Orthopteran Mating Systems
Sexual Competition in a Diverse Group of Insects

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Chapter 10

10. Pair Formation in the Katydid *Orchelimum nigripes* (Orthoptera: Tettigoniidae)

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Mating strategies are beginning to be examined from an evolutionary ecological perspective. What are, for example, the environmental factors that favor a mate-securing strategy involving territorial behavior by males, over strategies lacking such defensive behavior? The predictions we have to date regarding environmental influences on the evolution of mating strategies are based for the most part on data collected on avian and mammalian species (Brown 1975, Emlen and Oring 1977, Wittenberger 1981). It is in these groups that a large data base exists that details the social behavior for many species under natural conditions. The field study reported here, by investigating pair formation in **Orchelimum nigripes,** is (to the author's knowledge) the first attempt to furnish comparable data for a katydid species.

Many of the Tettigoniidae have long been presumed to be territorial because males have been observed calling from the same perches for a number of days (Alexander 1956, Blatchley 1920). For example, Blatchley (1920, p. 550) quotes McNeil's earlier report concerning a male of O. **nigripes** that "kept a place over the wooden finish of a doorway for more than a week". Males also have been reported to engage in fighting (grappling, biting and kicking) with the result that the male who won the encounter stayed in the area and the loser left (older references in Dumortier 1963 and Morris 1967, Busnel 1967, Morris 1971). Morris (1971) described fighting in two species of **Orchelimum (O. gladiator** and **O. vulgare)** and suggested that males were excluding rivals from areas utilized for mating. The present study on O. **nigripes** extends this work started by Morris by monitoring the movements and behavior of individual adults for two entire reproductive seasons. As well as examining the nature of the competitive interactions occurring between males, data were collected on those aspects of ecology and natural history that would enable the O. **nigripes**

mating system to be compared with those described
previously. For example, Alexander (1975) has suggested,
based on the assumption that calling males congregate and
the 'chorus' attracts receptive females, that katydid
systems may share characteristics in common with avian
leks. As yet, however, how such choruses form has not
been described. To what extent then do the data col-
lected in the present study support existing assumptions
and so speculations concerning factors that have played
an influential role in shaping the mating system of **O.
nigripes** and other katydids?

METHODS

     The study population was monitored for two complete
reproductive seasons, 1974 and 1975. Some data on
aggressive interactions were collected in 1976; however,
survivorship and movement of individuals were not
monitored that year because population densities were
very low. It was apparent from samples collected on and
adjacent to the study site that large numbers of eggs
failed to hatch in 1976.
     Biweekly canvassing of the entire study site
revealed areas where nymphal density was high. Because
first and second instar nymphs were small and proved too
difficult to locate among the dense vegetation, canvas-
sing was initiated as soon as third instar nymphs were
prominent. Transects were made every 10-15 m through the
study area and nymphs were counted as they jumped away
from the investigator. Thick vegetation was shaken with
the end of the insect net to reveal hiding nymphs.
     Adult animals, once located, were marked in two ways:
1) with a tegmino-pronotal clip code which served as a
permanent mark and 2) with a code employing dots of paint
which facilitated recognition of individuals from a
distance. After marking, males were weighed and
pronotum, wing, tegmen and body length recorded.
Morphological features, which suggested age and/or
fighting between males, were noted. Weights of
individuals were monitored periodically, usually every
4-5 days. Numbered stakes were placed at the site where
a male was originally captured. Every 3rd or 4th day,
males were relocated and their locations plotted in
reference to their original positions.
     Interactions between males were recorded using a
Uher tape recorder, model 400L. During an interaction,
the intensity of an individual male's signals on the tape
could be raised by bringing the microphone closer to him.
This technique together with individual peculiarities in
acoustical signals allowed recognition of individuals
during subsequent analysis. Tapes were analyzed

utilizing a Kay Electric Co., Sonograph, model 7030A, and NARCO-biosystems physiograph, model DMD 48. Background noise was minimized by passing the signal through a 2000 Hz high pass filter. This is well below the frequencies of **Orchelimum** spp. sounds (signals start at about 8000 Hz). In some cases, durations of taped signals were checked with a stopwatch. A few hours each day were spent observing a group of males. Animals did not seem to be disturbed by the presence of an observer if movements were kept to a minimum. In the beginning of the reproductive season, numbers were high and adults were found throughout the study site, making it difficult to monitor more than 10% of all the interactions that occurred. In contrast, later in the reproductive season, the clumping of males into the rather well defined areas of cattails and high sedge enabled the activities of about 50% of all calling males to be monitored. Much of the data presented on social interactions will be based on observations made after adults had moved to these areas and mating had begun.

Territory size was measured in several ways. 1) In all natural encounters the distance at which a stationary calling male oriented to an intruder and exhibited territorial defense by aggressive signaling was recorded. 2) Males, if previously disturbed by an observer (touched lightly), when approached again, moved away in a direction opposite the approaching disturbance. Males often continued to call while moving. In this way males could be induced to move toward a near neighbor, and the distance at which the neighbor exhibited territorial defense noted. 3) Males collected from another population were housed in cages attached to bamboo stakes. Such caged males were placed at various distances from a singing male and the distance at which the singing male exhibited acoustical aggression recorded. The last method proved the least satisfactory of the three. Caged males often failed to behave normally, and therefore, did not elicit normal acoustical aggression from the territorial male.

Laboratory populations were maintained during the study. Nymphs from neighboring populations were collected and kept in the laboratory until mature, or adults were raised from eggs laid by these females mated in the laboratory. Embryonic diapause was broken by exposing eggs to an 8-week cold period (temperature approx. 5°C) followed by a period of high temperature (25°C) and long days (16 h). Animals in the laboratory were fed a mixture of soybeans, lettuce, fishfood, oats, sunflower seeds, and a vitamin supplement. Laboratory-raised animals were comparable in size to those found in the field. Nymphs and females were housed in 5-gallon and 10-gallon aquaria. Mature males were housed

individually in cylindrical wire cages, 12 cm high and 5 cm in diameter. Mated females were housed in cylindrical wire cages, 15 cm in diameter. Several stems of known oviposition plants were available to females.

The following terms are utilized throughout the paper to replace lengthy descriptive statements.

1. Consistent singers or callers: males who stridulated throughout the active period (1000-1800 hours). However, they may have been silent for short periods of time during social interactions upon establishing close contact with conspecifics.

2. Silent males: males who did not stridulate or only stridulated for short periods of time (< 10 min) and then only a few times during the active period.

3. Territorial male: a male who 'defended' a site by responding to stridulation by an approaching male with aggressive signaling (see male-male interactions).

4. Dominant male: most often, a male who remained in an area and stridulated after an aggressive interaction. Less frequently, when the same two males continued to interact, it might signify a male who caused a near neighbor to stop stridulating by moving toward him.

5. Subordinate: a male who left an area or did not stridulate if he remained in an area after an aggressive interaction.

6. Two (2), four (4), six (6) days old (or days of age): days since the final molt or the age of an individual as a reproductive.

STUDY SITE

The study was conducted on the Edwin S. George Reserve, Livingston County, Michigan. The physiography and vegetation of this area have been described in detail in Cantrall (1943).

The O. nigripes study area was the northeast portion of Cattail Marsh (Fig. 1). A narrow belt of vegetation surrounded more open water in the center of the area. Water lilies (Nuphar advena) were found in the center section and cattails (predominantly Typha latifolia with some T. augustifolia) and sedge (largely Carex lanuginosa) predominated in the belt. A detailed description of the study site can be found in Feaver (1977). It is important to note for purposes of the following discussion that the patches of cattails and high sedge (> 1 m) were separated from one another by patches of low sedge and grasses. Mats of water lilies interdigitated into this belt and also served to separate patches of cattail and high sedge from one another.
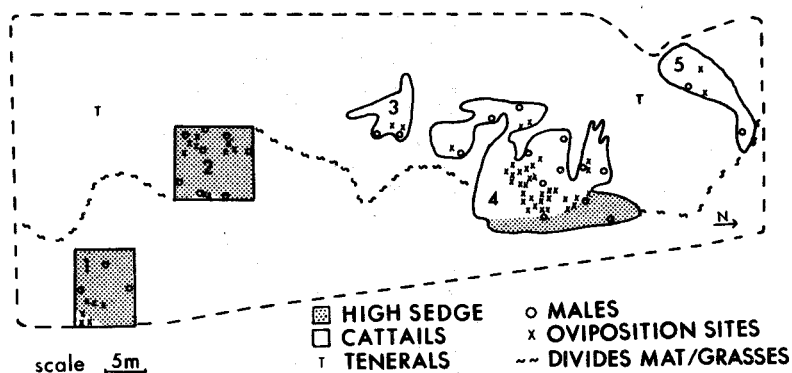
Fig. 1. **O. nigripes** study site 1975, the northeastern
tip of Cattail Marsh. Oviposition site distribution
(1975) and male distribution (for the first week after
large numbers of calling males were found) are
illustrated.

RESULTS

NATURAL HISTORY AND ECOLOGY

Aging

Adults reached maturity at different times during
the reproductive seasons and generally were not located
until their exoskeleton had hardened. Therefore, it was
necessary to develop an aging technique for adults. A
list of morphological changes accompanying aging was
compiled on 95 **O. nigripes** adults that were captured
with soft exoskeletons (20 while in the process of the
final molt).

The exoskeleton required 2 days to harden, there-
fore, all individuals captured with soft exoskeletons
were assigned an age of 2 days. Body color changed from
lighter to darker green over a period of 3-5 days.
Pigment streaks became apparent about 1-2 weeks after
molting. The intensity of these streaks increased with
age and very old individuals were mottled in appearance.
Eye color changed with age. Nymphs and newly molted
adults had yellow eyes which changed over a period of 2-4
days to orange.

Head color also changed. Late instar nymphs and
young adults had green, or rarely, yellow heads. By the
3rd or 4th day, the face started to show traces of beige
pigment, or brown in the case of yellow heads. By the
6th or 7th day all the green or yellow in the head had
disappeared. Later, more noticeably in the case of the

beige-faced individuals, the face became streaked with
darker pigment. It took 9-12 days for the head to appear
tan or rosy in these individuals.

On the basis of these color changes approximate ages
could be assigned to new adults and correlated with any
changes in behavior noted. For example, an individual
with a green head, yellow eyes and a light green body
when first captured, was assumed to be at least 2 days
old and so assigned to that age. An individual with
orange eyes, a dark green body, and some green on the
head was assigned an age of 4 days. An individual
similar to the latter, but with no green on the head,
was assigned an age of 6 days.

RECRUITMENT AND THE BEHAVIOR OF YOUNG ADULTS

Nymphs hatched in late May and early June from eggs
laid the previous fall. Adults appeared about 2 months
later in July and August. Populations persisted until
killing frosts occurred in October. Tenerals (newly
molted adults) were difficult to find, however, I was
able to locate 95 individuals with soft exoskeletons and
monitor the behavior of those that survived.

In any one area, large numbers of newly molted
females appeared 1-2 days after large numbers of newly
molted males. It appears then, that females generally
molted later than males.

Tenerals spent most of their time feeding in dense
vegetation. Often groups of two or three animals were
found feeding on the same plant. For the most part,
individuals behaved as though they were oblivious to each
other's presence. If two individuals contacted each
other while feeding, antennae were flicked and the
individuals moved apart. Two days after molting, adults
were more conspicuous, being found on lower vegetation,
such as the water lilies and arrowheads. Males started
to call (stridulate) 3-4 days after the final molt, and
called sporadically and for short periods during the next
day or two.

Once adults appeared, counts of stridulating males
were made every 3-5 days. Only consistent singers were
included. Numbers peaked early in the reproductive
season and then declined (Fig. 2). Young males actually
joined the calling populations throughout the
reproductive season, but later in the season, males
disappeared faster than they were added. Two newly
molted adults were found October 15, the last day any
adults were found in 1975.

Females began to interact with males when about 3 or
4 days old. Males, in contrast, did not begin to
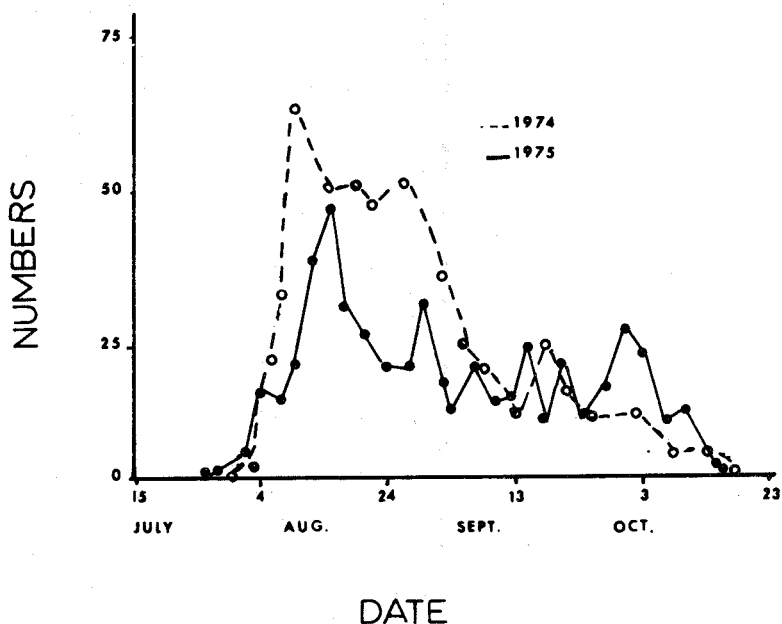interact with conspecifics until they started to call

Fig. 2. Changes in the number of calling males throughout the reproductive season.

consistently, or about 1-3 days after similar aged females had begun to interact socially.

SURVIVORSHIP

In 1975, 142 males <3 days old were captured. Only 51% (72) were recaptured, most of them within 2-3 days (90%, 65/72), the others after 4 or 5 days (10%, 7/72). At this stage males were moving throughout the habitat (see section on movement). In order to make sure that the males not recaptured had not emigrated, areas adjacent to the study area were censused. None of the marked males were located in these areas. It appeared then that about half of the newly molted males did not survive to call. In 1974, the results were similar; 75 2-day old males were marked and only 56% (42) survived to age 5 days. Mortality was also high in young females. Of 85 2-day females marked in 1975, 53% (45) survived to

age 5 days; in 1974, only 40% (12/30) of the 2-day
females marked, survived to age 5 days.
     There were indications that parasitic infections and
unsuccessful molting contributed heavily to mortality at
this stage. Forty to 60% of the late instar nymphs
collected for laboratory use died from infestations of
horsehair worms (Nematomorpha, Gordioida) and/or
nematodes (Nematoda, Mermithida). Several newly molted
adults were seen in the study area that apparently molted
unsuccessfully (having misshapen bodies). These adults
were never recaptured and it was assumed that mortality
resulted from the deformities.
     Once males started calling consistently (5-6 days
after the final molt), they were easily located.
Survivorship was low for the first few days after calling
became consistent, then it increased (Fig. 3). Both
years of the study 50% of the males disappeared within 6
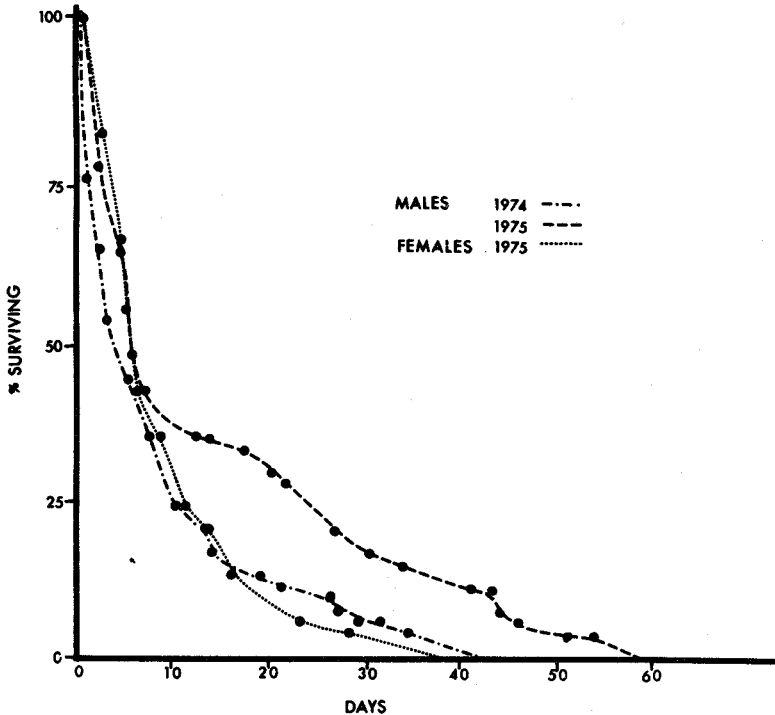days after they started to call consistently.

Fig. 3. Survivorship curves for calling males, 1974 and
1975, and females >6 days old as adults, 1975. All
pairwise comparisons (ANCOVA) of regressions significant
(p = 0.000) with the general form of the regression, log
survivorship = a+b (days), (r^2 for regressions =
0.921-0.994 and p = 0.000).

In 1975, data were compiled on the survivorship of
45 females marked when they were known to be about 6 days
old. Fifty percent of these females disappeared within 6
days. In 1974, only 29 females were marked at this age,
but the results were similar: 50% of these females
disappeared within 5 days.

A few individuals were parasitized by tachinid flies
(n=2), horsehair worms and nematodes (n=5). Two indivi-
duals were found in the webs of orb-weaving spiders. All
instances of observed predation were on moving individ-
uals, two males and two females swimming from one cattail
to another were taken by turtles. Two males also died
from injuries incurred during aggressive interactions.

Although the mean survivorships observed for the two
sexes were similar, some differences in the pattern of
survivorship between males and females older than 6 days
were noted. Twenty-five percent of the males disappeared
1 (1975) and 2 (1974) days after they started to call
consistently. Yet, 75% of the females were recaptured 3
(1975) and 4 (1974) days after first capture when at
least 6 days old. Thus females appeared to enjoy higher
survivorship at this time even though throughout the
study, fewer females were captured than males. Since
most of the physical combat took place early in the
season, mortality resulting directly or indirectly from
it may have accounted for the lower survivorship of males
compared to females (who did not fight).

Later in the season males appeared to enjoy higher
survivorship than females. In 1975, only 25% of the
females were recaptured when at least 24 days old. Yet
35% of the males were recaptured when they were at least
24 days old. Females began to oviposit when 10 days old
and when approached were not able to rapidly withdraw
their ovipositors from plants. Perhaps they proved more
conspicuous prey than males at this time. However, not
much significance should be assigned to the data
collected at this time. Few individuals in either sex
lived to this age. Sample sizes were therefore small and
silent females were always more difficult to locate than
singing males.

Density may have had a negative effect on survivor-
ships. Survivorships were lower in 1974 when densities
were higher ($0.042/m^2$), than in 1975 when densities were
lower ($0.038/m^2$).

ADULT/NYMPHAL HABITATS

Early instar nymphs and adults were found in
different areas of the study site. Nymphs occurred
mainly in areas containing low grasses, arrowheads and

water lilies; adults were most common among cattails and high sedge (Fig. 1). Although nymphal habitats bordered those of adults, in actuality, nymphs were found at a distance from where they would eventually establish adult residences. For example, during one census when early instar nymphs predominated, the mean distance from each nymph encountered to the nearest adult residence of the previous year was 10.3 m (n=47).

The shift in habitat, at least early in the reproductive season, occurred after the molt into the adult stage. Newly molted adults were found in the water lily mats or more grassy areas, but later were recaptured in typical adult habitats. Some 4-8 day old males were observed calling from the water lily mats (n=42), but only early in the season before large numbers of females appeared in the adult habitats. After females appeared in the patches containing cattails and high sedge, males were observed calling from these areas. Throughout the season, adults were observed frequently feeding in the water lily mats but never stayed in them for long periods of time (<20 mins). By September the water lilies and the arrowheads had finished flowering. Although late instar nymphs were often seen feeding with adults on heads of cattails, they associated with the water lily mats when not feeding. Perhaps the mats offered more cover and so protection from predators. Why then were the areas containing cattails and high sedges more suitable for adults? Perhaps it was because one resource offered by these areas was oviposition sites for females.

In 1974, only small areas of Patches 2 and 4 were surveyed for oviposition sites. Fifteen oviposition sites were located in cattails and one in sedge. In 1975, the entire study site was surveyed; 53 sites were discovered and the ratio of those in cattails to those in sedge was approximately 4:1 (Fig. 1).

The adult ages (days since the final molt) of 14 females that mated were known. These females on average were 12 days old (range 7-22). No female was observed to mate more than once. Females probably mate only once in the field, since in the laboratory females mated only once although given the opportunity for multiple matings (males were repeatedly introduced into their cages). Morris et al. (1975) also have laboratory data suggesting that females of **O. gladiator** only mate once. In **O. nigripes** oviposition occurred a minimum of 3 days after mating (n=10).

MOVEMENT

Younger adults moved more than older adults. Therefore, the displacements of individuals who had

molted less than 8 days previously were analyzed
separately from displacements undertaken by older
adults.   Displacements were grouped this way, since in
fact, movement data for animals engaged in different
activities were being segregated.   For example, the
youngest female of known age to mate was 7 days old; so
the displacements of females who were mating and
ovipositing (>8 days old) were examined separately from
those not as yet engaged in these activities (<8 days
old).

The differences in mean displacement between sexes
of adults older than 8 days were insignificant (p >0.10).
The means for females were 5.4 m (n=31, 1974) and 5.1 m
(n=54, 1975), for males were 6.0 m (n=107, 1974) and 5.2
m (n=191, 1975).   However, the patterns of displacements
observed were very different (Fig. 4).   Males had a much
larger variance (s^2 = 38.6, 1974 and 54.9, 1975) around
the mean displacement than females (s^2 = 14.9, 1974 and
13.2, 1975).   Males thus tended to undergo either large
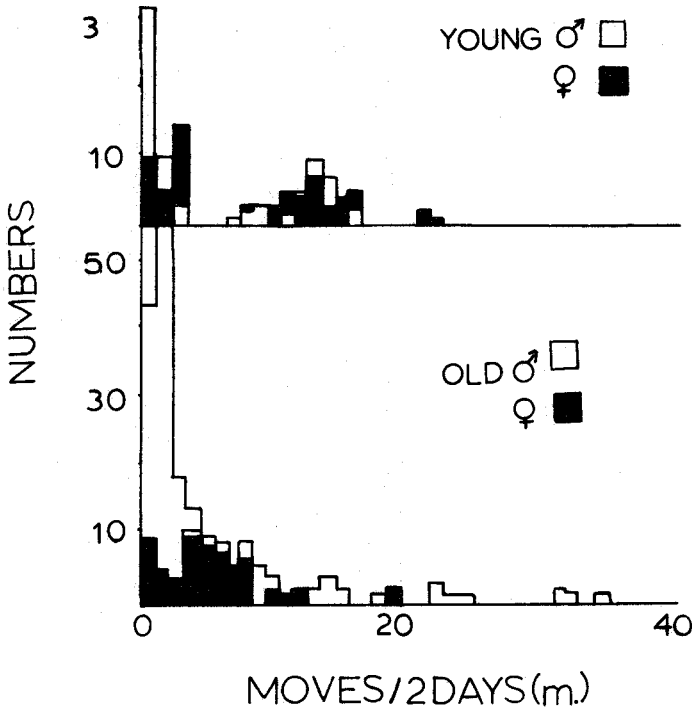or small displacements, while displacements for females

Fig. 4.   Pattern of distances moved over 2-day periods
for young and old adults.

were more consistently of intermediate length (p <0.05).
      Most of the movements by females were out of the
patch to feed or toward and away from different males
within a patch. In five instances, females were
observed to leave a patch after interacting with the
males there, but these females moved into adjoining
patches less than 5 m away (less than mean). The only
instances of older females undergoing displacements
greater than 9 m (= mean + SD) involved females moving
from predominantly sedge patches to predominantly
cattail patches. Females moved only after the few
cattails in the sedge patches (Patches 1 and 2, Fig. 1)
were used by more than one female for oviposition. All
females that moved were heavy and so probably carrying
numerous eggs. In one instance a female was observed to
test every cattail in the sedge patch before moving out
of that patch. It appears then that females preferred
to lay in the cattails more than sedges and sometimes
moved when there were no more cattails in predominantly
sedge patches that could be utilized as oviposition
sites. Small displacements by males were associated
with aggressive interactions and the back and forth
contesting for position that took place in these (see
male-male interactions). All the long moves (ca 10 m or
mean + SD) by males, occurred after the male had lost
several aggressive interactions that day within a
habitat patch.
      The mean displacements observed for adults <8 days
old were 7.2 m (n=63, 1974) and 6.7 m (n=86, 1975) for
males, 8.4 m (n=42, 1974) and 8.1 m (n=65, 1975) for
females. As for older adults then, differences in mean
displacement between sexes of young adults (<8 days old)
were insignificant (p >0.10). However, the mean
displacements for both sexes for young adults were
greater than for adults older than 8 days (p <0.10).
      The variances for young females were 38.2 (1974)
and 35.5 (1975), for young males 41.2 (1974) and 34.4
(1975). In contrast to older adults, the differences in
displacement patterns for males and females <8 days old
were insignificant (Fig. 4, p >0.10).
      In both years of the study, large numbers of newly
molted adults were captured in a 2 m x 2 m area of the
water lily-arrowhead-grass mat between cattail Patches 4
and 5 (Fig. 1). This part of the mat was located closer
to Patch 5 than Patch 4, but Patch 4 was larger than
Patch 5 and so probably more suitable in terms of the
amount of food and oviposition sites within it. All of
the males and females marked in the mat were <4 days
old. To investigate the factors responsible for the
greater average displacement of young adults <8 days

old, a special effort was made to monitor closely the movements of this group of young adults for 8 days after initial capture (Table 1).

Table 1. Pattern of movements by young adults; F = female, M = male.

| Days since first capture | Number recaptured in various areas | | | | | | | |
| | Water lily mat | | Cattail Patch 4 | | Cattail Patch 5 | | Other | |
	F	M	F	M	F	M	F	M
0	70	90	0	0	0	0	0	0
2	7	22	17	10	13	17	0	0
4	0	5	24	20	8	6	1	0
6	0	0	16	22	2	3	1	0
8	0	0	11	19	1	2	0	1

All except two of the individuals recaptured during the 8-day period confined their movements to the northern half of the study site. At the end of the 8 days, all except three individuals were in cattail Patch 4. During the 8-day period an equal number of females went to Patch 5 as to Patch 4. However, the females that went to Patch 4 remained there; while the females that went to Patch 5 left it and were later recaptured in Patch 4. The movements of males were similar to those of females (Table 1). However, proportionally more males left the water lily mat later than females. Three to 4-day old males remained in the mat and called for 1-2 days before moving to the cattail patches. The shift then in numbers of females from nymphal to adult habitats and from one adult habitat patch to another preceded similar shifts in the number of males.

The shifts in distribution that occurred within a habitat patch also deserve mention. In the larger patches (where such shifts were most noticeable), the most typical pattern was for calling males to be located along the entire border of the patch, spaced almost equidistant from one another. However, early in the season, males were typically found more clumped and calling only along one or two borders of the patch. This

pattern was observed when large numbers of newly molted adults were entering the patch. Interestingly, males were calling from borders of adult habitats that faced areas where large numbers of newly molted adults were found, and so along the borders where most adults (with females before males) were entering the adult habitat patches.
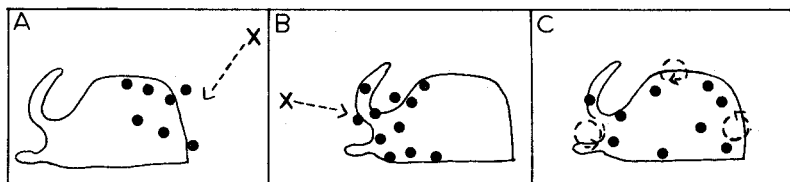

Fig. 5. Changing patterns of male distribution during recruitment in a habitat patch, 1974. Arrows indicate direction of female movements. In A, females were entering adult habitat from the north (nymphal habitat = X). Male territories (solid circles) were all located on the northern border of the adult habitat. In B, 2 days later, females were entering from the south. Male territories were located on the southern border of the adult habitat. In C, 4 days later, females entered along entire border as they moved in from other habitat areas. Females were also moving in and out of the adult habitat patch to feed.

Fig. 5 illustrates such shifts in calling male distribution in cattail Patch 4 in 1974. In 1974, this patch was bordered by two areas of mat where high numbers of newly molted adults were located. The mats were directly north and south of the patch. Newly molted females were present in the north mat 3 days before they were present in the south mat. Male territories were established first on the north side of the patch and then the south side. Males established territories along the entire border of the patch after females started moving from patch to patch. That male distribution so strongly paralleled that of females, indicated that males in some way were monitoring female location, perhaps by attempting to interact with highly visible (and so probably receptive) females.

Populations adjacent to the study site were censused at weekly intervals to see if migration was occurring. Seven cases of migration were noted. These males had emigrated to cattail patches that were within 20 m of the study site. Thus, individuals rarely emigrated to adjacent populations.

Also five likely immigrants were found during the
study. The five were injured and were probably males
from adjacent populations that emigrated after losing
physical aggressive encounters.

BEHAVIOR

Female/male interactions

Females <6 days old were more conspicuous than older
females and were found grooming or feeding on high
vegetation in the vicinity (<0.5 m) of calling males. At
intervals such females would move toward the stridu-
lating male, coming close enough to make body or antennal
contact. In older females, such approaches and
subsequent contact were preludes to mating. Fig. 6
illustrates the sequence of events observed in inter-
actions between older females and calling males. Males
responded to a female's approach by moving toward her.
In subsequent approaches, females underwent the greater
displacements (1-2 m), often moving back after a male's
approach (10-20 cm) and then toward a male again. They
executed semicircles about males who turned toward
females in response to each approach but only moved a few
centimeters toward them. At the minimum, interactions
between males and females consisted of a directed
approach by one partner, followed by an orientation or
approach by the other. During retreats of long duration
by a female, males resumed the calling positions observed
prior to a female's approach. If the interaction was not
ended by the female, the pair came to within 10 cm of one
another, facing each other. Such close contact was
maintained for several minutes to a few hours. Once
close contact was established, males, at least moment-
arily, stopped stridulating. Males more frequently
terminated interactions after durations of 20 min or
longer (n=37/58). If neither partner moved away,
the pair eventually moved down into the vegetation with
the female leading, where close contact was re-
established. The male eventually initiated genital
contact and if successful, mating took place. Males
remained slightly more responsive than females to
external stimuli while mating and terminating genital
contact after about 20 min (pulling away and kicking at
the female). In general, males appeared to be aware that
females were moving toward them and turned toward such
females. However, in 22 observations, females approached
males who gave no visible sign that they had seen them.
These females either retreated after a time or moved

close enough to a male to touch the rear of his abdomen
or tegmina (n=2). When touched, the male turned toward
the female.

Fig. 6. Sequence of events in typical male-female
interactions. The numbers are the number of
observations recorded of a particular outcome.

        Females only approached and interacted with stridu-
lating males. Occasionally (n=6), a female was observed
to pause or orientate toward a silent male that she
passed. In all cases such interactions were of brief
duration (<5 min) and the female soon left the male's
vicinity.
        Females were never observed to be pursued by an
established calling male after interacting with that
male, even if they terminated the interacion right after
orientating to that male, by moving away. Calling males
were observed to pursue females, but such females were

individuals who had traveled through the male's sphere of influence (see next section) without interacting with these males. Such females were followed until they paused and turned toward their pursuers, or these males interacted with other males they encountered.

In contrast, silent males in the proximity of calling males would pursue females as the females moved between patches (n=32). All of these males were of calling age or >4 days old, but either had not been calling or had only been calling sporadically for 3 days. If a female stopped to feed or groom for longer than a minute or two, the pursuing male would dart 1 or 2 meters ahead of the female and start to stridulate (n=6). This pursuing behavior exhibited by such males was apparently an attempt to interact with a female. Generally, the female did not approach such males (two exceptions) and moved past them quickly. These males continued to follow females until they entered another habitat patch. Here the following male attempted to call again but was usually forced out of the vicinity by an established calling male. In only one instance was a following male observed to enter into an aggressive interaction with an established territorial male and eventually force the territorial male out of his territory. By the time the aggressive interaction ended the female had moved onto the territory of a neighboring male. Also four of the followers became silent males after aggressive interactions with territorial males.

Females interacted with a number of males and with the same male a number of times before mating (Fig. 6). The mean time a female spent in the vicinity of a single male was 47 min. In a cluster of three to four stridulating males, females were observed to spend a mean of 3 days.

Male-male interactions

The signals utilized. Stridulating males except when feeding were highly aggressive toward other calling males and nonaggressive toward females, silent males, and nymphs. Individuals of all classes while feeding would lunge and bite at conspecifics on the same plant who moved close enough for contact (to within 1-3 cm), or others who attempted to feed on the same prey item.

During aggressive interactions, males exchanged acoustical signals and/or fought. Males faced one another before moving to a position opposite each other and grappling. While grappling, males would rake each other's wing covers (tegmina) and body with tarsal claws, kick and push each other using their legs; they bit at any exposed portion of the other's body (generally the abdomen and genitalia). Eventually one male, or rarely

both, would drop from the stem. After such a physical
encounter, the male forced off the stem usually moved
away. In about a third of the fights observed (n=31),
one or both males were injured or lost body parts. Two
males had their tegmina ripped and did not call although
they raised their tegmina in typical singing position and
vibrated them without sound. Fighting occurred
infrequently. Males fought in 95 of the complete
interactions observed (n=256). In 161 interactions males
only exchanged acoustical signals.

Males produced a typical stridulation or 'calling
song' that was a combination of individual pulses or
'ticks' and a sustained 'buzz' of variable length
(description after Alexander 1956). During an aggressive
interaction ticking was emphasized relative to the buzz.
The number of ticks, their rates of delivery and the
number of complete songs executed per time interval were
increased during an aggressive encounter. At intervals,
the two males engaged in rough sychronization or
alternation of such modified calling songs or what I have
termed' aggressive or defensive signaling'. Just prior
to physical combat, males often exchanged only ticks.
For a more detailed description see Feaver (1977). Since
such aggressive signals usually preceded a fight, they
were assumed to be threat of such. Such threats were
lacking only prior to fights initiated after males forced
off the stem during a previous physical encounter, did
not move far away and/or called soon after in the
vicinity of their dominant opponent. The dominant male
would often attack without signaling (n=11), jumping
toward the other male. After a few such attacks, the
deposed male moved away. Also, males appeared at
intervals to 'track' a near neighbor's position and
calls. A particular male could orient to one of his near
neighbors and acoustically track his calling songs,
adding or subtracting ticks and/or adjusting the interval
between his songs so that he essentially synchronized
with that neighbor. Tracking probably represents low
level aggressive or 'threatening' behavior. As in
aggressive or defensive signaling, ticking may have been
emphasized relative to buzzing, and stridulations were
somewhat synchronized. However, in tracking, rates of
ticking or complete song delivery were not modified (see
Feaver 1977 for sonograms). Also near neighbors did not
have to move toward a calling male to invoke tracking of
their songs. Aggressive signaling, in contrast, was only
observed when one calling male moved toward another
calling male and called in the second male's vicinity.

It was the approached male who first initiated aggres-
sive or defensive signaling. Tracking was utilized by
males who had engaged previously in several aggressive
interactions involving aggressive signaling and/or
fighting. Tracking was also most often practiced by
'central' males (see site defended) and so by males most
dominant and most often approached (challenged) by
near neighbors.

Daily cycle. Males started to call about 1000-1100
hours, after spending the night among heavy low-growing
vegetation. Males initially were heard exchanging
ticks. After a period ranging from 10-45 min, some of
the males would begin to call (tick and buzz). Males,
who had not yet started to call, would move away from
the males that initiated calling.

If a male started calling near a calling male, the
latter would signal defensively. Generally, this was
sufficient to cause the new calling male to move until
his singing failed to elicit aggressive signaling. Two
males who initiated calling about the same time,
responded to each other with defensive or aggressive
signaling. They then moved until they failed to elicit
this response in one another. By 1100 or 1200 hours in
good weather, the males were evenly spaced throughout
the habitat patch. This initial spacing was accom-
plished through acoustical aggression; no physical
combat was observed at this time.

Females began to interact with males at about 1200
hours and aggressive interactions were initiated when
one male tried to move closer to an approaching female
and in doing so, moved into the area defended by another
male. Dominance relationships between males at this
time were established through acoustical and physical
combat. This period lasted for 1 or 2 h. After this,
spacing and relationships between near neighbors
appeared to stabilize. Near neighbors continued to
'challenge' each other as they attempted to move toward
approaching females and into the territory of the other
male. Spacing, however, was readjusted through
acoustical aggression; very few interactions terminated
in physical combat. Tracking was prevalent at this
time.

About 1800 hours, calling became more sporadic;
males started to drop out of the chorus and began
feeding. The numbers of conspicuous females increased
as more females left the undergrowth and moved to the
tops of the forbs to feed. Females who became
conspicuous at this time were probably unreceptive.
Groups of two to four males and a female were observed
feeding on the same cattail head. No aggression was
observed unless individuals touched one another. By
1900 hours all calling had ceased.

Interactions between neighboring males in actuality continued throughout the day, although intensities of such interactions peaked from 1100 to 1500 hours.

The site defended and dominance. There appeared to be an area around each male where he could move freely without invoking aggressive signaling from neighbors. This small area was surrounded by a much larger area which was under continual contest. Males, therefore, defended areas from which they in part were excluded. If the distance between near neighbors was small, 1-2 m, a male could move about 10-15 cm toward his neighbor without invoking aggressive signaling. If the distance between two males was large, 5-8 m, a male could move 1-3 m toward his near neighbor without initiating an aggressive interaction. The distance a calling 'intruder' could approach before invoking aggressive signaling, varied from encounter to encounter for consecutive measurements on the same male. Three factors contributed to such variance. 1. Males who had engaged that day in one or two aggressive interactions allowed other males to approach closer than males who had engaged in several interactions. 2. Sectors of the defended site facing uninhabited areas were defended less vigorously than sectors facing other males. 3. Males who were tracking one near neighbor ignored, at least initially, other calling near neighbors who were moving closer. Yet small movements toward a male by a near neighbor who was being tracked, resulted in aggressive signaling by the tracking male. A good example of the variance contributed by tracking to territory size is demonstrated by three males: A and B, about 6-9 m apart, and B and C, separated by a road and about 15 m apart. A moved 3 m in B's direction with no response by B while B was tracking C. Yet B, while tracking C, responded to movements of less than 1 m by C with defensive signaling.

The smallest area defended acoustically had a radius of 70 cm; the largest had a radius of 18 m. Encounters initiated at these long distances, however, were terminated before males engaged in physical combat. The largest area defended with encounters that ended in physical combat had a radius of 8 m. Seventy-five percent of the encounters terminating in physical combat (n=95) were initiated by neighboring males separated by 2 m or less at the beginning of these interactions.

For 10 consecutive days the sizes of all males' territories in three patches were measured. A negative correlation was obtained between mean territory size and

the number of males in all three patches (p=0.000, r=0.87-0.90). Thus, the size of the area defended contracted under social pressure and expanded when such pressure was removed.

Although the size of the area defended within a patch increased as the density of males within a patch increased, the habitat patch was not simply being divided up among the resident males. For example, in the largest patch studied (Patch 4, Fig. 1), at peak density (0.16 males/m^2), calling males defended a mean circular area 2.6 m in radius. Since the territories overlapped, only half of the available area was occupied by the 12 males calling in this patch. In all patches during the first few days of recruitment, territories were smaller than later in the season. During this time females were entering the adult patches from the nymphal areas so that only those borders of the adult patch facing the nymphal areas were contested. Later (when females were moving from patch to patch or feeding just outside the patch) females were not entering the patch along a single border and males set up territories distributed around the entire patch. These territories were larger than the earlier ones. For example, in Patch 2 at a density of 0.16 calling males/m^2, the mean defended radius was 1.2 m during recruitment. After adults stopped moving into the patch 9 days later, the mean defended radius was 2.6 m.

Within a cluster of calling males there appeared to be favored calling sites. For example in Fig. 7, the most common distribution patterns for males inhabiting Patch 1 are illustrated. Pattern A was common when females were entering the patch from nymphal habitats along its western border. Pattern B occurred later, when females were moving into and out of the patch to feed. The central male controlled most of the patch by virtue of his location. Females were observed three times more frequently in the proximity of the central male than they were in the proximity of the distal males (n=11) probably because the central male controlled more of the patch border.

Males who placed themselves 'central' to female distribution moved toward (ca 1 m) near neighbors and tracked their songs (see signals). A north or east-facing neighbor would move toward a central male who was tracking a south or west-facing neighbor. In most instances such intruders would move back when the central male oriented toward them and tracked their songs (n=83/121). Near neighbors appeared more reluctant to move back when a female approached a central male. In fact, in 50% of the matings observed (n=18), females approached a central male who was also approached at the same time by a calling near neighbor. In three instances, the central male quickly asserted his dominance.

In another interaction, the central male withdrew after
fighting with a near neighbor and the neighbor eventually
mated with the female. In the other five instances, the
aggressive interactions between central males and
near neighbors continued until the female left the
patch. Females may have, by interacting with a number of
males before mating, been assessing the males' relative
dominance. In all five instances, the females were
observed to mate later with the central or the most
dominant male in other patches.
     The factors influencing dominance will be discussed
elsewhere in detail (manuscript in prep.). Age and
weight differential appeared to be the most influential
factors in **O. nigripes.** Males >9 days old were dominant
over same-sized males <9 days old. Heavier males
dominated in 96% of the interactions where the two males
differed by at least 10% in weight (n=106). As expected,
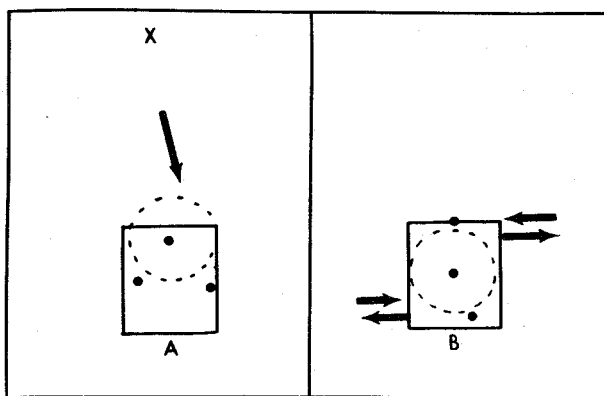dominant males did not hold central positions for long

Fig. 7. Distribution patterns of males (solid circles)
within a small habitat patch. Arrows denote the
direction of female movement. Pattern A was commonly
observed during recruitment periods. Females moved into
this adult habitat from nymphal habitats, X, along the
northern border. Pattern B was common at other times,
when females moved from adult habitat patch to habitat
patch, or in and out of the habitat patch to feed.
Territories were overlapping and equivalent to nearest
neighbor distance. Thus, the central male controlled
most of the habitat by virtue of his central position.
The dotted line indicates the boundaries of the central
male's territory.

periods of time.   The mean time that a male had continual possession of a central territory was 2 days (n=93).

Male-male attractiveness.   Young males just as young females, appeared to be attracted to calling conspeci- fics.   Males <3-4 days old moved out of the water lily mat and toward a stridulating male, and did not stop until <1 m away from him.   These young males would feed and groom in the vicinity of the calling male, but did not attempt to call until they had been there for 1 or 2 days (n=7).   Males of calling age also moved from the water lily mat toward a calling male in the cattail or high sedge patches (n=33 for males not following females). These males generally did not stridulate unless they encountered a calling male.   These approaching males first attempted to call at a distance of 1-2 m from the stridulating males.   If the established calling male responded with aggressive signaling, the younger male moved further away and attempted to call again.   In the three exceptions in which a young male called before coming close (1-2 m to a calling male) the young male had encountered a female.

Silent males.   Silent males <4 days old were found in the proximity of calling males (usually within 70 cm, n=24).   In a few cases (n=5), these young males were even feeding or grooming on the calling male's perch.
More surprising, silent males >4 days old were frequently (n=108) observed <70 cm away from calling males.   These males stayed near the same calling male for an average of 4 h.   Silent males of calling age were only observed near calling males when densities were high. Early and late in the season when densities were low, 4 and 5-day old males called.   If a calling male near a silent male was removed, the younger male began calling (n=32).   It appeared that when densities were high (0.019-0.021 males/m^2), older males held all the suitable territories, so the only way for younger males to stay in the vicinity of females was to be silent in the territory of a calling, older male.   Younger males were observed to be inhibited from calling by older established males even when near neighbor distances were well above the minimums recorded.

DISCUSSION

Morris (1967) investigated male spacing of **Orchelium gladiator** in a fairly homogeneous environment, a con- tinuous patch of sweet flag and sedge.   He found that: 1) males were uniformly distributed throughout the habitat;

2) males exhibited phonotaxis to bring them into the
vicinity of other males; and 3) after encountering
conspecifics, males often engaged in physical combat,
causing one of the males to leave the general vicinity.
He suggested that the observed spacing pattern of males
was the result of physical aggression, maintained by
calling, a threat of combat, and the areas defended might
serve as mating territories.

The density of **O. gladiator** on Morris' study site
was high (0.15 males/m^2) relative to the densities of
O. nigripes males encountered in my study (0.019-0.021
males/m^2). Also, my study site was more heterogeneous
than that utilized by Morris. This proved fortunate,
since it was the movement and behavior data collected on
individuals moving from nymphal to adult habitats that
indicated that the locations of calling stations were
determined in the following manner. Males molted and
matured before females. Early in the season, males set
up territories in areas where females were most abundant
at that time, the water lily mats where the females were
molting into adults. Later, these males, while
attempting to interact with the newly molted females,
followed them into the patches containing cattails and
high sedge and between such patches. If females entered
suitable habitat patches, they remained in them and so
would the males that followed them there. Males
continued to orient to and approach females in their
proximity. However, in most cases after densities
increased in the adult habitat patches, a male would only
be able to pursue the female for a few meters before
entering another male's territory, initiating an
aggressive interaction with that second male.
Displacements recorded for individuals over a 2-day
period became smaller and residences appeared to
stabilize although small shifts in distribution continued
to occur.

Morris (1972) has collected phonotactic evidence of
male-male attractiveness. In this study, **O. nigripes**
males who matured later in the season, or older subor-
dinate males forced out of a habitat patch, probably used
established calling males (moving in a straight line to
them) as clues of suitable areas from which to call,
i.e. where females were most dense. If they were
successful in establishing a territory, females would
approach and interact with them, and these males also
would stay in that area. Thus by attempting to interact
with conspicuous females and sometimes utilizing calling
conspecifics as clues to female presence, males even-
tually established territories in areas of high female
density.

It was also the shift from one habitat type to another, that occurred after the final molt, that prompted the natural history of **O. nigripes** to be examined to determine factors that distinguished adult habitats from nymphal habitats. In **O. nigripes,** the major factor appeared to be the availability of oviposition sites. The water lily mats continued throughout the reproductive season to serve as areas providing food and cover, if only intermittently, to adults as well as nymphs. Males also established calling stations in areas where oviposition sites could be found of **O. gladiator, Neoconocephalus ensiger,** and **Conocephalus nigropleurum,** (unpub. data and Feaver 1977). In **Orchelimum vulgare** and **Atlanticus testaceus,** the distribution of oviposition sites influenced adult distribution although males did not call from areas where such plants were most abundant (unpub. data and Feaver 1977).

In the present study, the low densities enabled any differences in relative suitability from one area to another to be manifested in the distribution pattern of adults. Noticeable changes in male distribution patterns within the adult habitat patches might not have been observed had densities been higher. Subordinate males may have been forced to occupy less desirable sites along borders opposite to those by which females were entering the patch in the beginning of the season. If that were true, later in the season, it would have appeared as if territory sizes simply decreased in response to increasing densities and that the pattern observed later, of males distributed more or less uniformly along the border of the patch (more like that observed by Morris), was one that persisted throughout the reproductive season. Instead, when females were entering the cattail and sedge patches along only one edge, male distribution as a whole became more clumped along that border. The sizes of male territories located there decreased in response to the social pressure exerted by males attempting to interact with these females (call and defend territories). Such shifts within habitat patches, so strongly associated with the shifts taking place in female distribution, indicated that males were monitoring female presence and so further confirmed that these defended areas serve primarily as mating stations.

Recent attempts to classify mating systems in an evolutionary perspective have focused on the role of male-male competition and how it acts to influence a female's mating decisions. Emlen and Oring (1977), for example, have divided existing polygamous systems into three major categories: 1) those in which males control resources needed by females, 2) those in which males

attempt to control and so monopolize females directly and
3) those in which males compete for dominance status, in
an effort to increase their probability of mating. The
latter system (male dominance) includes explosive
breeding assemblies, leks, and probably the system of
O. nigripes.
     Borgia (1979) recognized four major mating systems:
1) in which males control resources, 2) in which males
control females, 3) in which males collect resources that
may be exchanged for mating privileges and 4) in which
males do not utilize resources in any way and females
choose on the basis of 'good' genes. He also ranked
these with regard to their likelihood of evolving, given
the ecological possibility of more than one system, from
most likely to least likely: 1 and 2, then 3, followed by
4. He feels that 4, or the system where males do not
utilize resources, is the least likely to evolve since it
allows the females the most freedom in mating decisions
and whenever possible males should attempt to restrict
female choice in their favor. Again the **O. nigripes**
system should probably be ranked with systems under 4, in
which males are not monopolizing resources or controlling
females in any way to influence female mating decisions,
for the following reasons.
     Although males in all species established calling
sites in proximity to various resources utilized by the
female, there was no indication that males utilized these
resources in any direct fashion to enhance their
competitive advantage in pair formation. Such use of
resources has been reported in other territorial species
where males have been observed to be aggressive toward
females, forcing copulatory attempts on reluctant females
who come into male territories to utilize the resources
found there (Alcock et al. 1977, 1978; Barrows 1976;
Borgia 1981; Eickwort 1977; Jaycox 1967; O'Neill 1979;
Pezalla 1979; Spieth 1974). In **O. nigripes,** there was
no evidence that resources were limiting. Nor was there
any indication that resources were distributed in such a
manner that some males could restrict female access to
needed, or to the most suitable of them, and demand
mating privileges in return. Male katydids were non-
aggressive toward conspecifics other than calling males.
Males did not even pursue females who rejected their
approaches as long as females at least paused and
oriented to these males before moving on. In katydids
males produce a complex spermatophore during copulation
(Gwynne 1982b). Struggles with an unwilling female would
probably have interfered with the successful transfer of
the spermatophore.
     In fact, it was fairly obvious that **O. nigripes**
males were not even utilizing the resources found in
adult habitat patches as indicators of the areas'

suitability to attract females, since males did not
aggregate in adult habitat until after females were found
there. A closer examination of the association between
the distribution of adults and resources in this and
other species, indicates that this may be because females
eventually resided in areas that varied in the quantity
and quality of the resources offered. The cattail
patches offered oviposition sites and food, but in some,
little in the way of cover (less that 20% in some
areas). In fact, all four instances of predation
observed took place in the cattail patches. The sedge
patches offered dense cover, but females moved out of
these to feed. These areas were also less suitable for
oviposition than the cattail patches. The only instances
recorded of older females undergoing large displacements
involved females moving from predominantly sedge patches
to predominantly cattail patches. Yet the sedge patches
continued to attract tenerals and three females mated in
these patches after some females had departed for the
cattail patches. Just where females would reside prior
to mating appeared somewhat unpredictable. Considering
the number of plants utilized for oviposition and feeding
in some of these species, their distributions relative to
each other and the temporal variation that may have
occurred in the suitability for use of each plant (Feaver
1977 and unpub. data), the best strategy for males
appeared to be to monitor the females' presence directly
and not rely on a priori judgements of an area's suita-
bility for drawing receptive females at some future date.
     Some researchers (Alcock et al 1978, Campanella 1975,
Emlen and Oring 1977) have suggested insect mating terri-
tories should be found in areas that predictably attract
females. In katydids, mating stations were defended even
though where females will mate was unpredictable. Of
course this initial unpredictability was reduced by the
monitoring of female presence practiced by males.
     Females did not appear to be utilizing the resources
in a male's territory as a basis for selecting him as a
mate. Such use of resources has been reported in other
insect species, especially some dragonfly species where
males defend oviposition sites (Campanella 1975,
Campanella and Wolf 1974, Jacobs 1955, Wittenberger
1981). In one of the first detailed field studies on
insect territoriality, Jacobs (1955) observed that male
Perithemis tenera followed potential oviposition sites
that they defended if the sites were moved and rejection
of these sites by females resulted in a male 're-
examining' his site and attempting to set up a territory
elsewhere. In O. nigripes, there was no indication that
females laid eggs only in plants found in a male's
territory. Also, oviposition occurred a minimum of 3

days and on average 8 days after mating. Males and
females were observed most frequently feeding after males
ceased holding territories for the day, so the food
resources did not appear to be used to attract females.
Often groups of males and females would feed next to each
other on top of the same cattail head.

Males did transfer some resources via the spermato-
phylax, the external portion of the spermatophore which
the female feeds upon after mating. Male **O. nigripes**
examined, lost about 10% of their weight upon transfer of
a spermatophore; in **A. testaceus**, although the mean was
10%, the maximum was 17% (unpub. data). Gwynne (1982a)
has suggested that in **C. nigropleurum,** since heavier
males produce heavier spermatophylaxes, females may be
seeking the heaviest male because of the resources they
obtain this way. Females are able to judge how heavy a
male is by utilizing the intensity of substrate vibration
caused by tremulation of the courting male at short
distances or by the intensity of a male's calling song at
longer distances, larger males having louder songs. Most
of the **C. nigropleurum** females in choice trials moved
straight to and mated with the larger of two calling
males

There was no indication in my study that females
were assessing male weight directly. **Orchelimum** males
were not observed to tremulate. Females who mated
interacted with a number of males and/or the same male a
number of times. During an interaction with a female, a
male will stop stridulating, the two partners will face
each other and may antennate each other. Females could
be utilizing visual cues to assess male size, and so
weight, at this point, but I question whether they are
capable of such discrimination. There was a correlation
between length and weight in **O. nigripes** (p=0.000) but
the variance among males of the same length was great
(r=0.290). Also neighboring calling males differed by
less than 0.5% in weight (Feaver 1977). Rather the data
indicated the females were evaluating a male's relative
dominance probably by interacting with a number of males
or the same male a number of times. The only females
observed to leave a patch or group of males were females
who were heavy (so carrying eggs and probably seeking
oviposition sites) or younger females who left when a
central male's dominance status continued to be
challenged by near neighbors. In one case such a young
female eventually mated with a male who was the most
dominant male in a neighboring habitat patch, but only
weighed two-thirds of that weighed by the males in the
patch she originally rejected. In choosing a relatively
dominant male however, a female does ensure she has
chosen a male who can give an adequate spermatophylax.
Males who have recently mated (and so lost 10% of their

weight) would have a 96% chance of losing an aggressive
interaction with a near neighbor of similar weight and so
almost always be subordinate to unmated males.

Males do not appear then to influence female choice
by demonstrating their ability to give resources as much
as by demonstrating overall 'vigor' through relative
dominance. The selective regime appears to have most in
common with mating systems included under Borgia's 'good
gene' model or Emlen's male dominance category. Male
O. nigripes are in some sense 'war propagandists' (Borgia
1979, after Fisher), advertising their dominance status
by their calls. Females did not interact with silent
males. In two instances previously silent subordinate
males placed themselves between an approaching female and
a calling male, moved their tegmina as if calling, but
made no sound. Obviously these males were attempting to
intercept the approaching females, but only while behav-
ing as if 'calling'.

Although the O. nigripes system is characterized as
one in which female choice is relatively unrestricted,
there are some indications that this system could easily
be replaced in other species by one that gives males more
influence over female mating decisions. It is obvious
that males in O. nigripes terminate many interactions
(see Fig. 6), particularly those of long duration. In a
few instances (n=5) males left a female (including one
instance where a male eventually returned to mate) to
initiate aggressive interactions with near neighbors who
had moved into and were calling in the territory. The
data are anecdotal but do suggest the priority placed on
dominance status. In most instances, however, males
resumed calling or immediately moved toward another
female. Perhaps males evaluate at least to some extent
the time they spend with any one female. Couple this
tendency to interrupt courtship or perhaps even postpone
mating, with delivery by males of a resource in short
supply, and males are in a position to restrict female
choice. Gwynne (1981, 1982b) observed in Anabrus
simplex, males weighing females and rejecting the lighter
females who will eventually lay less eggs than heavier
females. He observed this role reversal only at high
densities when food was in short supply and so the
spermatophylax probably represented a significant
contribution to a female's reproductive success.

Because dominance allowed a male to call in a
position that increased his chances of interacting and so
mating with females relative to near neighbors, the
selective pressure on katydid males may resemble that on
males in species said to lek. The term has traditionally
been applied to avian breeding systems where males
display communally, each male defending a small mating

territory within the larger area or court (Emlen and Oring 1977, Lack 1968). In leks, dominant males on certain territories have been observed to enjoy greater mating success, sometimes almost to the total exclusion of subordinate or satellite males (Hogan-Warburg 1966, Lill 1976, Robel 1966, and Wiley 1973). However, the term has also been used in conjunction with courts used year after year by males that are removed from areas providing resources such as food and nesting sites, and visited by females only for the purposes of mating (Alexander 1975, Brown 1964, Lack 1968). In katydids, the sizes and the distribution of territories, i.e. the court, changed throughout the season and mating territories did offer access to resources utilized by the females.

Recently Alexander (1975) has suggested the term lek be used to refer to any system where males actively aggregate, that is males or groups of males can be shown to attract males as well as females, even if such assemblies occur in regions where females are dense for reasons other than mating alone. He designated these as resource-based leks, the more traditional bird leks that have no function but mating for either sex as non-resource-based leks. There are, however, problems in referring to the mating system of **O. nigripes** even as a resource-based lek. Male-male attraction did occur, although it appeared to play a secondary role to direct monitoring of female presence in establishing the spacing patterns observed. Early in the season, most males followed females, eventually aggregating where these females did. However, the utilization of calling males as clues to locations where females were most dense was probably practiced by males who molted later in the season and by subordinate males forced out of a habitat patch.

For leks, Alexander (1975) predicted intragroup competition among males for females, such that larger groups would attract more females, and in some species selection would begin to favor cooperation among males, at least in regard to the signal used to attract conspecifics. In **O. nigripes** the opposite appeared to be true, in that it was the number of highly visible females that determined in some sense the 'attractiveness' of an area for young males. This may be why no behavior of any sort that could be construed as 'cooperation' among males was observed during the course of the study. Males did synchronize and alternate their threat or defense signals, but only in the context of interacting aggressively and this type of behavior appeared to repulse, not attract, females.

The mating system of **O. nigripes** shared one important characteristic in common with the 'leks' postulated

by Alexander: females appeared to be unrestricted by males in their choice of mates and so the potential influence of the female-choice component of sexual selection in shaping the mating system should be substantial. Dominant males did not pursue reluctant females until they were, in some sense, forced to mate with them. Also females were not forced to exchange mating privileges for unharrassed access to resources. In fact, the competition that occurred among males may have enhanced the relative influence of female choice by providing a setting by which males advertised their relative 'vigor' and thus suitability as mates, in much the same fashion suggested for traditional avian leks (Alexander 1975, Borgia 1979).

This paper, in characterizing the pair formation strategy, begins to also characterize the sexual selection regime predominating and to examine the factors that may have been influential in its maintenance and evolution. To complete this characterization, the criteria females are using in making their choices and the factors that shape such mating preferences will have to be examined in more detail. Such an examination should also include factors that may, more indirectly than male restriction, influence mating decisions. In **O. nigripes** for example, 50% of the females did not survive to mate. Females first captured when 6 days old, had on average only 5 (1974) or 6 (1975) days to live. So even if females mated early (the youngest female observed to mate was 7 days old), they had less than a week to oviposit. Obviously in a species like **O. nigripes,** the influence of indirect considerations on female choice, such as survivorship schedules, is expected to be substantial, limiting in some sense the time a female can spend making a mating decision.

SUMMARY

This study examined the behavior associated with intraspecific competition among males for females in the katydid, **Orchelimum nigripes**. The behavior of individually marked adults was monitored in the field for two reproductive seasons.

Teneral adults were first found in the water lily mats where nymphal density was high. Adults then moved into patches of tall sedges and cattails where females would later oviposit. In a group of newly molted adults, females entered and established residences in these areas before males.

Males excluded other stridulating males from an area averaging 2 m in radius around their calling perches.

The borders between neighboring territories involved broad areas neither male could enter without eliciting aggression. The size of the area defended decreased with increases in the density of calling males. Silent young males were found close to older calling males at the beginning of the reproductive season when densities were high.

During an aggressive interaction, males exchanged acoustical signals that were modifications of the calling song. If after such an exchange, neither male left the vicinity, they fought. More aggression occurred among males who defended more centrally located sites in regard to receptive female proximity and during the reproductive season, males changed their calling sites as females moved. Calling males were nonaggressive toward nymphs, females, and silent males, and did not appear to deny conspecifics any resource other than females found in the areas they defended. Females only interacted with calling males. Females also interacted with several males or the same male more than once prior to mating.

O. nigripes males did not attempt to force females to mate with them or exchange mating privileges for unharrassed access to resources as suggested for some other insect species. Female mate choice appeared to be relatively unrestricted and so female mating preferences have probably played a prominent role in shaping the mating system of this species. As suggested for avian leks, the male competition that occurred may have provided a setting by which males advertised their relative dominance or 'vigor' to females and thus their suitability as mates.

ACKNOWLEDGEMENTS

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