443	3	41	0	18	15	6	0	2	1.85	3	4.00
+ 445	1	35	0	3	15	12	2	3	2.63	10	3.33
		1755	20	397	246	574	235	283	2.83		

+ reared under crowded conditions in a cool room (66-72°F)

Experiment 4

453	21	55	0	18	16	15	4	2	2.20	0	-
454	22	33	0	7	1	9	2	14	3.45	9	4.67 *
469	2	30	0	17	4	8	0	1	1.80	2	3.00 *
470	7	41	0	5	8	18	4	6	2.95	4	4.25 *
472	6	40	0	6	9	21	1	3	2.65	3	3.00
474	11	32	0	4	6	16	3	3	2.84	4	3.50
480	7	43	0	4	5	20	4	10	3.26	3	4.67 *
490	12	27	0	3	4	10	2	8	3.30	3	4.33

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Table 23. (Continued)

No. Exptl.	F.E.I.	No. Inter-actions	Level of Encounter						A.L.A.	I.C.C.	
			0	1	2	3	4	5		No.	A.L.A.
498	8	3	0	0	1	2	0	0	2.67	0	-
500	10	35	0	9	6	5	4	11	3.06	4	3.50
503	5	27	0	6	13	7	1	0	2.11	0	-
504	6	13	0	1	7	5	0	0	2.31	0	-
505	1	48	0	5	8	18	3	14	3.27	4	4.50 *
		427	0	85	88	154	28	72	2.80		

Experiments 5 & 6

No. Exptl.	F.E.I.	No. Inter-actions	0	1	2	3	4	5	A.L.A.	No.	A.L.A.
508	2	23	0	3	5	12	1	2	2.74	2	3.00
510	1	50	0	8	3	30	2	7	2.94	4	3.75
511	6	48	0	0	2	22	6	18	3.83	9	3.78
514	1	34	1	2	10	15	6	0	2.68	3	3.33
518	5	34	0	0	3	19	5	7	3.47	9	3.67
522	3	41	1	4	13	23	0	0	2.41	3	2.33
524	1	40	0	17	14	5	2	2	1.95	1	2.00
528	1	46	0	6	12	16	9	3	2.80	1	5.00
529	10	33	0	2	4	18	7	2	3.09	1	4.00
533	3	48	0	6	8	14	6	14	3.29	3	4.67 *
537	1	52	0	2	8	18	8	16	3.54	4	4.00
539	2	49	0	6	8	17	16	2	3.00	3	2.67
541	4	45	0	1	10	20	12	2	3.09	0	-
545	3	29	0	2	5	8	5	9	3.48	3	5.00 *
549	2	44	0	0	4	26	8	6	3.36	1	3.00
551	1	43	2	6	12	7	9	7	2.84	6	3.67
		659	4	65	121	270	102	97	3.05		

* Significant P< 0.05   Mann-Whitney U test (one-tailed)

Table 25. Aggression data for experimental male G. integer in Experiments 1-6, including average level of aggression (A.L.A.), number of interactions involving Level 5 aggressive encounters, intensity (maximum and average) of Level 5 encounters (no. of IM's/duration of face-off in seconds), incidence of dominance by resident experimental (E) and by intruder (I), number of interactions during which the experimental was actively chased (A.C.) by the intruder, and adult longevity (in days) for the experimental and its appropriate control.

No. Exptl.	A.L.A.	Level 5 Interactions			Dominance			A.C.	Longevity	
		No.	Max.	Ave.	E	?	I		Exptl.	Control

Experiment 1

43	2.95	3	5/90	4.3/55	7	6	9	2	77	115
44	3.89	6	9/60	2.7/37	12	2	4	0	80 +	50
45	3.60	5	4/45	2.0/66	19	2	4	1	84	109
48	3.20	3	1/65	1.0/42	16	4	10	2	97	123
50	3.07	3	1/5	1.0/5	10	5	0	0	56	96
52	3.48	8	10/60	3.4/56	9	7	13	0	74 +	95
54	2.88	10	3/10	1.3/32	18	16	7	2	77	93
56	3.53	3	10/210	4.3/83	13	3	3	0	97	123

Experiment 2

64	2.46	5	3/15	1.6/23	0	8	16	0	88 +	104
74	1.89	2	2/30	1.5/18	0	12	6	2	68 +	80
76	1.68	1	1/6	1.0/6	0	13	6	3	69	71
113	2.59	2	1/8	1.0/8	0	6	11	0	57	84
114	2.60	1	2/13	2.0/13	1	5	14	4	64	80
115	2.85	3	1/45	1.0/22	8	6	20	11	94	85
121	2.52	3	2/35	1.7/41	1	8	14	4	69	92
128	3.85	16	17/229	5.2/60	3	4	26	8	87	72

Table 25. (Continued)

No. Exptl.	A.L.A.	Level 5 Interactions			Dominance			A.C.	Longevity	
		No.	Max.	Ave.	E	?	I		Exptl.	Control
129	3.58	10	14/80	5.2/86	8	3	22	8	89	101
133	2.71	5	5/100	2.0/53	1	10	17	0	75 +	62
139	3.46	6	4/40	1.8/40	13	1	27	1	102	65
142	2.53	0	-	-	5	8	19	10	86	82
144	3.56	7	2/26	1.1/14	2	2	21	7	65 +	57
149	2.30	4	3/48	1.5/39	0	9	14	1	61	66
154	2.74	7	4/46	2.3/19	8	8	11	0	64 +	125
156	3.83	10	3/35	1.3/19	3	3	23	3	66	115
158	2.25	3	3/60	2.3/31	1	15	20	3	80	156
163	2.67	7	7/270	2.8/87	6	8	7	0	40 +	93

Experiment 3

No. Exptl.	A.L.A.	No.	Max.	Ave.	E	?	I	A.C.	Exptl.	Control
165	3.75	7	8/130	3.3/33	10	2	4	1	71	104
167	4.06	7	7/34	3.6/24	13	0	3	0	70 +	119
170	2.73	1	6/20	6.0/20	18	4	0	0	78 +	87
171	2.86	3	4/53	3.0/27	4	4	13	3	74	93
174	3.80	4	6/47	4.0/20	9	0	1	1	53	107 +
175	1.48	0	-	-	7	14	0	0	72	86
176	3.17	1	6/30	6.0/30	7	2	14	6	79 +	127
179	3.81	7	6/20	2.9/11	10	2	15	8	81	147
180	2.29	0	-	-	3	6	12	8	73 +	71
183	3.38	3	1/10	1.0/9	2	2	4	4	47	99
185	3.23	2	2/6	1.5/9	0	1	12	6	57 +	91
186	3.38	5	5/25	2.0/12	1	2	23	5	81 +	85
188	3.93	8	6/25	2.5/15	0	0	15	8	58 +	133
191	3.12	2	1/12	1.0/10	0	3	23	15	80	125
192	3.21	4	2/14	1.5/13	2	3	19	13	77	44

Table 25. (Continued)

No. Exptl.	A.L.A.	Level 5 Interactions			Dominance			A.C.	Longevity	
		No.	Max.	Ave.	E	?	I		Exptl.	Control
194	2.85	2	7/31	4.5/35	1	3	16	7	66 +	71
199	2.97	1	1/8	1.0/8	26	1	4	0	92 +	88
201	2.30	2	2/22	1.5/50	2	12	13	1	80	115
202	2.00	0	-	-	0	10	10	1	66 +	85
204	1.94	2	1/17	1.0/16	0	21	12	4	91	61
205	3.88	7	5/15	2.0/11	0	1	16	5	59 +	99
207	4.43	20	13/55	3.5/27	13	4	11	9	79 +	113
209	3.00	1	1/8	1.0/8	2	1	16	4	59 +	127
211	1.76	0	-	-	0	12	13	0	71	108
214	3.96	9	1/80	1.0/21	2	0	21	15	68	102 +
216	3.63	7	2/15	1.3/20	1	5	13	11	58	113
217	3.29	3	2/23	1.3/17	0	2	26	14	78 +	128 +
220	3.00	5	5/50	2.4/31	3	7	39	13	120 +	77
221	3.26	3	2/8	1.3/8	0	1	37	22	96 +	114
224	2.88	10	11/80	3.0/23	7	12	5	0	67 +	52
226	2.88	6	2/30	1.5/24	16	10	6	0	84 +	133
228	2.89	5	2/35	1.2/18	1	9	17	0	72	156
231	1.20	0	-	-	4	16	0	0	46	124
232	1.97	3	1/16	1.0/10	12	19	6	0	81	91
233	2.36	7	4/28	1.6/34	18	20	6	0	102 +	108
235	2.86	6	3/32	1.5/17	0	12	31	8	93 +	129
238	1.93	7	4/54	2.0/44	3	28	10	6	90 +	139
239	3.62	15	18/131	3.6/41	15	7	30	16	109	116
241	2.97	6	5/31	1.7/18	2	6	28	9	78 +	131
244	2.13	2	1/37	1.0/24	23	25	4	0	110 +	118
246	2.39	1	2/30	2.0/30	4	8	6	0	51	106
322	2.72	7	4/45	2.3/23	24	12	7	5	97	194
324	2.68	4	5/26	3.2/30	12	3	22	6	80 +	144
326	3.23	5	2/40	1.4/18	18	2	2	0	63 +	146
328	2.96	3	2/16	1.3/9	0	7	21	7	79	106

Table 25. (Continued)

No. Exptl.	A.L.A.	Level 5 Interactions			Dominance			A.C.	Longevity	
		No.	Max.	Ave.	E	?	I		Exptl.	Control
387	3.56	9	11/46	2.8/18	23	0	4	0	64 +	156
389	2.76	3	1/22	1.0/16	3	8	27	0	95 +	92
395	1.69	0	-	-	0	8	8	1	35	99
397	2.71	1	1/12	1.0/12	0	5	23	7	102 +	114
400	3.46	3	2/22	1.3/13	25	1	0	0	88 +	91
401	3.86	8	7/68	3.9/46	9	1	11	7	74 +	141
404	3.13	5	3/17	1.6/28	4	2	25	3	96	82
405	3.04	8	6/56	2.4/30	5	8	11	2	75	84
408	2.88	6	3/10	1.5/10	1	4	36	4	107	148
409	2.30	0	-	-	2	7	21	2	83	103
412	2.96	7	8/87	3.3/49	27	7	11	1	105	85
*413	1.91	2	2/41	1.5/23	0	28	29	0	127	113
*416	3.81	11	7/138	2.7/51	13	2	17	9	69	109
*417	2.51	12	8/147	2.0/50	5	24	12	1	95 +	196
*443	1.85	2	1/32	1.0/22	4	18	19	0	83	105
*445	2.63	3	3/30	1.7/27	7	6	22	0	70	83

* Showed very retarded development. #413-#417 were approx. 110 days old, #443 was 197 days old, and #445 was 208 days old at time of adult molt. Comparable data for their controls.

Experiment 4

453	2.20	2	3/50	2.0/53	0	19	36	12	126	87 +
454	3.45	14	9/84	5.7/45	10	7	16	9	86 +	124
469	1.80	1	1/5	1.0/5	3	17	10	0	59 +	37
470	2.95	6	10/50	3.0/27	5	5	31	6	88 +	132
472	2.65	3	6/72	3.0/30	11	7	22	8	81 +	120
474	2.84	3	2/18	1.3/18	10	6	16	10	73	54

Table 25. (Continued)

No. Exptl.	A.L.A.	Level 5 Interactions			Dominance			A.C.	Longevity	
		No.	Max.	Ave.	E	?	I		Exptl.	Control
480	3.26	10	3/30	1.5/15	13	8	22	5	90 +	113
490	3.30	8	3/10	1.2/18	2	3	22	11	63	137
498	2.67	0	-	-	0	0	3	1	14	120
500	3.06	11	6/55	2.0/28	2	9	24	4	76 +	41
503	2.11	0	-	-	0	9	18	1	56 +	88
504	2.31	0	-	-	0	1	12	1	30	74
505	3.27	14	14/62	3.2/38	3	6	39	8	91 +	75

Experiments 5 & 6

No. Exptl.	A.L.A.	Level 5 Interactions			Dominance			A.C.	Longevity	
		No.	Max.	Ave.	E	?	I		Exptl.	Control
508	2.74	2	2/23	1.5/21	13	3	7	6	47 +	104
510	2.94	7	2/20	1.4/15	36	8	6	2	100 +	132
511	3.83	18	22/70	5.6/42	41	0	7	3	102 +	124 +
514	2.68	0	-	-	16	0	15	11	66 +	155
518	3.47	7	1/15	1.0/9	23	0	11	6	73 +	77
522	2.41	0	-	-	34	5	2	1	84	76 +
524	1.95	2	4/35	3.5/38	13	21	6	4	78 +	95
528	2.80	3	3/30	1.7/19	24	6	16	6	91 +	79
529	3.09	2	1/40	1.0/30	2	3	28	19	74 +	185
533	3.29	14	21/500+	5.0/80+	8	6	34	19	96 +	125
537	3.54	16	5/30	1.5/24	6	2	44	13	111	71
539	3.00	2	1/11	1.0/8	9	8	32	12	97 +	116
541	3.09	2	3/420+	2.0/240+	0	1	44	18	98	124
545	3.48	9	54/300	13.8/103	9	5	15	7	60 +	125
549	3.36	6	9/78	3.0/52	15	0	29	15	92	111
551	2.84	7	3/25	1.6/75	3	8	32	8	85 +	113 +

+ definite paralysis at death

Table 28. Analysis of stability of the dominant-subordinate rela-
tionship for the total number of interactions experienced
by each experimental (E) male $\underline{G}$. integer exposed to intru-
der(s) (I) in Experiments 1 to 6.

No. Exptl.	Inter- actions	No. Intruders	No. Runs	Dominance E	Dominance I	Significance of Difference
			Experiment 1			
43	22	Varied	10	7	12	
44	18		4	14	4	
45	25	"	3	20	5	**
48	30		9	16	14	*
50	15	"	1	14	0	Stable
52	29		6	12	17	**
54	41	"	12	31	10	
56	19		3	13	5	**
			Experiment 2			
64	24	3	1	0	24	Stable
74	18	4	1	0	18	Stable
76	19	4	1	0	19	Stable
113	17	3	1	0	17	Stable
114	20	2	2	2	18	*
115	34	2	9	8	26	*
121	23	1	2	1	16	Nearly Stable
128	33	1	2	7	26	**
129	33	2	8	8	24	*
133	28	1	3	2	25	**
139	41	2	5	14	27	***
142	32	1	4	5	23	**
144	25	2	5	2	23	
149	23	2	1	0	17	Stable
154	27	4	3	9	18	**
156	29	3	7	3	26	
158	36	4	2	2	34	***
163	21	2	6	8	9	

Table 28. (Continued)

No. Exptl.	Inter-actions	No. Intruders	No. Runs	Dominance E	I	Significance of Difference
				Experiment 3		
165	16	2	5	12	4	
167	16	1	4	13	3	
170	22	1	1	22	0	Stable
171	21	1	3	6	14	**
174	10	1	3	9	2	
175	21	2	1	21	0	Stable
176	23	2	2	7	16	**
179	27	2	10	11	16	
180	21	3	2	6	15	**
183	8	2	4	2	6	
185	13	1	1	0	13	Stable
186	26	2	2	2	24	***
188	15	2	1	0	15	Stable
191	26	2	1	0	26	Stable
192	24	1	2	2	19	*
194	20	2	2	1	19	Nearly Stable
199	31	2	9	27	4	
201	27	3	4	4	23	**
202	20	1	1	0	20	Stable
204	33	1	1	0	33	Stable
205	17	1	1	0	17	Stable
207	28	4	12	17	11	
209	19	2	2	2	17	*
211	25	2	1	0	25	Stable
214	23	1	2	2	21	*
216	19	2	2	1	18	Nearly Stable
217	28	1	1	0	28	Stable
220	49	4	5	5	44	***
221	38	2	1	0	38	Stable
224	24	2	5	9	12	**
226	32	1	6	25	7	**
228	27	1	2	1	26	Nearly Stable
231	20	1	1	14	0	Stable
232	37	3	2	15	20	**
233	44	3	8	33	8	**
235	43	3	1	0	39	Stable
238	41	3	4	5	36	***
239	52	4	4	16	31	***
241	36	3	3	2	34	**
244	52	3	3	38	6	**

Table 28. (Continued)

No. Exptl.	No. Inter-actions	No. Intruders	No. Runs	Dominance		Significance of Difference
				E	I	
246	18	4	5	8	10	*
322	43	4	2	27	7	***
324	37	3	2	12	25	***
326	22	2	2	19	2	*
328	28	4	1	0	28	Stable
387	27	2	2	23	4	**
389	38	2	3	3	35	***
395	16	3	1	0	16	Stable
397	28	3	1	0	28	Stable
400	26	2	1	26	0	Stable
401	21	2	3	9	12	**
404	31	3	2	6	25	***
405	24	5	4	9	15	**
408	41	1	3	1	40	Nearly Stable
409	30	4	4	2	27	
412	45	3	4	31	14	***
413	57	5	1	0	52	Stable
416	32	3	4	13	18	***
417	41	6	5	18	20	***
443	41	4	4	6	25	***
445	35	3	11	7	28	

Experiment 4

No. Exptl.	No. Inter-actions	No. Intruders	No. Runs	Dominance		Significance of Difference
				E	I	
453	55	4	1	0	55	Stable
454	33	4	10	14	19	*
469	30	1	3	8	22	**
470	41	3	5	5	36	***
472	40	2	4	15	25	***
474	32	3	5	14	18	**
480	43	4	4	16	27	***
490	27	2	4	2	25	
498	3	1	1	0	3	Stable
500	35	5	5	6	29	***
503	27	1	1	0	25	Stable
504	13	1	1	0	13	Stable
515	48	5	5	3	45	***

Table 28. (Continued)

No. Exptl.	No. Inter- actions	No. Intruders	No. Runs	Dominance		Significance of Difference
				E	I	

<center>Experiments 5 & 6</center>

No. Exptl.	No. Inter- actions	No. Intruders	No. Runs	E	I	Significance of Difference
508	23	3	3	15	7	**
510	50	4	5	40	8	***
511	48	1	10	41	7	
514	34	3	4	18	16	**
518	34	2	10	23	11	*
522	41	3	4	36	4	***
524	40	2	2	29	10	***
528	46	1	2	29	17	***
529	33	3	2	2	31	***
533	48	4	4	11	37	***
537	52	4	5	6	46	***
539	49	3	4	12	34	***
541	45	2	1	0	45	Stable
545	29	2	4	14	15	***
549	44	2	2	15	29	***
551	43	4	7	6	37	**

Significant *P< 0.05   **P< 0.01   ***P< 0.001

Significance determined by a one-sample runs test (two-tailed), from
S. Siegel. 1956. Nonparametric Statistics for the Behavioral
Sciences, McGraw Hill Book Co., Inc., 312 p.

Table 30. Analysis of stability of the dominant-subordinate relationship for each experimental (E) male G. integer exposed to the same intruder (I) male for nine or more consecutive interactions in Experiments 2 to 6.

No. Exptl.	Inter-actions	No. of Intruder	No. Runs	Dominance E	I	Significance of Difference
				Experiment 2		
63	14 (#3-16)	Blue-4	1	0	14	Stable
76	10 (#10-19)	Black-6	1	0	10	Stable
113	11 (#5-15)	Green-5	1	0	11	Stable
114	18 (#1-18)	Blue-8	1	0	18	Stable
115	11 (#1-11)	II	1	0	11	Stable
	23 (#12-34)	Black-8	8	8	15	
121	23 (#1-23)	IV	2	1	16	Nearly Stable
128	33 (#1-33)	V	2	7	26	**
129	30 (#1-30)	VI	7	6	23	*
133	28 (#1-28)	VII	3	2	25	**
139	38 (#1-38)	VIII	5	14	24	***
142	32 (#1-32)	IX	4	5	23	**
144	23 (#3-25)	X	4	2	21	
149	21 (#3-23)	XI	1	0	17	Stable
154	18 (#3-20)	Black-3	2	6	10	**
156	25 (#3-27)	Black-4	7	3	21	
158	23 (#11-33)	Black-7	1	0	23	Stable
163	18 (#4-21)	Blue-9	6	8	9	
				Experiment 3		
165	11 (#1-11)	F3I-1	3	9	2	
167	16 (#1-16)	F3I-2	4	13	3	
170	22 (#1-22)	F3I-3	1	22	0	Stable
171	21 (#1-21)	F3I-19	3	6	14	**
174	10 (#1-10)	F3I-6	3	9	1	
175	20 (#2-21)	F3I-30	1	20	0	Stable
176	16 (#8-23)	F3I-9	1	0	16	Stable
179	20 (#8-27)	F3I-8	8	7	13	
180	11 (#7-17)	F3I-21	1	0	11	Stable
185	13 (#1-13)	F3I-31	1	0	13	Stable
186	24 (#1-24)	F3I-23	1	0	24	Stable
188	9 (#7-15)	F3I-32	1	0	9	Stable
191	20 (#7-26)	F3I-24	1	0	20	Stable
192	24 (#1-24)	F3I-33	2	2	19	*

Table 30. (Continued)

No. Exptl.	No. Inter- actions	No. of Intruder	No. Runs	Dominance E	I	Significance of Difference
194	11 (#1-11)	F3I-29	1	0	11	Stable
	9 (#12-20)	F3I-67	2	1	7	
199	26 (#6-31)	F3I-35	8	22	4	
201	20 (#8-27)	F3I-55	1	0	20	Stable
202	20 (#1-20)	F3I-36	1	0	20	Stable
204	33 (#1-33)	F3I-37	1	0	33	Stable
205	17 (#1-17)	F3I-38	1	0	17	Stable
207	13 (#11-23)	F3I-68	6	9	4	
209	17 (#1-17)	F3I-41	1	0	17	Stable
211	21 (#5-25)	F3I-53	1	0	19	Stable
214	23 (#1-23)	F3I-43	2	2	21	*
216	16 (#1-16)	F3I-44	2	1	15	Nearly Stable
217	28 (#1-28)	F3I-45	1	0	28	Stable
220	26 (#1-26)	F3I-46	2	1	25	Nearly Stable
	11 (#27-37)	F3I-8	1	0	11	Stable
	10 (#38-47)	F3I-69	2	2	8	*
221	11 (#1-11)	F3I-47	1	0	11	Stable
224	12 (#1-12)	F3I-52	2	1	8	Nearly Stable
	12 (#13-24)	F3I-70	4	8	4	
226	32 (#1-32)	F3I-50	6	25	7	**
228	27 (#1-27)	F3I-51	2	1	26	Nearly Stable
231	20 (#1-20)	F3I-10	1	14	0	Stable
232	15 (#23-37)	F3I-82	1	15	0	Stable
233	20 (#1-20)	F3I-13	2	14	3	**
	17 (#21-37)	F3I-77	3	15	2	
235	10 (#1-10)	F3I-14	1	0	10	Stable
	32 (#11-42)	F3I-42	1	0	32	Stable
238	30 (#8-37)	F3I-16	1	0	22	Stable
239	29 (#8-36)	F3I-15	3	1	28	Nearly Stable
	13 (#37-49)	F3I-50	2	12	1	Nearly Stable
241	32 (#1-32)	F3I-17	3	2	30	**
244	32 (#1-32)	F3I-18	1	24	0	Stable
	14 (#39-52)	F3I-96	1	14	0	Stable
322	21 (#23-43)	F3I-92	1	20	0	Stable
324	22 (#1-22)	F3I-6	1	0	22	Stable
	13 (#25-37)	F3I-95	2	12	1	Nearly Stable
326	19 (#4-22)	F3I-71	1	19	0	Stable
387	12 (#1-12)	F3I-32	2	8	4	**
	15 (#13-27)	F3I-74	1	15	0	Stable
389	33 (#1-33)	F3I-72	3	3	30	***
397	23 (#1-23)	F3I-19	1	0	23	Stable
400	23 (#4-26)	F3I-90	1	23	0	Stable
401	17 (#5-21)	F3I-91	2	9	8	**
404	22 (#7-28)	F3I-43	1	0	22	Stable

Table 30. (Continued)

No. Exptl.	No. Inter- actions	No. of Intruder	No. Runs	Dominance E	I	Significance of Difference
405	10 (#15-24)	F3I-81	1	0	10	Stable
408	41 (#1-41)	F3I-89	3	1	40	Nearly Stable
409	14 (#8-21)	F3I-55	1	0	14	Stable
412	12 (#1-12)	F3I-84	2	2	10	
	29 (#13-41)	F3I-97	1	29	0	Stable
413	11 (#1-11)	F3I-93	1	0	11	Stable
	10 (#12-21)	F3I-71	1	0	9	Stable
	16 (#22-37)	F3I-96	1	0	16	Stable
416	12 (#1-12)	F3I-94	1	11	0	Stable
	9 (#13-21)	F3I-91	1	0	9	Stable
	11 (#22-32)	F3I-98	3	2	9	
417	10 (#16-25)	F3I-92	2	6	4	*
	11 (#31-41)	F3I-89	1	9	0	Stable
443	13 (#6-18)	F3I-101	3	1	12	Nearly Stable
	18 (#19-36)	F4I-1	1	0	18	Stable
445	28 (#8-35)	F3I-102	9	4	24	

Experiment 4

No. Exptl.	No. Inter- actions	No. of Intruder	No. Runs	Dominance E	I	Significance of Difference
453	30 (#1-30)	F4I-3	1	0	30	Stable
	17 (#39-55)	F4I-23	1	0	17	Stable
454	25 (#3-27)	F4I-6	8	12	13	*
469	30 (#1-30)	F4I-5	3	8	22	**
470	32 (#1-32)	F4I-2	4	5	27	**
472	16 (#1-16)	F4I-8	3	15	1	Nearly Stable
	24 (#17-40)	F4I-11	1	0	24	Stable
474	11 (#1-11)	F4I-9	2	4	7	*
	11 (#12-22)	F4I-1	3	10	1	
	10 (#23-32)	F4I-17	1	0	10	Stable
480	12 (#1-12)	F4I-10	1	12	0	Stable
	16 (#18-33)	F4I-15	2	4	12	**
	10 (#34-43)	F4I-10	1	0	10	Stable
490	20 (#1-20)	F4I-13	4	2	18	
500	19 (#1-19)	F4I-14	3	1	18	Nearly Stable
503	27 (#1-27)	F4I-20	1	0	25	Stable
504	13 (#1-13)	F4I-18	1	0	13	Stable
505	24 (#8-31)	F4I-22	1	0	24	Stable
	9 (#33-41)	F4I-10	3	2	7	

Table 30. (Continued)

Experiments 5 & 6

No. Exptl.	No. Inter- actions	No. of Intruder	No. Runs	Dominance E	Dominance I	Significance of Difference
508	10 (#1-10)	F_1I-1	2	7	2	
510	27 (#1-27)	F_1I-2	3	24	1	Nearly Stable
	13 (#28-40)	F_4I-4	1	13	0	Stable
511	48 (#1-48)	F_1I-3	10	41	7	
514	19 (#1-19)	F_1I-4	3	18	1	Nearly Stable
	14 (#20-33)	F_1I-11	1	0	14	Stable
518	28 (#1-28)	F_1I-5	9	23	5	
522	36 (#1-36)	F_1I-6	1	35	0	Stable
524	35 (#1-35)	F_1I-7	2	29	5	***
528	46 (#1-46)	F_1I-8	2	29	17	***
529	22 (#1-22)	F_1I-9	2	2	20	*
	10 (#23-32)	F_1I-20	1	0	10	Stable
533	22 (#7-28)	F_1I-14	2	7	15	**
	16 (#29-44)	F_1I-19	1	0	16	Stable
537	25 (#1-25)	F_1I-12	1	0	25	Stable
	12 (#26-37)	F_1I-22	1	0	12	Stable
	9 (#44-52)	F_1I-32	4	6	3	
539	31 (#1-31)	F_1I-13	1	0	31	Stable
	12 (#38-49)	F_1I-31	2	10	2	*
541	26 (#1-26)	F_1I-15	1	0	26	Stable
	19 (#27-45)	F_1I-28	1	0	19	Stable
545	19 (#1-19)	F_1I-16	2	5	14	**
	10 (#20-29)	F_1I-21	2	9	1	Nearly Stable
549	26 (#1-26)	F_1I-18	1	0	26	Stable
	18 (#27-44)	F_1I-29	2	15	3	**
551	17 (#1-17)	F_1I-17	1	0	17	Stable
	15 (#29-43)	F_1I-25	5	2	13	

Significant *P< 0.05   **P< 0.01   ***P < 0.001

Significance determined by a one-sample runs test (two-tailed), from S. Siegel. 1956.

Table 36. Aggressive calling (ACa) by dominant (Dom.) and subordinate (Sub). experimental C. integer before (during) and after Level 3-5 aggressive encounters during interactions with intruders.

No. Exptl.	No.	ACa Before Dom.	ACa Before Sub.	ACa After Dom.	ACa After Sub.	No.	ACa Before Dom.	ACa Before Sub.	ACa After Dom.	ACa After Sub.
	Level 3 Interactions					Level 4-5 Interactions				
Experiment 2										
64	5	1	0	4	0	5	3	1	3	0
74	3	0	0	3	0	2	0	1	2	0
76	3	0	0	2	0	2	0	0	2	0
113	6	0	0	4	0	4	1	1	4	1
114	11	0	0	9	0	2	0	0	1	0
115	21	7	2	14	0	7	2	4	5	0
121	5	2	0	3	0	6	4	2	6	0
128	5	1	0	3	0	23	11	13	12	0
129	10	6	2	7	0	17	12	10	17	0
133	5	2	0	4	0	11	2	3	8	0
139	20	6	0	15	0	17	10	4	11	0
142	18	4	1	13	0	4	1	1	2	0
144	10	5	2	10	0	12	7	5	11	0
149	3	3	0	3	0	6	4	4	5	0
154	5	2	0	3	0	10	5	2	7	0
156	8	4	1	5	0	18	6	3	15	1
158	12	7	0	7	0	8	0	2	3	0
163	3	1	1	3	0	8	6	7	5	0
	153	51	9	112	0	162	74	63	119	2
Experiment 3										
165	4	1	1	2	0	9	1	2	3	0
167	6	3	1	3	0	10	7	5	9	2
170	11	2	1	5	0	4	1	0	2	0
171	11	5	1	10	0	4	2	0	1	0
174	6	3	1	3	0	4	2	1	4	0
175	2	0	0	0	0	0	-	-	-	-
176	14	8	1	8	0	7	3	3	6	0
179	7	2	0	7	0	18	2	1	14	0
180	9	2	1	7	0	2	1	1	2	0
183	1	0	0	1	0	5	1	2	5	0
185	7	1	2	3	0	4	1	2	3	0
186	16	1	1	7	0	8	0	4	5	0
188	5	2	0	2	0	8	2	0	5	0
191	16	1	0	13	0	7	0	0	4	0
192	15	4	1	11	0	6	3	1	2	0

Table 36. (Continued)

No. Exptl.	No.	Level 3 Interactions ACa Before Dom.	Sub.	ACa After Dom.	Sub.	No.	Level 4-5 Interactions ACa Before Dom.	Sub.	ACa After Dom.	Sub.
194	11	6	1	8	0	4	3	2	4	0
199	20	4	1	10	0	5	2	2	3	0
201	4	2	1	1	0	8	2	6	3	0
202	8	2	1	5	0	1	0	0	0	0
204	4	0	0	3	0	7	1	3	6	0
205	4	2	2	4	0	11	5	6	10	0
207	1	1	0	0	0	24	18	11	19	1
209	15	0	1	10	0	2	1	0	1	0
211	4	1	0	4	1	1	0	0	0	0
214	10	4	1	8	0	13	5	7	10	0
216	2	0	1	1	0	13	2	4	12	0
217	17	4	1	9	0	9	7	5	5	0
220	21	6	2	12	1	15	9	11	8	1
221	26	8	1	18	0	10	5	3	8	1
224	1	1	1	0	0	11	8	9	9	0
226	6	0	0	3	0	13	8	8	11	1
228	6	0	1	0	0	11	3	2	3	0
231	1	0	0	1	1	0	-	-	-	-
232	9	5	1	4	0	3	2	1	0	0
233	13	9	3	7	0	8	4	2	5	1
235	18	11	4	13	0	12	6	7	8	0
238	2	0	1	1	0	8	2	3	4	1
239	12	2	4	9	0	32	16	23	23	1
241	18	5	0	11	1	8	4	2	7	0
244	9	3	0	8	2	9	3	4	3	0
246	4	4	2	4	0	4	3	1	4	0
322	17	10	2	11	0	11	6	6	9	0
324	9	6	1	7	0	11	9	7	6	0
326	12	2	0	11	0	6	4	3	4	0
328	17	5	4	7	1	6	4	3	5	0
387	15	7	2	6	0	9	6	3	4	0
389	16	9	4	16	4	8	6	4	6	1
395	3	1	0	2	0	0	-	-	-	-
397	16	6	2	9	0	4	1	1	4	0
400	11	3	0	4	0	12	5	5	9	1
401	6	3	1	2	1	13	12	11	8	0
404	13	4	4	6	0	9	3	5	4	2
405	2	0	0	0	0	11	5	6	9	0
408	10	5	0	8	0	12	5	3	9	0
409	8	2	0	7	0	4	1	2	1	0
412	4	1	1	2	0	19	17	13	12	2
413	8	2	3	6	0	6	0	2	3	0
416	15	1	1	4	0	16	12	12	7	0
417	0	-	-	-	-	15	7	7	5	2

Table 36. (Continued)

No. Exptl.	|	Level 3 Interactions				|	Level 4-5 Interactions			
	No.	ACa Before Dom.	Sub.	ACa After Dom.	Sub.	No.	ACa Before Dom.	Sub.	ACa After Dom.	Sub.
443	6	2	0	6	0	2	1	1	1	0
445	12	3	0	5	0	5	1	0	0	0
	576	187	66	355	12	517	250	238	337	17

Experiment 4

No. Exptl.	No.	ACa Before Dom.	Sub.	ACa After Dom.	Sub.	No.	ACa Before Dom.	Sub.	ACa After Dom.	Sub.
453	15	4	0	1	0	6	3	3	2	0
454	9	2	3	7	0	16	6	5	15	0
469	8	1	0	2	0	1	0	0	0	0
470	18	8	3	13	0	10	8	6	7	0
472	21	11	4	18	0	4	2	2	3	0
474	16	6	2	11	0	6	2	1	5	1
480	20	5	0	16	0	14	7	4	10	1
490	10	2	0	10	0	10	1	1	8	0
498	2	1	0	1	0	0	-	-	-	-
500	5	2	1	4	0	15	7	8	10	0
503	7	6	3	5	0	1	?		0	0
504	5	1	1	4	0	0	-	-	-	-
505	18	10	5	18	2	17	16	15	13	2
	154	59	22	110	2	100	52	45	73	2

Experiments 5 & 6

No. Exptl.	No.	ACa Before Dom.	Sub.	ACa After Dom.	Sub.	No.	ACa Before Dom.	Sub.	ACa After Dom.	Sub.
508	12	2	1	4	0	3	1	1	3	0
510	30	12	7	18	0	9	4	5	8	0
511	22	10	4	18	1	24	20	19	19	3
514	15	2	2	14	0	6	5	4	4	0
518	19	9	3	15	3	12	3	4	12	1
522	23	12	0	20	0	0	-	-	-	-
524	5	1	0	5	0	4	2	4	4	0
528	16	8	4	10	0	12	7	5	12	0
529	18	5	1	13	0	9	3	6	6	0
533	14	1	1	8	0	20	13	16	18	0
537	18	5	1	17	0	24	11	12	21	0
539	17	8	3	12	0	18	8	7	12	0
541	20	7	0	18	0	14	14	1	14	0
545	8	0	0	7	0	14	7	5	10	0
549	26	10	3	26	0	14	9	7	14	0
551	7	3	1	5	0	16	10	7	13	0
	270	95	31	210	4	199	117	103	170	4

APPENDIX

II

Molting

I.   Final molt of F_2 male - 5-29-69 - 2:55 p.m. - 84° F

2:55   Head downward on screen, periodically arching and positioning body; wing buds extended out from thoracic segments.

3:04   Region of 1st and 2nd thoracic segments lightening; pronotum splits along ecdysial line and pinkish-white pronotum visible beneath.

3:07   Head, thorax, most of flight wings, and first six abdominal segments visible; 1st pair of legs free.

3:09   Flight wings and hind femora free.

3:11   Hind limbs completely free.

3:13   Cricket moves free of cuticle, freeing antennae and cerci, then turns and moves up screen.

3:25   Anterior ½ of the flight wings inflated.

3:32   Cricket immobile with fairly rhythmic contractions of abdomen every 2-5 seconds; flight wings nearly fully inflated.

3:39   Cricket shifts position and abdomen noticeably shortens; abdominal contractions continuing.

3:43   Flight wings beginning to fold over each other (right over left).

3:47   Slight rustling and further folding of flight wings; pronotum noticeably darkening.

3:50   Cricket turns and begins eating molted exoskeleton.

4:12   Entire exoskeleton nearly consumed; head and pronotum light black, wings a dirty-white color.

II.   Final molt of F_2 female #77 - 5-22-69 - 9:38 a.m. - 78° F

9:38   Completes emergence; quickly turns around and lies motionless on sand.

9:45   Ovipositor moving slowly up and down; hind legs periodically lifted off substrate.

10:11   Flight wings completely inflated and extended; still motionless except for movements of ovipositor and occasional contractions of abdomen.

10:32   Wings folding slightly.

10:44   Cricket begins eating ecdysed exoskeleton and continues until 11:30 a.m. Everything consumed except hind tibiae and tarsi, antennae, and some pieces of mouthparts.

III.   Final molt of F_3 female #355 - 8-10-69 - 3:25 p.m. - 88° F

3:25   Moving about on sand, continually changing position. Finally moves to screen and turns head downward; pronounced arching and contracting of body; wing buds flanged out from body surface.

3:39   Area beneath thoracic segments 1-2 lightening.

3:40   Wing buds greatly flanged out; pronotum splits down middle.
3:41   Head, pronotum, thorax, and 1st abdominal segment visible; continual 'buckling' movement of soft white pronotum evident.
3:43   Anterior two pairs of legs free. Antennae of a nearby adult cricket contact molting female. Molting female violently jerks body; other cricket moves away.
3:44   Elytra free.
3:45   Flight wings free but highly compressed together distally.
3:47   Hind legs free.
3:49   Complete emergence.

IV.   Final molt of F_4 male #457 - 2-23-70 - 5:08 p.m. - 70° F

5:08   Moving about on sand, attempting to find position, etc.
5:12   Male has now localized to one position, but continues to adjust position by moving slightly; wing pads held out from thoracic surface.
5:15   Ecdysial line on pronotum evident. More positioning movements; antennae 'testing' sand.
5:19   Still positioning, but no locomotion; occasional 'pumping' movements visible beneath pronotum.
5:20   Moves forward slightly on sand; antennae lashing substrate; 'pumping' movements occurring more frequently.
5:24   Splitting along ecdysial line on thorax between wing pads and continuing onto pronotum.
5:25   Split widening. Wing pads now at 90° angle from thorax and soon approximately at 145° angle from body.
5:27   Most of pronotum and thorax visible; ecdysial line now prominent on head.
5:28   Exoskeleton on head splitting.
5:30   Proximal parts of wings visible; eyes visible and head free.
5:33   Fore- and mid-legs free.
5:35   Elytra free and unfolded.
5:36   Flight wings free and highly compressed distally.
5:39   Proximal $\frac{1}{2}$ of hind tibiae free
5:40   Hind legs free; cricket resting.
5:46   Cricket moves forward, freeing antennae and cerci.

APPENDIX

III

Behavior of Permanently Paired Males

Pair #87-88

From 5-24-69 to 6-15-69 during daily observations of this pair, #87 was always dominant (five Level 3 encounters and many Level 2 encounters). On 6-15-69 at 2 p.m. #87 began courting and #88 approached and mounted on two different occasions, both resulting in spermatophore transfer attempts by #87. After the first mount #88 remained nearby the courting #87, lashing antennae, rearing up and jerking its body, and acting distinctly aggressive before approaching and mounting the second time. During such mounts #88 responded by opening mandibles and aggressive calling.

Seven hours later at 9:30 p.m. #88 actively chased #87 around the jar, frequently stopping to call aggressively. This new change in the dominance relationship remained stable until 7-18-69 when #87 reassumed the dominant role.

Pair #93-94

At 10:30 p.m. on the 14th day of adulthood, both males were observed courting back to back. After one minute, #93 stopped, turned, and briefly mounted; at dismount both males resumed courtship calling in the back to back position.

Pair #95-96

After mutual courtship calling back to back for over one minute, #96, the subordinate in all observed aggressive encounters (all Level 2) up to that time, turned and mounted; an attempted spermatophore transfer occurred. This was quickly followed by three brief mount/dismount sequences, one of which also involved a mating attempt. Although most mountings observed for this pair were of short duration, during a mount with attempted mating two weeks later, #96 remained astride #95 for over 40 seconds.

Pair #99-100

This pair was grouped together 5-25-69, and from 6-4-69 to 6-20-69 male #99 dominated all recorded aggressive encounters. On 6-22-69 male #100, with a spermatophore visible, quickly pursued #99 around the jar, and 19 days later #100 charged and chased #99 during a Level 2 encounter.

Pair #101-102

Four dominance switches were noted for this pair (Table 11).

On 7-6-69 male #102 courtship-called and backed into #101; male #101 turned and kicked back with its hind legs and #102 ceased calling, approached and mounted. Male #101 briefly vibrated its cerci, then moved away and resumed courtship calling.

This unique interaction is interesting in that #102, initially exhibiting the typically male behavior of courting, quickly responded to the aggressive behavior of kicking with the typically female response during copulation (i.e., mounting), then immediately resumed the male courting behavior once again.

Pair #106-107

Male #106 had defective wings that produced no sound when vibrated. For this pair courtship calling by one male frequently initiated agonistic responses by the other. Twelve days after their adult molts, #107 courted and #106 mounted several times during a half-hour observation period; but before and after each mount #106 jerked its body and highly arched and vibrated its wings in an apparent attempt to call aggressively. Minutes later the first aggressive encounter was noted for this pair when #106 charged and briefly chased #107, then stopped and attempted to stridulate.

Pair #111-112

On 6-9-69 when both were 11-day old adults, #112 courted at various times throughout the day, with frequent mounting and occasional chasing bouts by #111; #111 occasionally called aggressively while mounted. During one sequence #111 mounted/dismounted three times in quick succession. During each mount both males lashed antennae, and at each dismount #111 briefly chirped. These behavior patterns lasted off and on for nearly two hours and during this time after one particular dismount #111 suddenly switched from aggressive to courtship calling. Male #112 soon stopped courting and approached; at antennal contact #111 immediately reverted to aggressive calling then switched back to courtship. This was followed by both males mutually courting back to back and soon thereafter by both males aggressive calling leading to a face-off with open mandibles. After several seconds both animals turned away and moved to opposite sides of the jar to continue aggressive calling.

Three days later this pair was observed rapidly switching back and forth between Level 4 aggressive encounters and courtship sequences with #112 courting and #111 mounting, all mounts terminating after abortive mating attempts. One hour and three known mating attempts later, a Level 5 encounter occurred; after three IM's #112 turned away, but instead of retreating, immediately resumed courting.

Three days later both were observed mutually courtship
calling back to back, after which #111 turned and mounted and
#112 attempted spermatophore transfer. This homosexual encounter
was followed by three more mounts, all resulting in mating
attempts by #112. Prior to each mount #111 approached with
open mandibles, and at the last dismount #112 remained with its
abdomen highly upturned in the mating posture for 20 seconds.

Minutes later both males were orienting towards and antennat-
ing each other, both calling aggressively.

Pair #252-253

This pair exhibited numerous encounters of uncertain dominance,
a frequent phenomenon among permanently paired males. On several
occasions both males engaged in Level 4 encounters, aggressive
calling and antennal fencing, but with closed mandibles during
the face-off. The encounters terminated with both animals sepa-
rating, often to continue aggressive calling, with definite retreat
by either male not apparent.

Pair #266-267

Two known dominance switches (i.e., three runs) occurred for
this pair during the experiment. Male #267 assumed dominance first
and during daily observations for nearly two weeks chased #266
around the jar. Then at 9 p.m. 9-17-69, several hours after a
Level 4 encounter of uncertain dominance, #266 chased #267.
Male #266 was still dominant, frequently chasing #267, at 8:30
a.m. the following day, but when next observed at noon, #267 had
reassumed dominant rank. At 4:30 p.m. another Level 4 encounter
was witnessed, ending in a draw. Both males fenced with antennae
and called aggressively during a face-off with closed mandibles,
before moving apart.

APPENDIX

IV

Sequential Appearance of Paralytic Symptoms

I. F_3 experimental #224 - 11-3-69

8 a.m.   Found lying stretched out on sand, hind legs extended and
            palpi moving continually. Cerci stimulated with probe and
            male drags itself forward with anterior appendages.
            Hind legs nonfunctional in locomotion; mid legs moving
            sluggishly.
10 a.m.   Only movements of palps, antennae, and fore legs discernible.
11 a.m.   Hind legs stiff and held high off substrate. Fore legs
            still capable of movement.
Noon   No change.
2 p.m.   Faint palp movements. Cricket immobile, with occasional
            slight twitch of fore appendages.
3 p.m.   Near death. Only very faint palp movements discernible.

II. F_3 experimental #387 - 12-2-69

10 a.m.   During grouping with intruder it was noted that this male
            was entering the first stages of paralysis as evidenced by
            a beginning stiffness in the hind legs and slight difficulty
            in locomotion.
11 a.m.   Hind legs becoming increasingly non-functional. Hind legs,
            in contact with the substrate, suddenly 'spring up,' are
            held off substrate, and quiver slightly for 20-30 seconds.
Noon   Increased difficulty in locomotion. Slight prodding of
            cerci with probe induces cricket to locomote forward.
            Within seconds an exaggerated single spasm of several seconds
            duration occurs in both hind legs and cricket becomes immobile.
1 p.m.   Complete immobility. Only slight palp movements visible.

III. F_3 experimental #324 - 12-11-69

8 a.m.   Early stages of paralysis.
9 a.m.   Progressive difficulty in locomotion. Hind legs stiffening.
10 a.m.   Hind legs paralyzed and useless in locomotion.
1 p.m.   Mid legs paralyzed; hind legs stiff and held high off substrate.

IV. F_4 experimental #469 - 5-22-70

8 a.m.   Beginning stages of paralysis. Locomoting with difficulty;
            hind legs extended and stiffening.
9 a.m.   Hind legs now held high in air, tibia over 5 mm. from the
            sand surface.
Noon   Hind legs in same upraised position. Fore legs drag body
            forward slightly when cerci are prodded.
1 p.m.   Twitch of large amplitude of left hind leg occurs. Both
            hind legs now widely extended from body axis and fully

extended with no bend at the femoro-tibial joint. Only palp movements visible.

2 p.m. Near death. Hind legs held high off substrate. Body immobile when prodded. Antennae curling, and only occasional faint palp movements (see Fig. 29).

V. F_1 experimental #528 - 7-29-70

10 a.m. Advanced paralysis. When cricket is lightly prodded the hind legs quiver slightly several times, followed by a final tremor at which time the hind legs, originally bent, become fully extended and rise up off the substrate; immobility, but slight wing vibrations and voidance of fluid fecal material.

Noon Dead in paralysis.

VI. F_4 pair #493-494 - 6-15-70

9 a.m. Male #494 in beginning stages of paralysis. Locomotion by fore legs and mid legs only; hind legs held in air but occasionally contact substrate and move slightly.

11 a.m. #494 near death. Immobile, with curling antennae and laterally compressed desiccated abdomen. Only faint palp movements. #493 locomoting normally. #494 removed from jar.

2 p.m. Male #493 observed spending extended periods attempting to climb glass sides of jar.

4 p.m. #493 in early stages of paralysis. Hind legs stiffening and held off substrate, but not extended.

10 p.m. #493 dead. Hind legs stiff and high off substrate.

VII. F_3 experimental #416 - 1-14-70

9 a.m. Found lying on back. Cricket remained motionless after righting, with occasional slight tremors of hind legs.

11 a.m. Motionless. Body prodded lightly, and mid legs quiver slightly, then hind legs quiver several times, then right hind leg (followed by left hind leg) extends backward, but both remain bent at the femoro-tibial joint.

Noon Cricket near death. Appendages loose and body flaccid.