7. Predation and Sperm Competition in the Evolution of Coupling Durations, Particularly in the Stick Insect *Diapheromera veliei*

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Ejaculate transfer is not inherently time consuming. A cricket, **Cyrtoxipha** sp., accomplishes the task in less than one second (Alexander and Otte 1967). It seems indicative of some noninseminatory complication, then, that a fellow orthopteroid, the stick insect **Necroscia sparaxes**, devotes 79 days to a coupling (Gangrade 1963). What accounts for this and other only slightly less extensive time investments? After all, to a male of most species, time is a determinant of how many females can be found and inseminated, a major component of reproductive success. Females, as well, could presumably be feeding, ovipositing, or dispersing more efficiently without an attached male (exceptions, such as the phoretic copulations of certain Hymenoptera and phoroid Diptera, are likely secondarily evolved elaborations of prolonged matings, see Evans 1969, Schmitz 1950).

Couplings may be prolonged simply because copulation is a convenient time or the only time for the performance of other behaviors. Time might be taken to lodge accessory gland materials such as mating plugs, anti-aphrodisiacs, nutrient investments and perhaps sperma-tocides in the female system (Gwynne 1982, Leopold 1976). The potentially laborious job of removing previously inserted ejaculates could also prolong couplings (brush-like sperm extractor in a damselfly, Waage 1979). Members of sexual unions sometimes pass and accept nuptial gifts such as insect prey, predigested seeds, or nutritious spermatophores (Thornhill 1976). Their presentation and consumption could prolong the time required for mating. Pairing might even serve as a stage for male displays with time required to deliver information to a discriminating mate, e.g. communication through the form and motions of genital structures in the carabid beetle **Pasimachus punctulatus** (Alexander 1959).

Most of these time-consuming adjuncts to sperm transfer, however, are themselves subject to selection

for brevity. They appear insufficient to explain the
several days of pairing that are commonplace among
phasmids. Rather, it seems more reasonable to look for
benefits that are inherent in mating itself. Selection
acting to enhance such advantages could prolong copu-
latory positions. Two such forces of extension are (1)
increased protection from predators due to amplification
of warning signals by pairs and/or the pooling of
mechanical and chemical defenses (e.g. Eisner 1965) and
(2) the avoidance by attached "blockading" males of sperm
competition (Parker 1970; the competition between the
sperm of two or more males for the fertilization of an
ovum). What follows is a search for these forces acting
on the coupling durations of insects, particularly stick
insects, and specifically the phasmid Diapheromera
veliei.

Some natural history of Diapheromera veliei

     D. veliei is widely distributed over the western
United States. The population I studied occurs in the
arid grasslands of New Mexico's central Rio Grande
valley. The single annual generation lives almost
exclusively on the microphyllus shrubby legume, Dalea
scoparia. Nymphs first appear in May, and adults are
present from June through September. Adult D. veliei
live about 80 days in the laboratory. Sex ratios will be
discussed later; suffice to say here that adult, but not
nymphal, sex ratios change radically over time. Density
is high for a phasmid; in some locations nearly every
bush (= 1 cu m of volume) will contain 1-20 insects.
     Eggs are reminiscent of small apple seeds, and weigh
an average of 3.5 mg. A female drops a mean 6.0 eggs on
the substrate daily, principally in the late afternoon,
although oviposition can occur at any time. Seven
captive females, whose lifetime fecundity was measured,
produced 322-589 eggs ($\bar{x}$ = 456). Oddly, female size is a
poor predictor of egg production (r = -0.204, p>.25; see
also Neumann, 1976, for a similar case in the phasmid
Didymuria violescens).
     Males mount females dorsally and grip their mates,
anterior to the vulva with a powerful cercal clasping
organ. Coupling lasts 3-156 h in captive pairs and during
this time the penis is periodically inserted and with-
drawn up to 9 times. These intromissions occupy ca 60%
of the pairing duration. Males have considerable control
over female terminalia with their clasper, and it appears
that, in a proximate sense, males have control over
mating duration. Females with attached mates are capable
of oviposition.

COUPLING AS A DEFENSIVE ALLIANCE

Potential benefits

A copulating insect acquires properties it lacked while single. It becomes part of a larger object, perhaps discouraging predators by appearing beyond their abilities to capture. If the union is tenacious, it becomes a more unwieldy object that a predator might lose control of or abandon. Should the pair be easily broken apart, a predator could be confused by the sudden appearance of two moving objects. And by mating, an insect is shielded by the possibility that, if a predator attacks one insect, it may be the partner that is consumed (see Hamilton, 1971, for a discussion of the "selfish herd" concept). In addition to these inevitable consequences of copulation, some sexual partners, as well as members of other types of groups, take on further beneficial properties. The effectiveness of some defenses is multiplied in aggregations and, presumably, could be magnified in mating pairs. In sawfly larvae, for instance, neighbors turn on a pentatomid predator and smear it with more of a sticky exudate than an isolated individual can apply (Tostowaryk 1972). Grouped owlfly larvae present a thicket of mandibles to an attacker (Henry 1972). Eisner (1965) has proposed that pooling of chemical defenses is the selective cause for the extension of coupling position in the walkingstick Anisomorpha buprestoides. The heavy, thick-bodied females and diminutive males of A. buprestoides discharge a potent terpenoid spray from prothoracic glands that could become even more repulsive with increased volume. Adults are typically found joined (matings in the laboratory last up to 3 weeks) and even juveniles are sometimes found attached in sexual postures.

In addition to enhancing the potency of defenses, groups tend to amplify warning colorations (Cott 1957). Presumably some predators will be more apt to see an enlarged display or notice one sooner and be less likely to complete a mutually unpleasant attack. Chaplin (1973) proposed that lengthy and interspecific pairings of unpalatable Hemiptera aid in broadcasting aposematic displays. The comparative evidence is weak. Both cryptic and conspicuous bugs engage in lengthy and/or frequent matings (Walker 1980). Such amplified advertising in phasmids would not be common as they are seldom aposematically colored. A. buprestoides, however, is not particularly cryptic; the bright black and white morph of north central Florida is even less so (Hetrick 1949). Some Australian stick insects, such as Podacanthus wilkinsoni, take on conspicuous patterns of black, yellow, and white at high densities (Key 1957).

I know of no record of copulation duration changing with
density. The large Moluccan phasmid **Megacrania wegneri**
(male up to 165 mm, female 190 mm) is gaudy, with a
· blue-green body, black-edged segments, bright orange
antennae and legs and reddish wing bases. Pores in
dome-like prothoracic turrets are directed fore and aft
and spray an evil-smelling fluid up to 50 cm. Wegner
(1955) found a number of single adults but rarely mating
pairs, suggesting that coupling is short relative to
adult life span and is not extensively used to increase
communication with predators.

Mating glows in some phengodid beetles could be
cooperatively amplified aposematic signals. Biolumines-
cent nonmate-orienting signals of Coleoptera may serve as
facultative warnings (Sivinski 1981a). **Phrixothrix
tiemanni** females possess lights, but probably advertise
for mates with only a pheromone. Both males and females
glow when copulating (Tiemann 1970). Ceylonese **Dioptoma
adamsi** females luminesce to attract males. Males,
however, were thought to be dark until Green (1913)
captured a coupled pair and found the male bore 26 green
lights that glowed "under sexual excitement". Note that
female, but not male, copulatory glows could have the
sexual explanation of attracting additional males and so
arranging informative confrontations between potential
mates, as might the cries of cow elephant seals (Cox and
LeBoeuf 1977, Lloyd 1979).

In insects where coupling does amplify aposematism,
signal patterns might be adapted to mating position or
copulatory postures modified to accommodate warning
signals. Assuming most visually oriented attacks from
learning predators (i.e. birds) are from above, apose-
matic males might be expected to abandon ancestral dorsal
mounts which hide the female signaling surface and
copulate end to end. In all phasmids, both drab and
bright, the male assumes a position above the female
while mating. In beetles, there are a variety of mating
positions, but no obvious correlation between warning
coloration and sexual position. Among generally
unpalatable taxa, meloids and some cantharids mate end to
end. Coccinellids and lycids, however, mate with the
male astride the female's back (Wojcik 1969, Balduf
1935).

Defenses of D. veliei and survival from attack

Insect defenses are of two types: primary defenses
that prevent discovery and secondary defenses that
discourage predation following discovery (Robinson
1969). D. veliei resembles a twig, a resemblance in
color and form that is furthered by periodic rocking (a
breeze-blown motion). Extension of the front legs hides

the head, disguises the forelimbs, and creates a still
more elongate, plant-like appearance. Cryptic posture in
the male, at least, is disrupted by mating. The abdomen
is bent in a sigmoid shape and the front legs are used to
grip the female. It is worth noting that 21 human
observers detected no difference in the crypticity of
single or mating pairs (for explanation of methods and
more detailed results of this and other experiments in
this section see Sivinski 1980).

     There are two forms of chemical secondary defenses
in D. veliei. Both sexes regurgitate when handled,
though females are more likely to do so (72% of females
compared to 34% males). The female crop is much larger
and may provide more voluminous and effective protection.
Crop contents are unpalatable to the carnivorous ant,
Pogonomyrmex rugosus, and an insectivorous rodent,
Onychomys leucogaster (the latter occasionally removes
the stick insect's crop before eating it).
(Orthopteroid gutting by predators is considered in
Robinson 1969b, Edmunds 1974, Walker 1980, Schultz 1981).
Both sexes of D. veliei reflex bleed. Drops of bright
yellow fluid appear at virtually any articulation in the
body, but most commonly between tarsal segments. Males
are more apt to bleed than females (19% compared to 7%).

     Besides the chemical assets combined at copulation,
mating pairs could present unusual physical problems for
predators.   D. veliei is a large insect (male length $\bar{x}$ =
74 mm, female $\bar{x}$ = 80 mm), and males often maintain a grip
on females, particularly if only the female is directly
handled.

     When coupled pairs and single individuals were
placed in a large enclosure with two Mexican jays
(Aphelocoma ultramarina), there was no difference in
single and paired male mortality (see Table 1). Female
survival, however, improved considerably with coupling.
By survival, I mean that the bird took the insect off the
bush but did not eat it; it escaped in transit to or at
the the perch. Male survival was lower than female, pro-
bably because of the vulnerable dorsal mating position.

     In D. veliei, extended matings are apparently not a
form of male self defense. There is no evidence that
males are protected by copulation. In other cases, males
may obtain this kind of protection. However, selection
need not favor males that reach old age securely attached
to a protecting mate but who have foregone inseminating
new females. For prolongation of a defensive alliance to
be adaptive, increased survival from coupling must be
greater than the reciprocal of the lower rate of insemi-
nation. In D. veliei, for example, mated males tapped by
a pencil run less than half the distance of single indi-
viduals. If general mobility is also halved, then a male
remaining in copulo until a new female is discovered

would have to live twice as long as a single male to have
a similar number of sexual encounters (even this presumes
that males direct the course of the pair or that
undirected females are as likely to find other females as
single males).

Males unprotected by pairing might prolong coupling
to guard future offspring through defense of the mother,
a kind of paternal care of zygotes still unformed. This
assumes female mortality to be so extreme or mates so
rare that males cannot locate new females as fast as
previous mates containing their sperm are consumed.
Prolonged couplings resulting from mate protection alone
require a higher mortality in single adult females than
single adult males. This condition may sometimes be met
in phasmids. The tachinid parasitoid Thrixion
halidayanum attacks only female walkingsticks (Clausen
1940) and a number of birds consume more female than
male Didymuria violescens, often at rates surpassing 10:1
(Readshaw 1965). Female D. veliei also appear to be a
preferred prey, presumably due to their greater bulk
(males are 92% the length of females but only a third
their weight). Adult sex ratios (male:female), near 1:1
in early June, become 3:1 or even 4:1 through much of
July. Late instar nymphs have more nearly equal sex
ratios throughout the season, so that differential matur-
ation is unlikely to account for the bias in adults. The
plunge in female numbers does, however, correspond to the
peak nesting season of local birds. Adult females, but
not males, are polychromatic with brown, green, and
greyish color morphs. Such polymorphisms are often due
to frequency-dependent selection exerted by search image-
forming predators (Clark 1962). Unfortunately, D. veliei
data are insufficient to test a mate guarding hypothesis.

One sort of phasmid armature, the enlarged spines of
certain males, has been supposed to serve in the defense
of mates. Both Bedford (1975) and Walker (1980) have
proposed that big spiny males, (e.g. Eurycantha horrida)
protect associated females. But Robinson (1968) argued
that the larger femoral spines of Oncotophasma martini
males are due to the greater exposure to predators males
suffer while searching for mates. This difference of
opinion over whether male or female vulnerability is the
raison d'etre for inflated male spines is based on the
assumption that spines function solely in defense. In
D. veliei this is not the case. Both sexes have spines
on the distal end of the midfemora. Those of the male
are longer than the female's, and hooked at the tip.
When either sex is grasped, the insect may assume a
rigid, stick-like position or flail with its legs. But
the better-endowed males are not more likely to strike out
than females, as might be expected (57% of 110 males, 47%
of 47 females, p>.10). Spines are used, however, by

males in combats over females. The body of a rival is
caught between the tibia and femur. By flexing the leg,
the hook is driven into an opponent. In the closely
related D. covillea, spines have been seen to puncture
the integument and draw blood (Sivinski 1978). Other
enlarged male spines may have similar functions. Some of
the largest male spines and greatest male sizes occur in
species that live in high densities, where encountering a
sexual rival may be commonplace. Male armature and bulk
reach an extreme in Melanesian Eurycanthinae, some of
which roost in heaps inside hollow trees (Bedford 1975,
see also illustrations in Gurney 1947; spikes on male
hind tibiae have been used as fish hooks).

Mate manipulation by females and mating duration

D. veliei females may not necessarily benefit from
numerous inseminations, but under certain conditions at
least, they find an advantage in the presence of a mate.
Males in this and similar circumstances may be held in
copulo against their best reproductive interests. A
female, for instance, might simply grip the inserted
penis.
Male phasmids occupy what seems to be a vulnerable
dorsal mating position derived from ancestral ventral
ones (Alexander 1964). Might females erect males over
their backs as shields by rearrangements in their genital
structure or copulatory postures? Some of the peculiar
rearrangements of male terminalia in other insects are
suggestive of 'differences of opinion' with females over
mating position. For instance, the entire genital
capsule of male sawflies has been rotated 180° on its
long axis, allowing males to couple end to end rather
than being forced to climb upon the female's back (Tuxen
1970; also note in this reference rotations of 90° in
some Coleoptera and 180°-360° in Diptera; the latter bear
an external arrangement similar to the supposed ancestral
state, but internal structures, such as the vas deferens,
have been twisted around the gut). A large number of
insects with penile contortions couple however, in the
male above position (e.g. Adephaga, Cyclorrhapha),
suggesting that either females are winning, or males are
in fact attempting to attain a position on their mates'
backs (see section on sperm competition).
Where males monitor a process, they might alter
their behavior in response to changes or apparent changes
in the actions of their partners. For instance, if males
attempt to transfer a minimum amount of ejaculate, a
female accepting sperm at a slower rate might be accom-
panied by a mate for a longer period of time. There is
no evidence of this particular hypothetical maneuver in
phasmids. Intromission is usually followed by a longer
period when the genitalia are not engaged.

SPERM COMPETITION

Facultative coupling durations in D. veliei.

An inserted penis or the occupation of a mating position can protect a male's ejaculate from being removed, displaced or diluted by a sexual rival (Parker 1970, 1974). It may benefit a male to so protect his gametes, particularly when the last male to mate receives most of the fertilizations (as is typical of the small sample of orthopteroids tested, see citations in Walker 1980).

How much time a male should invest is dependent, among other things, on the degree of competition (Parker 1974). At times when males are abundant and females scarce, a male might be expected to increase his guarding time. When new mates are common and rivals to reinseminate past mates are rare, guarding durations might become shorter. Are male D. veliei time investments consistent with such a prediction? Changes in population composition that could influence mating decisions are certainly common in D. veliei demes. As discussed earlier, sex ratio, i.e. relative abundance of mates and competitors, varies over time. D. veliei live in dense populations, where monitoring of population composition is feasible and an individual can potentially live through a large part of an annual population cycle and experience radical changes in its sexual environment.

In the laboratory, three males: one female (n=3), 2:1 (n=8), 1:1 (n=8), 1:2 (n=8) and 1 male:3 females (n=3) were placed in 10 gal. aquaria. They were checked every 2 h from 0800h-2000h and their sexual behavior noted. The longest pairing duration of the various replications are plotted against sex ratio in Fig. 1. There is a significant regression (F=4.3, p<.05, r^2=.13).

A puzzling aspect of the point scatter is the increased variance in mating times at sex ratios of 1:1 and higher. One explanation might be the previously mentioned male combats that frequently result in mate 'takeover'. Males confronted with rivals might adaptively extend guarding, but in the presence of an aggressor could regularly be cut short. Variance would increase with competition. This does not explain the mysteriously high variance at an equal sex ratio, and I am cautious about these results pending their successful repetition. A similar extension in presumed male guarding time with increasing sex ratios has been found in the stink bug Nezara viridula (McLain 1981). High male encounter rates result in prolonged copulations in the lasiocampid moth Malacosoma disstria (Bieman and Witter 1981). Males of the luminous fungus gnat Arachnocampa luminosa cling to a female's pupa and mate as she
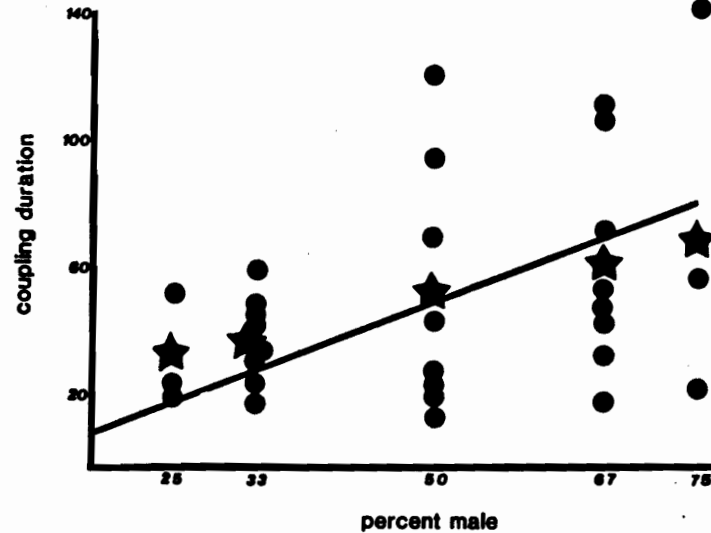
Fig. 1. The relationship between coupling duration (in hours) in D. veliei and the male proportion of captive populations: (F=4.3, df=1,28, r=.36).

emerges. Richards (1960) notes a copulation of 7 h when two males were present compared to a 1 h and 13 min pairing that occurred in the absence of rivals. In the biting fly Culicoides nubeculosus, matings that are initiated in swarms but consummated on the ground last about 2 min. Copulations that occur on hosts where rival males are frequently present last about 1 h (Downes 1955). Male Photinus collustrans fireflies increase coupling duration when rival males are present (S. Wing, pers. comm.).

It remains to ask why many phasmid matings are so long in the first place, often measured in days, weeks, or months (see, for example, Gustafson 1966, Korbott 1961, Gangrade 1963). One possibility is based on the typical oviposition pattern of stick insects. Ova are usually large in relation to adult size. As a rule, from one to several of these big eggs are laid each day over long life spans (Bedford 1978). The result is a great deal of homogeneity, as far as males are concerned, in the reproductive value of females. The time until next fertilization is apt to be very much alike between

neighboring females. This contrasts with females that
produce batches of eggs at widespread intervals who
become less valuable after laying than other females
about to oviposit. Unlike males guarding batch-laying
females there is no instant, particularly in the short
run, for a male walking stick to leave to search for a
better mate. Phasmid reproductive value declines slowly
with age, over periods that parallel some mating
durations, i.e. days, weeks, or months (in D. veliei
female daily oviposition falls at the shallow slope of
b=-0.07 for the first 6 weeks of maturity; see also
citations in Bedford 1978). When past mates are as
likely to couple with rivals as deserting males are to
find new mates the sexual landscape for a male stick
insect may be a succession of equally green pastures. If
valid, the argument fails to be inclusive. Male
Necroscia sparaxes couple for months to batch-ovipositing
females, (Gangrade 1963).

    Opportunities to maintain long attachments may be
more abundant for stick insects than for more mobile
insects. The mechanics of coupling are probably simpler
where sluggish females remain on large, persistent
resources (i.e. phasmids on shrubs and trees). A male
might, with some difficulty, accompany a female on
movements between scattered ephemeral oviposition sites.
But if his presence substantially lowers her searching
ability, he may gain little from his guarding (see
however the following subsection).

    Males avoiding sperm competition are expected to
occupy good defensive positions while mating. All stick
insects, to my knowledge, are mounted above the female's
back. This high ground allows control of the area around
the pair, and D. veliei males often strike out with
their forelegs at nearby rivals.[1]

Costs to Females

    Male and female reproductive interests are commonly
in conflict (Trivers 1972, Parker 1979). A male may

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[1] Sperm and spermatophores are proteinaceous, and
     sometimes eaten by females or predators. Both nuptial
     secretions and guarding by males have been supposed
     responses to that danger (Richards 1927, Alexander
     1961). It is possible that females go about har-
     vesting ejaculates with very little 'intention' of
     having their contents end up in zygotes. If so, males
     might rapidly pass multiple spermatophores so that as
     one is eaten, the others empty into the female (parti-
     cularly if the first ones are large and/or hard

burden the female with some stratagem that protects his
ejaculate from competition but lowers his mate's fecun-
dity or survival.

While coupling may shelter some species from their
predators, it's apt to be an awkward and precarious
position for others (Richards 1927, Daly 1978; an unusual
instance is the greater parasitization of mating meloid
beetles by mirid bugs — Pinto 1978). Struggle by
females to remove their dangerous companions might result
in yet another advantage to dorsal mounts by males. In
end to end copulation, females can pull against an
inserted male and perhaps gain control of coupling
duration (as might be the case in the carpenterworm moth
Prinonoxystus robiniae, Solomon and Neel 1973).
Male-above positions not only provide better control but
are useful in capturing mates. Female cooperation is
usually required in reaching female-above couplings, the
ancestral position in orthopteroids (Alexander and Otte
1967). It is difficult to catch and force an ejaculate
into a female by backing under her ('force' in the sense
of making refusal unadaptively expensive, Parker 1974).

Often there is little a female can do to inexpen-
sively remove a persistently clinging male (Parker 1970b,
1979). Precopulatory choice of mates may be females'
sole means of minimizing the price they pay. Female yel-
low dung flies apparently accept the risks of coupling,
but choose large males that are most likely to be able to
lift the female during aerial escapes (Borgia 1981).

Who wins in conflicts of sexual interest depends on
"...1. the rates of evolutionary adaptation (i.e.
selection intensity) in the two 'opponents', and 2. the
relative effectiveness of each quantum of adaptation
against the opponents' current level of adaptation"
(Parker 1979). Males, however, may have an additional
advantage in most systems due to their higher variance in
reproductive success. Because the best male, i.e. one
with a successful countermeasure to a female adaptation,

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(Footnote [1] contin.) to chew; perhaps these were
early spermatophallaxes?; see Alexander and Otte,
1976, for the occurrence of multiple spermatophores
and Gwynne 1982). Only a few phasmids have an
external spermatophore exposed to such danger.
There is, however, an interesting case of a coupled
male South African Phalces longiscaphum that
kicked vigorously at ants removing his spermatophore
from a mate (Le Feuvre 1937). The period of
vulnerability in this and other stick insects is
only a fraction of the time the male is perched
above his mate.

can potentially leave more offspring than the correspond-
ing best female, selection will occur more rapidly in
males. On this basis alone, the odds are better than
even that at any given time, females will be behind in a
copulation related arms race.

Lost female reproduction is usually a loss to the
male as well. It is expected that males minimize the
burden they place on their mates. For instance, the
effort to partially or completely support a male's weight
during a prolonged attachment is apt to drain female
resources away from reproduction. Long-mating males
might become diminutive, trading bulk for offspring. In
the stick insects I am aware of that mate for over a
week, males are of below average length relative to their
females (Sivinski 1978; this is perhaps another reason
for dwarfism and degeneration in parasitic males, such as
those of deep sea ceratoid anglers; such males are
discussed in Ghiselin 1974).

CONCLUSION

The function of extended mating in D. veliei
remains undemonstrated. Changes in coupling duration
with the intensity of male-male competition tend to
support the contention that males invest their time to
avoid sperm competition.

However, the possibility that males protect females
from predation has not been discounted, particularly
since one qualification for the evolution of such a
tactic, higher adult female mortality, is apparently met.

Actually, the proposal of two exclusive selective
forces may be simplistic. Predator defense and sperm
competition could simultaneously direct the behaviors of
one or both sexes.

SUMMARY

Effects of inseminatory postures and behaviors may
serendipitously be of value to mating insects. If so,
these effects can become the function of couplings that
last beyond the requirements of ejaculate transfer. Two
such advantages are greater safety from predators and
prevention of sperm competition by blocking access to
female genitals. It is difficult to find a clear example
of the former in phasmids. Juvenile couplings in the
stick insect Anisomorpha buprestoides are suggestive,
but could be cases of sequestering a future mate (Eisner
1965). In Diapheromera veliei, mating females are
sheltered from bird attacks by attached males. The data
are insufficient to determine whether males remain

mating to protect mates. One requirement, greater single
female than single male mortality, may be met. Females
appear to suffer a higher death rate, but the magnitude
of difference necessary to maintain the male's presence
is unknown. There is more support for the contention
that male D. veliei prolong coupling as a means of
avoiding sperm competition. Preliminary results show a
correlation between the level of competition (i.e. sex
ratio) and the time investment per pairing (i.e. mating
duration).

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LITERATURE CITED

Alexander, R.D.   1959. The courtship and copulation of
     Pasimachus punctulatus (Haldemann) (Coleoptera:
     Carabidae). Ann. Entomol. Soc. Am. 52: 485.
Alexander, R.D.   1961. Aggressiveness, territoriality,
     and sexual behavior in field crickets. Behaviour
     17: 130-223.
Alexander, R.D.   1964. The evolution of mating behavior
     in arthropods. Roy. Entomol. Soc. Lond. Insect
     Symp. No. 2: 78-94.
Alexander, R.D., and D. Otte. 1967. The evolution of
     genitalia and mating behavior in crickets
     (Gryllidae) and other Orthoptera. Misc. Pub.
     Mus. Zool., Univ. Mich. No. 133.
Balduf, W.V. 1935. The bionomics of entomophagous
     Coleoptera. E.W. Classey, Hampton, Middlesex,
     England.
Bedford, G.O.   1975. Defensive behavior of the New
     Guiana stick insect Eurycantha (Phasmatodea:
     Phasmatidae: Eurycanthinae). Proc. Linn. Soc. New
     S. Wales 100: 218-221.
Bedford, G.O.   1978. Biology and ecology of the
     Phasmatodea. Ann. Rev. Entomol. 23: 125-149.
Bieman, D.N., and J.A. Witter. 1981. Influence of
     demography on the intensity of sexual selection in
     Malacosoma disstria (Lepidoptera: Lasiocampidae).
     Ann. Entomol. Soc. Am. (in press).
Chaplin, S.J.   1973. Reproductive isolation between two
     sympatric species of Oncopeltus (Hemiptera:
     Lygaeidae) in the tropics. Ann. Entomol. Soc. Am.
     66: 997-1000.

Clark, B. 1962. Balanced polymorphism and the diversity
    of sympatric species. Pages 47-70 in D. Nichols,
    ed. Taxonomy and geography. Syst. Assoc. Publ. 4.
Clausen, C.P. 1940. Entomophagous insects.
    McGraw-Hill, New York.
Cott, H.B. 1957. Adaptive coloration in animals.
    Methuen, London.
Cox, C., and B. Le Boeuf. 1977. Female incitation in
    the northern elephant seal. Am. Nat. 111: 317-355.
Daly, M. 1978. The cost of mating. Am. Natur.
    112: 771-774.
Downes, J.A. 1955. Observations on the swarming flight
    and mating of Culicoides (Diptera:
    Ceratopogonidae).   Trans. Roy. Entomol. Soc. Lond.
    106: 213-236.
Edmunds, M. 1974. Defense in animals. Longman,
    New York.
Eisner, T. 1965. Defensive spray of a phasmid insect.
    Science 148: 966-968.
Evans, H.E. 1969. Phoretic copulation in Hymenoptera.
    Entomol. News 80: 113-124.
Gangrade, G.A. 1963. A contribution to the biology of
    Necroscia sparaxes Westwood (Phasmidae: Phasmida).
    Entomologist 96: 83-93.
Ghiselin, M.T. 1974. The economy of nature and the
    evolution of sex. Univ. of California Press,
    Berkeley.
Green, E.E. 1913. On some luminous Coleoptera from
    Ceylon. Trans. Roy. Entomol. Soc. Lond.
    1912: 717-719.
Gurney, A.B. 1947. Notes on some remarkable Australian
    walkingsticks including a synopsis of the genus
    Extatosoma (Orthoptera: Phasmidae). Ann. Entomol.
    Soc. Am. 59: 59-61.
Gustafson, J.F. 1966. Biological observations on
    Timema californica (Phasmoidea: Phasmidae). Ann.
    Entomol. Soc. Am. 59: 59-61.
Gwynne, D.T. 1982. Male nutritional investment and the
    evolution of sexual differences in Tettigoniidae and
    other Orthoptera. Pages 337-366 in D.T. Gwynne and
    G.K. Morris, eds. Orthopteran mating systems:
    sexual competition in a diverse groups of insects.
    Westview Press, Boulder, Col.
Hamilton, W.D. 1971. Geometry for the selfish herd.
    J. Theor. Biol. 31: 295-311.
Henry, C.S. 1972. Eggs and repagula of Ululodes and
    Ascaloptynx (Neuroptera: Ascalaphidae): a
    comparative study. Psyche 79:1-22.
Hetrick, L.A. 1949. Field notes on a color variant of
    the two-striped walkingstick Anisomorpha
    buprestoides (Stoll). Proc. Entomol. Soc. Wash.
    51: 103-104.

Key, K.H.L. 1957. Kentromorphic phases in three species
    of Phasmatodea. Aust. J. Zool. 5: 247-284.
Korbott, K. 1961. Observations of the life histories of
    Acrophylla tessellata Gray and Extatosoma tiaratum
    Macleay (Phasmida). Univ. Qd. Pap. Entomol.
    1: 161-169.
Le Feuvre, W.P. 1939. A phasmid with a spermatophore.
    Proc. Roy. Entomol. Soc. Lond. (A) 14:24.
Leopold, R.A. 1976. The role of male accessory glands
    in insect reproduction. Ann. Rev. Entomol.
    21: 199-222.
Lloyd, J.E. 1979. Sexual selection in luminescent
    beetles. Pages 293-342 in M.S. Blum and N.A. Blum,
    eds. Sexual selection and reproductive competition
    in insects. Academic Press, New York.
McLain, D.L. 1981. Sperm precedence and prolonged
    copulation in the southern green stinkbug Nezara
    viridula. J. Ga. Entomol. Soc. 16: 70-76.
Matsuda, R. 1976. Morphology and evolution of the
    insect abdomen. Pergamon Press, New York.
Neumann, F.G. 1976. Egg production, adult longevity and
    mortality of the stick insect Didymuria violescens
    (Leach) (Phasmatidae: Phasmatinae) inhabiting
    mountain ash forest in Victoria. J. Aust. Entomol.
    Soc. 15: 183-190.
Parker, G.A. 1970. Sperm competition and its
    evolutionary consequences in the insects. Biol.
    Rev. 45: 525-527.
Parker, G.A. 1974. Courtship persistence and female
    guarding as male time investment strategies.
    Behaviour 48: 157-184.
Parker, G.A. 1979. Sexual selection and sexual
    conflict. Pages 123-166 in M.S. Blum and N.A. Blum,
    eds. Sexual selection and reproductive competition
    in insects. Academic Press, New York.
Pinto, J.D. 1978. The parasitization of blister beetles
    by species of Miridae. Pan-Pac. Entomol. 54: 57-60.
Readshaw, J.L. 1965. A theory of phasmatid outbreak
    release. Aust. J. Zool. 13: 475-490.
Richards, A.M. 1960. Observations on the New Zealand
    glow-worm Arachnocampa luminosa. Trans. Roy. Soc.
    N. Zeal. 88: 559-574.
Richards, O.W. 1927. Sexual selection and allied
    problems in the insects. Biol. Rev. 2: 299-364.
Robinson, M.H. 1968. The defensive behavior of the
    stick insect Oncotophasma martini (Griffin)
    (Orthoptera: Phasmatidae). Proc. Roy. Entomol.
    Soc. Lond (A) 43: 183-187.
Robinson, M.H. 1969a. Defenses against visually
    hunting predators. Evol. Biol. 3: 225-259.
Robinson, M.H. 1969b. The defensive behavior of some
    orthopteroid insects from Panama. Trans. Roy.
    Entomol. Soc. Lond. 121: 281-303.

Schmitz, H. 1950. Uber die Gattung Thaumatoxena nebst
    Beschriegung einer neuen Art... Rev. Zool. Bot.
    Afr. 43: 39-57.
Schultz, J.C. 1981. Adaptive changes in antipredator
    behavior of a grasshopper during development.
    Evolution 35: 175-179.
Sivinski, J. 1978. Intrasexual aggression in the stick
    insects Diapheromera veliei and D. covillea and
    sexual dimorphism in the Phasmatodea. Psyche
    85: 395-405.
Sivinski, J. 1980. The effects of mating on predation
    in the stick insect Diapheromera veliei Walsh
    (Phasmatodea: Heteronemiidae). Ann. Entomol. Soc.
    Am. 73: 553-556.
Sivinski, J. 1981a. The nature and possible functions
    of luminescence in Coleoptera larvae. Coleopt.
    Bull. (in press)
Solomon, J.D., and W.W. Neel 1973. Mating behavior in
    the carpenterworm moth Prionoxystus robiniae
    (Lepidoptera: Cossidae). Ann. Entomol. Soc. Am.
    66: 312-314.
Thornhill, R. 1976. Sexual selection and parental
    investment in insects. Am. Nat. 110: 153-163.
Tiemann, D.L. 1970. Nature's toy train, the railroad
    worm. Nat. Geogr. 138: 56-67.
Tostowaryk, W. 1972. The effect of prey density on the
    functional response of Podisus modestus (Hemiptera:
    Pentatomidae) to the densities of the sawflies
    Neodiprion swainei and N. pratti banksianae
    (Hemiptera: Neodiprionidae). Can. Entomol.
    104: 61-69.
Trivers, R.L. 1972. Parental investment and sexual
    selection. Pages 136-179 in P. Campbell, ed.
    Sexual selection and the descent of man, 1871-1971.
    Aldine-Atherton, Chicago.
Tuxen, S.L.P. 1970. Taxonomist's glossary of genitalia
    in insects, 2nd ed. Scan. Univ. Books, Copenhagen.
Waage, J.K. 1979. Dual function of the damselfly
    penis: sperm removal and transfer. Science
    203: 916-918.
Walker, W. 1980. Sperm utilization strategies in
    nonsocial insects. Am. Nat. 115: 780-799.
Wegner, A.M.R. 1955. Biological notes on Megacrania
    wegneri Willemse and M. alpheus Westwood
    (Orthoptera, Phasmidae). Treubia 23: 47-52.
Wojcik, D.P. 1969. Mating behavior of certain stored
    product beetles (Coleoptera: Dermestidae,
    Tenebrionidae, Cucujidae) with a literature review
    of beetle mating behavior. M.S. Thesis, Univ.
    Florida.

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