Orthopteran Mating Systems

Sexual Competition in a Diverse Group of Insects

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Chapter 14

14. Mating Behavior of the Primitive Orthopteran Genus *Cyphoderris* (Haglidae)

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The Haglidae (formerly Prophalangopsidae) were a large and diversified orthopteran family in the lower Triassic (Sharov 1968). Zeuner (1939) considered them ancestral to modern Gryllidae and Tettigoniidae (katydids and crickets). Only five extant species in three genera are known. **Cyphoderris monstrosa, Cyphoderris buckelli** and **Cyphoderris strepitans** occur in northwestern North America (for biological observations and distributions see Morris and Gwynne 1978). The two remaining species, **Prophalangopsis obscura** (Zeuner 1939) and **Paracyphoderris erebeus** (Storozhenki 1980), are Asian; nothing is known of their acoustic behavior. **C. strepitans** has been the main focus of study including experiments in the field to be published elsewhere (Morris and Gwynne, in prep.). Due to their ancestral taxonomic standing and the uniqueness of their mating habits, they are of special interest to evolutionary biologists.

Cyphoderris have a mating system akin to many acoustic Ensifera in which males produce a calling song by tegminal stridulation and attract females. They are crepuscular and nocturnal animals; sporadic stridulations by males typically begin late in the afternoon and become more consistent with increasing darkness. It is extremely difficult to approach males without causing them to stop calling, especially during the early evening.

Observations of mating behavior are further complicated by the fact that females are rarely found in the field and most of those observed are not interacting with males. Searches for females were conducted by moving through an area of approximately 0.3 hectares, checking the vicinity of all calling males. Thirteen nights of

searching revealed only eight females close enough to
males to be even potentially involved in courtship
activity. Only one complete copulation was observed
during this period and only once during other field
work. Exactly where females are located during this time
remains uncertain. The description of **Cyphoderris**
mating behavior which follows is based on two sources:
field observations of all three species, and observations
of **C. strepitans** individuals released into an open
enclosure (80 x 27 cm), subject to natural temperature
fluctuations and supplied with soil and plants obtained
from their natural habitat.

CALLING

        Characteristics of the perch from which individuals
call should be important to all acoustic orthopterans.
It can be argued that elevated sites increase broad-
casting range so long as the site is not so high that
amplitude at ground level becomes limiting (see Paul and
Walker 1979).   **C. monstrosa** was commonly heard calling
from over 10 m up in lodgepole pine **(Pinus contorta)** and
western yellow pine **(Pinus ponderosa)**. **C. buckelli**
and **C. strepitans,** on the other hand, typically called
at approximately knee height, the particular perch depen-
dent on the site.   **C. strepitans** males seem to prefer
sagebrush **(Artemesia tridentata)** where it is available,
but understory junipers, tree trunks, fallen branches and
grass blades are also used. Individuals in sagebrush
tended to call from the tops of plants suggesting that
they would move higher if possible. However, in every
habitat there were potential avenues, e.g. trees, to
higher calling perches going unused. One advantage of
bushes over tree trunks is that sound can be broadcast in
more directions. Male **C. strepitans** position them-
selves in a head-downward orientation (80% of 354
observations of 143 calling males were head downward).
This position might serve to direct the sound over the
maximum area possible, or as Paul and Walker (1979)
suggested for **Anurogryllus arboreus,** it may aid in
visual detection of approaching females or predators.
        Calling males were well spaced in the field (nearest
neighbors with a mean distance of 2.7 m) apparently as a
result of acoustical interactions (see below). Some
individuals called from lower perches (<20 cm) such as
grass stems, possibly as a result of intermale competi-
tion forcing them into peripheral areas. Certain popula-
tions are found in meadows which do not contain bushes,
so elevated calling sites may be important only on a
relative basis associated with advertisement competition.
        One of the most striking aspects of **Cyphoderris**
biology is the lower limit of temperatures at which males

are known to call. Adult male **C. strepitans** in north-
western Wyoming start calling in late May or early June,
just after the snow melts. **C. strepitans** males on Mt.
Washburn in Yellowstone National Park called regularly at
an ambient temperature of −4°C, recorded at their perch
height. Isolated individuals have been heard at tem-
peratures as low as −8°C. In comparison the lowest
temperature previously reported for singing in acoustic
Orthoptera was 7°C (Fulton 1925, Frings and Frings
1957). Individuals of all three species have also been
recorded either in the field or laboratory at tempera-
tures above 25°C. There is a positive linear relation-
ship between pulse rate and temperature. (See Morris and
Gwynne (1978) for the acoustical characteristics of these
three species.) The ability to sing at these extreme
temperatures allows males to be acoustically active from
early evening until just before dawn on many nights.

    C. strepitans males do not show high fidelity to
singing sites. While a few individuals reused the same
plant as a calling site on consecutive nights, others
moved considerable distances between the times that we
located them. The average distance moved by (nonvirgin)
males from the singing location of the previous night of
active calling (i.e. nights of unsuitable weather were
discounted) was 4.4 m (n = 34 measures of 28 males).
Some individuals were not heard for several nights in the
study area, but would show up again later. Despite
exhaustive searches we have not been able to determine
with certainty where males spend the day. In 1981, two
males were found just beneath the litter at the Pacific
Creek site. However, on 2 nights at the Mt. Washburn
site, the perches of eight consistently calling males
were marked late in the night without disrupting
calling. One-meter square areas around these perches
were searched the following morning to the point of
turning up the top layer of soil, but none of these
individuals were found. It appears that they do not
simply descend to a hideaway just beneath their present
perch.

    Male weight can fluctuate widely from one day to the
next. Copulating males lose weight (see below) as a
result of nutrient investment. Calling activity alone is
apparently costly on a caloric level. Seven males were
weighed before and after 1 h of calling activity with no
females present. Initially they had a mean weight of 839
mg (± 43.31, SD). After calling, mean weight loss was
1.9% of their body weight. The same experiment was
repeated a different night with 11 individuals left for 2
h, again no females present. Mean weight of 818 mg
(± 91.6, SD) for these males was reduced by an average of
3.1% by the end of the period. A certain minimum weight
must be important for survival reasons, so these

individuals would have a lot of weight to replenish after many hours of calling. Individuals are capable of consuming substantial amounts when food is available. Three individuals collected in the field weighed 667, 709, and 709 mg. After being provided apples and oatmeal for one day, they gained 250, 230, and 212 mg respectively. This may explain the previously mentioned absence of some individuals from the calling population for one or more nights, as they may be feeding.

The physical stresses associated with calling and mating may increase the mortality rate of males over females. In the field, females that can be found, are typically sitting passively and feeding or moving very slowly. In the laboratory males and females were maintained under the same conditions with identical choices of food. Over a 1-month period, nine of 29 males died while none of 29 females died.

MATING

Another feature of **Cyphoderris** mating systems that sets them apart from other Orthoptera is an unusual, nutritional contribution made by males during copulations. Both sexes are flightless, females having only two pairs of rudimentary wings. Males have short forewings (tegmina) each possessing a functional file and scraper.[1] Beneath the tegmina is a pair of cream-colored, fleshy hindwings. When a receptive female arrives at a male she mounts him so that her mouthparts are positioned above his wings. Males cease calling, lift and separate the tegmina, exposing the hindwings. **C. strepitans** males in the enclosure typically presented their hindwings just prior to or simultaneous with tactile contact by the female. At this point a female may move away, following rapid antennation, or she may begin to consume hindwing material and the resulting

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[1] The left and right tegmina are mirror images and both sets of files and scrapers are fully functional. A curious reversal of tegminal overlap is known to occur within the lifetimes of individual **Cyphoderris** and offers some interesting possibilities for courtship communication (Morris and Gwynne 1978, Spooner 1973).

flow of haemolymph.[1] While she is feeding in this
manner, the male, with the aid of his telescoping abdomen
and dorso-posterior gin trap (pinching organ)[2], attempts
to grasp and draw her genitalia into contact with his
own. Observations of nine C. **strepitans** copulations and
three additional interactions involving hindwing feeding
but no copulation, made it clear that females are capable
of making genitalic contact difficult or impossible. In
several instances, females feeding, or at least
attempting to feed, on a male's hindwings, interrupted
their feeding activity in order to bite at his abdominal
tergites, backing away from the probing male. One of us
(GKM) witnessed an interaction in the lab in which a
tarsus and hind femur of a C. **monstrosa** male (whose
wings were chewed to stubs in previous matings) were
severed by a female with whom he eventually copulated.
C. **strepitans** males, and the one C.**buckelli** male whose
mating is reported here, used their legs to push
backwards against females in an apparent attempt to gain
a positional advantage during this process. When and if
genital contact is completed, the female continues to
feed on the hindwing material and the male's abdomen
immediately begins to pump up and down. A spermatophore
with an external spermatophylax is transferred during
copulation, but it was not possible to determine exactly
when. The mean duration of copulation for eight C.
strepitans matings was 3 min 15 s (see Table 1). The one
observed C.**buckelli** copulation lasted approximately 2
min. The haglid spermatophore itself is relatively large
when compared to other orthopteran spermatophores (see
Gwynne 1982a) and it may take 3 min or so to transfer
it. However, there is evidence that no correlation
exists between duration of copulation and spermatophore
size among the Tettigoniidae for which data exist (Morris
1980). Three min is not at all short for crickets (Tom
Walker, pers. comm.), and although there are tettigoniids
in the same range (e.g. Mormon crickets copulate for 6-7
min -- Gwynne, in prep.), several are known to copulate
from 30 min up to several hours (see Morris 1980 and
references).

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[1] Female **Hapithus** (Gryllidae) also feed on male wing
     material (Alexander and Otte 1967), but it is the
     tegmina rather than hindwings.

[2] Morris (1979) discussed the structure and possible
     significance of the gin traps on male **Cyphoderris.**

Table 1. Summary of 12 **C. strepitans** and
1 **C. buckelli** mating interactions.
Conservative ranges are provided where an
exact onset or ending to an activity was
difficult to determine.

Mating histories of males	Duration of wing feeding prior to coupling (min:s)	Coupled Yes	No	Duration of copulation (min:s)
C. strepitans				
virgin	2:00	X		4:57
once-mated	9:31		X	
virgin	4:50		X	
once-mated*	7:34	X		3:33
virgin	1:06-2:55	X		2:38-4:27
virgin**	0:44	X		3:21
once-mated	20:10		X	
virgin	?	X		2:30-3:30
virgin	10:00-11:20	X		1:16-2:36
virgin	5:00	X		1:45
virgin***	3:00	X		3:57
unknown***	Less than 12 min for total hindwing feeding including copulation.			
C. buckelli				
mated	ca. 7:00	X		ca. 2:00

 * wings fed upon twice previously, but only resulting
   in one copulation.
 ** unmated but its wings chewed previously in the lab
    by another male.
*** occurred in the field.

Copulations were terminated by males in all cases; immediately after spermatophore transfer males began to pull away from females who typically held their positions and obtained a few more seconds of wing feeding. In seven of nine observed copulations of **C. strepitans**, males resumed stridulation immediately after mating. In three of these instances stridulation was resumed even before the male and female were uncoupled. In one case a male pulled away from a female and silently moved over to and began feeding on the hindwings of a nearby, calling male (see below). In the final instance, a male moved 4–5 cm away, called once and then moved around for several minutes before calling again. Since there is probably associated risk with sound production in Orthoptera (Cade 1979, Walker 1964) and there is no known advantage for haglid males in attracting females they cannot inseminate, their behavior may indicate that males are capable of mating again just after a copulation. Although they were allowed to continue calling undisturbed in the enclosure, no males mated twice in the same night (it is not known whether this was due to a lack of sexually receptive females in the enclosure or rejection of these just-mated males). One male did mate 2 nights in a row (see Table 1).

Females, on the other hand, moved away from the site of mating immediately after uncoupling in all cases. No females were ever observed eating the externally attached spermatophylax despite the fact that some were left undisturbed for over an hour. One female was observed bending around in an apparent attempt to eat the spermatophylax before being disturbed. This action occurred 37 min after she had copulated. In all cases the spermatophylax had disappeared by the following morning. It can be stated with some certainty that females do not consume the spermatophylax very soon after its transfer. In three instances (one in the enclosure and two in the field) females were observed feeding on plant material within minutes after copulating.

None of 29 females kept in the laboratory were known to have mated more than once. Since we had no way of checking their prior mating histories (without dissecting them) we cannot be certain that they do not mate repeatedly. However, all 12 females known to have mated once (taken in the field with spermatophore attached or copulating in the enclosure) were given additional opportunities to remate on subsequent evenings but showed no indication of receptiveness. No eggs were laid by any females during the period that they were kept in soil-filled containers in the laboratory (up to 2 months). Two females dissected late in the summer contained 17–23 eggs.

Males then, contribute both a sizeable spermato-
phylax and hindwing material as a result of mating. A
C. strepitans male, weighed in the lab immediately before
and after mating, lost approximately 10% of his body
weight. Virgin males of **C. strepitans** showed an average
body weight of 701 mg (n = 25) at a low-elevation site
(2195 m) in Grand Teton National Park. Nonvirgins from
the same location, individuals whose wings indicated
mating activity within 24 h of capture (n = 8), had an
average body weight of 629 mg. A Student's two-tailed
test shows this difference to be significant at the 1%
level; this is also a difference of approximately 10% in
body weight.

Cyphoderris are not the only Orthoptera to make a
dual 'investment' as part of mating. Various gryllids
(Gwynne 1982a) and many species of cockroaches(Breed
1982) have specialized glands on the dorsum of males
which secrete substances fed upon by females. This
feeding takes place during, and in some cases, before and
after copulating (Gwynne 1982a). An important difference
between feeding on glandular secretions and feeding on
hindwing material, is that wing material is not
replaced.   Contributions such as these can be classified
as nonpromiscuous mating effort (as defined by Gwynne,
1982b), in that they occur prior to fertilization (and
thus cannot be parental effort -- Alexander and Borgia
1979), but they do "provide material or risk-lowering
benefits to the female and/or her offspring and result in
a decrease in the probability of a male locating other
mates".

Using the wound incurred by wing feeding as an
indicator of a mating, one could potentially monitor a
population over time by mark-recapture technique and
measure reproductive success among individual males. If
the wing material and spermatophylax are nutritional
resources that enhance female fitness (Gwynne 1982b),
sexual selection theory predicts that females should be
selective about mates, opting for those individuals that
can provide more of the resource. It seems logical that
virgin haglid males, not having given up any wing
material or spermatophylax components, would be capable
of providing more of these materials than nonvirgin males
and should, therefore, be preferred by receptive
females. On the other hand, females do not devour all of
a male's hindwings during a mating. It is possible,
therefore, that as long as wing material is present all
males are equally able to provide nutrition to females.
This seems unlikely for three reasons. Nonvirgin males'
wings are shortened, and the remaining wing material may
be more difficult for a female to reach. Old wounds
harden and may not be as easily fed upon or as palatable.
Finally, there is reason to believe that males cannot

produce full-sized spermatophores at every mating.[1]   If
chewed wings indicate that a male has already transferred
at least one spermatophore, selection should favor
females who seek out virgins.
     If this male nonpromiscuous mating effort repre-
sents a relatively large investment per mating (and it
appears that it does), sexual selection theory further
predicts that there should be low variance in male
reproductive success and high confidence of paternity
(Trivers 1972). Using wing wounds as reasonable evidence
of mating, Morris and Gwynne (in prep.) have found that
virgin male C. strepitans are more likely to obtain a
mating than nonvirgin males. This differential in mating
success could occur either because females exercise
choice or because virgins out-compete nonvirgins. Also
noted was a low variance in male mating success, in that
the population was found to be only mildly polygnous and
almost all males obtained at least one mating. No data
exist with regard to confidence of paternity, although in
the study reported here no females were observed to mate
a second time.
     There are complications which should be taken into
account concerning the use of wing wounds as indicators
of matings. During calling periods in the laboratory we
found that C. strepitans and C. buckelli were not
reluctant to offer their hindwings, even in the absence
of a female. We were consistently able to elicit
sustained exposure of hindwings and genitalic groping by
males of both species simply by probing the animal from
behind. Additionally, hindwing feeding did not always
culminate in a copulation (Table 1). Whether or not such
behavior is important in nature is not known, but there
is no reason to believe otherwise. On one occasion in
the field a C. strepitans female was observed position-
ing herself over the back of a male. She interacted
for the next 6 min, at least once nipping at his hind
wings, until he fell from the plant while maneuvering.
In addition, duration of hindwing feeding was quite
variable whether it culminated in a copulation or not
(Table 1), ranging from 44 s to 11 min 20 s when followed
by a copulation and from 4 min 50 s to 20 min 10 s

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[1]   There is evidence (Gwynne 1982a) for the tettigoniid
     Orchelimum delicatum that newly mated males which
     mated a second time after 24 h had a significantly
     smaller spermatophore.

when it did not.[1] It is assumed that the extent of
damage to the wings would be related to the duration of
feeding, but there is no assurance that even a large
amount of damage always represents a copulation. Lab
data suggest, however, that wing damage seen in the field
clearly represents mating opportunities which have a very
high probability of having culminated in a copulation.
     There is one other complication (alluded to above):
a male feeding upon the hind wings of another male. The
incident, observed in the laboratory, involved a male who
had just copulated and a nearby calling male.
Immediately after mating, the first male moved silently
over to chew on the wings of the unresisting caller. It
then appeared that the feeding male stopped of its own
accord and moved off. On other occasions males with
intact wings have been left together in enclosures
overnight and were found with chewed hindwings the
following morning. This behavior is less likely to occur
in a field situation since they were unnaturally close in
the laboratory.
     Evidence for a lack of cautious discrimination by
males with regard to the offering of wing material comes
primarily from the laboratory. However, one reason to
expect similar behavior in nature is the temporal
limitation on mating in these populations. Although they
apparently live for more than one year, males are
sexually mature for only one season (only virgin males
are found when adults first emerge). A newly emerging
adult population on Mt. Washburn was censused on 28 June
1981. Examination of most of the calling males (n = 14)
revealed that all had intact wings. On 2 July, 21 of 40
calling males had intact wings. On the following night
17 of 34 males had intact wings. It would appear then,
that matings can take place in a great flurry over a
short time interval. Apparently 50% of the population
had mating opportunities over just 3 nights. If
receptive females are as scarce as they appear to be on
most nights, it might be reproductively expensive for a
male to pass up mating opportunities of any kind.

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[1] Times given for duration of hindwing feeding do not
necessarily represent continuous feeding. In most
instances, females interrupted their feeding inter-
mittently, apparently in response to the maneuvering
and groping by males. In the cases where times of
20:10 and 11:20 were recorded, a stopwatch was stopped
and restarted each time these females interrupted
their feeding. Actual feeding times of 6:08 and 10:15
respectively were measured.

MALE-MALE AGGRESSION

Species in which male nutrient investment is negligible, such as field crickets, often have mating systems consisting of male dominance hierarchies (Burk 1982). Dominant males win physical aggressive interactions, a fact which ultimately results in their mating more often than subordinates. Species with larger nutrient investments might be expected to forgo costly aggression, competing instead for access to females through advertisement of their potential to contribute nutritionally. **Cyphoderris** males (and females) have large, powerful mandibles and are capable of inflicting severe damage and even killing one another (as occurred when they were kept under abnormally high densities in the laboratory). Male **C. strepitans** held in jars or released into the enclosure interacted acoustically (usually by alternating stridulations) and occasionally physically grappled (15 instances during 31 h of observation). No **C. strepitans** males were observed fighting in nature.

Infrequency of physical contact does not necessarily mean that intensive aggression is not occurring. Stridulation is also considered an aggressive device (Alexander 1961). We found that calling males tended to be well spaced in the field (see above). It is possible that noncallers, undetected by us, were occasionally between callers. One of us (GND) over a total of 11 nights noted seven instances of 'pairs' of calling males within a half meter of each other. They appeared to be interacting acoustically. There was no obvious pattern in their orientation with respect to each other. However, these males were highly predictable regarding the condition of their wings. In six out of the seven pairs, both individuals' hindwings were examined. All six pairs consisted of one male with chewed wings and one with intact wings. On these same nights, censuses of the male population as a whole, revealed more than twice as many males with chewed wings as with intact wings. These data suggest a rate of interactions between virgins and nonvirgins which cannot be explained by chance.

CONCLUSIONS

The dual investment of **Cyphoderris** males leads one to certain predictions about their mating system. These predictions, i.e. low variance in male reproductive success, high confidence of paternity, decreased levels of potentially injurious aggression and possibly even an increase in the potential for mate discrimination by

males -- all are discussed in detail by Gwynne(1982b) --
are based on the assumption that the male contribution is
substantial. A more complete understanding of the
relative value to females of the male contribution will
require an analysis of hind wing tissue and the
spermatophylax. What kinds of materials are males
actually supplying and of what use are they to females?
     The offering by males appears to be a substantial
one as most males do mate and there is some evidence for
discrimination by females on the basis of male mating
history. There is also a lack of overt, physical
aggression, although males are acoustically spaced. A
critical need exists however, for more information on the
elusive females. Is there any maternal care? Do they
mate more than once and, if so, what is the degree of
sperm precedence?
     It seems that in the case of an ancient orthopteran
family, being around longer than most is not a result of
leading the simple life.

SUMMARY

     The mating behaviors of three species of
Cyphoderris (Haglidae) are discussed. Males call from
elevated perches at temperatures as low as -8°C.
Receptive females appear to be scarce relative to males
on most nights. Females feed on the fleshy hindwings of
males prior to and during copulation and consume a
relatively large external spermatophylax. **C. strepitans**
copulations averaged 3 min 15 s in duration and were
terminated by males. Wing wounds of males can be used as
indicators of probable reproductive activity to test
theoretical predictions that virgin males are more likely
to obtain a mating than nonvirgins. There is low
variance in male mating success through the season.

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