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The University of Michigan,
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ASPECTS OF THE BEHAVIORAL ECOLOGY OF THREE SPECIES OF ORCHELIMUM (ORTHOPTERA: TETTIGONIIDAE)

by

Marianne Feaver

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Zoology)
in The University of Michigan
1977

Doctoral Committee:

Professor Richard D. Alexander, Chairman
Professor Irving J. Cantrall
Professor Donald W. Tinkle
Professor Warren H. Wagner

To

those I love

Paul,

Mom and Dad,

and

Busia

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INTRODUCTION

Few published studies have dealt with the reproductive or behavioral ecology of the Tettigoniidae (see review by Dumortier, 1963; exceptions are Isely, 1949, Morris, 1967). Most ecological studies have been concerned with documenting geographical distributions, seasonal occurrences, and general habitat preferences of adults of various species (Rehn and Hebard, 1915a, 1915b; Blatchley 1920; Cantrall, 1943). Behavioral studies for the most part, have outlined repertoires (Spooner, 1964, 1968; Alexander, 1956) or analyzed various aspects of sound production in the laboratory (Dumortier, 1963 for review of older works; Jones 1966a, 1966b, 1974; Shaw, 1968; Morris et al., 1970, 1972, 1974, 1975a; Walker, 1975). Behavior in the field is known largely from anecdotal observations made in conjunction with studies of acoustical repertoires (Fulton, 1932, 1933; Spooner, 1964; Alexander, 1956).

This study investigates the behavior associated with intraspecific competition among males for females in three species of Orchelimum, O. gladiator Bruner, 1891, O. nigripes Scudder, 1875 and O. vulgare Harris, 1841. The behavior of individually marked adults was monitored in the field during the reproductive season, so that the function of

such behavior could be hypothesized in the light of their ecology and life history.

Orchelimum species are especially well suited for a study of the behavior associated with intraspecific mate competition and the factors that may have influenced its evolution. Males produce acoustical signals which attract sexually responsive females (Spooner, 1968; Morris, Kerr and Gwynne, 1975; for other references see Alexander, 1967). Males are active and produce these signals during the day. Calling is intense and continuous. Thus, males can be easily located acoustically and their interactions with conspecifics observed.

Morris (1971, 1972) found that males also are attracted to calling males. However, males in close proximity often engaged in physical combat, with the result that one male forced the other to leave the general vicinity. Males appeared to be setting up "calling" territories about their calling perches. The nature and function of these territories were not elucidated by Morris' study, although he suggested that they were mating territories, in some sense, because conspecific males are excluded from them and females attracted to them.

The present study continues the investigation into intraspecific competition in this genus begun by Morris and answers two major questions. 1) What environmental factors, physical and social, influence intraspecific competition

between males for mates? 2) What is the relationship of territoriality and the associated behavior to other aspects of the life history and natural history of these species?

The data collected in conjunction with answering these questions is presented topically in the sequence that follows: I. Brief accounts of the natural history introduce the study animal. Aggression including site defense is briefly characterized so that II. the nature and function of territoriality in the three species of Orchelimum can be investigated. In order to do this: a) areas where males call are described. They are characterized in terms of resources they may provide to males and females; b) observations are presented on the behavior and interactions between the sexes during periods of high recruitment. It is during these periods that territories are established; c) the relationship between aggression and density is discussed. III. In order to render the account of the overall strategy complete, the influence of the territorial strategy on life history parameters is considered. IV. The relationships between neighboring males are then characterized in more detail by a) examining the factors influencing dominance status, b) describing acoustical aggression and its role in maintaining dominant-subordinate relationships. V. Finally, katydid territories are compared to territories of other groups of insects.

METHODS

The study was conducted on the Edwin S. George Reserve, Livingston County, Michigan. The Edwin S. George Reserve is a two-mile-square protected area, reserved for biological studies undertaken under the auspices of the University of Michigan.

Three species of the genus Orchelimum were studied, O. gladiator Bruner, 1891, O. nigripes Scudder, 1875, and O. vulgare Harris, 1841 and all are abundant on the Reserve. For vulgare, it was possible to mark and monitor a distinct and isolated population of individuals. The study site is bounded on three sides by forest, on the fourth by a tree line and field containing woody vegetation not inhabited by this species during the course of the study. No other singing males belonging to this species were found within 200 meters of the study site. Unfortunately, in all similarly isolated sites inhabited by the other two species, populations of adults proved too sparse for a study of this type (5-10 adults at any one time). Therefore, it was necessary to monitor portions of large populations. The selected sites were bounded by vegetation and contours that seemed likely to inhibit movement into and out of the study site.

Portions of the populations located outside the study site and/or nearby populations were periodically checked for the presence of marked individuals. Every effort was made to discover whether an individual which disappeared had died or migrated from the study site.

The study populations of vulgare and nigripes were monitored for three complete reproductive seasons (1974-1976); that of gladiator for two (1975, 1976). In addition, some data are presented from a pilot study on vulgare started in August (1973), about midway through this species' reproductive season.

Adult animals once located were marked in two ways: 1) with a tegmino-pronotal clip code and 2) with a code employing dots of paint. The latter facilitated recognition of individuals from a distance. The former served as a permanent mark by which individuals could be recognized in the event that the paint marks were obliterated. Muted colors of model airplane paint, mostly greens and grays, were used to reduce conspicuousness.

After they were marked, 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, in the case of new adults. An accurate scale was available in a laboratory about a mile away. After being weighed animals were returned to the capture site.

Numbered stakes were placed at the site where a male was originally captured. Males were subsequently relocated every third or fourth day, weather permitting, and subsequent locations plotted in reference to the original position.

Bi-weekly canvassing of the entire study site (in all three species) revealed areas where nymphal density was high. Transects were made every 10-15 meters through the study areas, and nymphs were counted as they jumped away from the investigator. Thick vegetation occasionally was shaken with the end of an insect net to reveal hiding nymphs. Canvassing was usually initiated as soon as third instar nymphs were prominent. First and second instar nymphs are small and proved too difficult to locate among the dense vegetation. As noted previously, the population of gladiator was only monitored for two years. Transects to measure nymphal density were only made the last year of the study in this species.

All aspects of behavior were recorded. In general, a few hours each day were spent observing a clump of males. Animals did not seem to be disturbed by the presence of an observer if movements were kept to a minimum. Males and females often chewed on the observer's clothes or the leather tape recorder straps.

Interactions were recorded on Scotch brand #306, magnetic recording tape, using an Uher tape recorder,

model 400L. During an interaction, the intensity of one 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. Disturbances in the patterns of the signal caused by background noise were minimized by passing the signal through a filter blocking frequencies below 2000 HZ. This is well below the frequencies utilized by these animals (signals start at about 8000 HZ). In some cases, durations of taped songs were checked with a stopwatch.

Field findings on female cycles (maturation/receptivity/oviposition) were validated in the laboratory. Usually nymphs from neighboring populations were collected and kept in the laboratory until mature. Adults were also successfully raised from eggs laid by females mated in the laboratory. Embryonic diapause was broken by exposing eggs to an 8 week cold period (temperature ~5°C), followed by a period of high temperatures (~25°C) and long days (16 hours). Animals in the laboratory were fed a mixture of soybeans, lettuce, fish food, 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. Males, when mature, were housed individually in 5-inch cylindrical wire cages, 2 inches in diameter. Two or four males were introduced at 2-day intervals into female cages. Mated females were housed in cylindrical wire cages, 6 inches in diameter. Several stems of known oviposition plants were available to females. Two males were introduced into the cages at 2-day intervals to monitor female receptivity relative to egg deposition.

Procedures utilized to examine a small subset of the data will be presented just prior to such data.

PRELIMINARY REMARKS

The Study Animal

The species studied are about 2 cms in length. Their basic color is green. Individuals of nigripes have distinctive black legs and beige or brown heads. In the other two species, the heads are green, and the legs green and light brown.

All three species are widely distributed. Orchelimum nigripes and vulgare are found throughout the central United States, and gladiator throughout the northern United States (see Morris and Walker, 1976, for current range maps). These three species have been cited as among the most commonly encountered species in the states of Indiana, Illinois, Ohio, and Michigan (Blatchley, 1920; Alexander, 1956; Cantrall, 1968).

All three species have been found in a variety of habitats including damp meadows, prairies, and marshes. In Indiana, vulgare is more common in drier uplands than is nigripes which is a lowland marsh species (Blatchley, 1920). Orchelimum vulgare and gladiator have frequently been taken from the same sites (Blatchley, 1920; Cantrall, 1943, 1968). Cantrall (loc. cit.) reports that vulgare is often found

in mixed grass-herbaceous upland habitats. During the course of this study, vulgare was more common in old fields in the heavy Rubus growth. Orchelimum gladiator was more abundant in wetter, marshier situations. Orchelimum nigripes was most abundant in the cattail-sedge marshes.

Nymphs hatched in late spring from eggs laid the previous fall. Adults appeared about two months later (see Table 1). The reproductive seasons of nigripes and vulgare overlap. Adults of both species began to appear in the latter part of July but nigripes generally reached peak population density 1-2 weeks later than vulgare. (The nymphs of nigripes also hatched 1-2 weeks later than those of vulgare.) Populations of both species persisted until killing frosts occurred, usually in October. Orchelimum gladiator nymphs hatched in late March and early April. Adults were found in early June and the population disappeared in early August, before the population sizes of the other two species peaked.

Males of all three species called almost continually from about 10 AM to about 6 PM. If night temperatures remained above 75°F, calling could continue until 2 or 3 AM. On cloudy days, when temperatures remained below 60°F, males did not call. On sunny days, however, males were observed to sing at temperatures as low as 52°F.

Males of the three species used a variety of plants as calling sites. No distinct preferences for any one species of plant were observed and choice was probably dictated by

TABLE 1

RECORDS ON SEASONAL DISTRIBUTION
IN ORCHELIMUM

Species	Year	Hatched Nymphs	First Adults	Last Nymphs	Last Adults
O. gladiator	1975	?	June 29	Aug. 17	Aug. 29
	1976	March 15-April 1	June 20	July 22	Aug. 13
O. nigripes	1974	June 2-June 23	July 29	Sept. 29	Oct. 18
	1975	May 27-June 18	July 27	Oct. 12	Oct. 15
	1976	May 30-July 7	July 26	Sept. 21	Sept. 28
O. vulgare	1974	May 20-June 6	July 15	Sept. 23	Oct. 8
	1975	May 19-June 12	July 20	Sept. 27	Oct. 1
	1976	May 12-June 2	July 23	Sept. 21	Oct. 1

availability. For example, most vulgare males sang from Liatris stems in areas where Liatris was the most abundant forb, and from goldenrod (Solidago spp.) where it was the predominant forb.

Singing was interrupted by short periods of grooming and feeding, especially in the late afternoon. When singing ceased in the evening, feeding activity continued until the temperature dropped below approximately 70°C.

Gangwere (1961) described the Conocephalinae (Orchelimum and Conocephalus) as indiscriminate feeders, although preferences were recorded for flowers of forbs and seeds of grasses. He and others also reported that animal matter was taken frequently (Gangwere, 1961; Blatchley, 1920).

Females lay their eggs in stems of plants. The females use their mandibles to make incisions in the stems at one-half to one cm intervals. After making the incision, the female turned around or moved down the stem until the ovipositor could be inserted into the opening; eggs were then deposited into the center of the stem.

Metcalf and Colby (1930) reported that previous investigators had found eggs of vulgare in a number of different plants including sugar beets, corn stalks, elder twigs, dogbane, lambs' quarters, timothy, horse nettle, and crab grass. The authors also stated that the females may show preferences among the plants locally available. They state that the insect "prefers to lay its eggs in the respberry when this is convenient." Hancock (1915)

reported that in the laboratory a vulgare female tested different plants by biting the stems before deciding to lay in bur marigold. No data on oviposition is available for the other two species. The data on feeding and oviposition for the three species compiled in this study are presented in the section on male selection of calling sites.

Preliminary Studies

Most of the thesis will be concerned with factors influencing male-male spacing. To see why such factors are important in a consideration of the nature of intraspecific competition for mates in this group, a few remarks on the general aspects of aggression in these three species are warranted.

Calling males were highly aggressive toward one another, but, with few exceptions (see section on feeding) were totally nonaggressive toward females, silent males, and nymphs. Aggressive interactions between males frequently involved physical combat during which males "grappled" with one another (term from Morris, 1967). The basic sequence of events observed in male-male aggressive interactions was as follows: Males, prior to fighting, faced one another. One male would move past the second until he was opposite his opponent. Males would then bite at each other's abdomen and genitalia, rake each other's wing covers, tegmina, and body with tarsal claws, and kick and push each other using the hind legs. Eventually, one male, or rarely both males, would drop from the stem. After such a physical encounter, the male who was forced off the stem usually moved away.

In about one-third of the fights observed, one or both males were injured. Tarsi and antennae were torn or bitten off during the combat; wings and tegmina were torn

and tattered by the tarsal raking. Scars occurred on the body where small incisions had been made with tarsi or mandibles. On two occasions, males were observed to tear the section of the opponent's tegmina bearing the sound-producing apparatus. Males so injured did not call again, although they raised their tegmina in typical singing positions and vibrated them without producing sound.

Fighting occurred infrequently. Males actually fought in only 25% of the aggressive interactions observed. More commonly, interactions involved only exchanges of acoustical signals. When one male entered the vicinity of another singing male, signals were exchanged and shortly thereafter one male left the area. The patterns of signals in this acoustical aggression were always observed prior to physical combat, and so were assumed to be a threat. (These signals will be described later.) The only exceptions to this occurred when males forced off the stem during a physical encounter, did not move away, and/or called in the vicinity of the opponent. The opponent would often attack without signalling, jumping on the calling male's back. After a few attacks, the deposed male moved away.

All aggressive encounters were initiated when one calling male moved toward another, decreasing the distance

between himself and a calling neighbor. Males appeared to defend an area around their calling perch from occupation by other males. The actual size of the area defended by a calling male 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 acoustical signal 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 "coaxed" into moving toward a near neighbor, and the distance at which the neighbor exhibits 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.

The data indicated that males defended roughly circular areas around their calling sites. Borders of the territories facing areas in the study area not inhabited by adult males were sometimes defended less vigorously than borders facing areas where other males were located.

The smallest territory defended acoustically had a radius of 70 cm; the largest had a radius of 18 m. Encounters initiated at these distances, however, were terminated before males engaged in physical combat. The largest territory defended with encounters involving physical combat had a radius of 8 m. In all three species, however, over 75% of the encounters terminating in physical combat were initiated by neighbors separated by 2 m or less at the beginning of the encounter.

Territories of near neighbors overlapped extensively and the radius of the territory defended was almost equivalent to nearest neighbor distance. If the distance between near neighbors was small, 1-2 m, a male could only move 10-15 cm toward his neighbor without invoking aggressive signalling in that neighbor. If the distance between neighboring males was large, 8 m or more, a male could move as much as one meter toward his neighbor without provoking territorial defense.

Since the radius of the territory defended by a male was almost equivalent to his distance from his near neighbor, explaining the function of territoriality in this group of animals becomes, in part, a problem of explaining the pattern of male-male spacing. In order to understand the spacing patterns of males, the areas where males were found were characterized in terms of the resources they may have provided, behavior was monitored during the establishment

of adult residences and the effect of density on territory size was analyzed.

THE TERRITORIAL STRATEGY OF ADULT MALES

The Distribution of Adult Males

Habitat Descriptions

Figures 1 through 4 show the major features of vegetation for the study sites for the three species. They show the male distribution within these sites for the week following peak recruitment.

The nigripes study area was the northeast portion of Cattail Marsh (Figure 1): A narrow belt of vegetation surrounded the relatively open water in the center of this 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. 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 cattails and high sedge from one another. Arrowhead (Sagittaria latifolia), bur reeds (Sparganium eurycarpum) and three-way sedge (Dulichium arundinaceum), were common in the areas of the mat bordering cattails and sedge patches. Early in the season (May and June) bladderwort

FIGURE 1. Orchelimum nigripes study site, the northeastern tip of Cattail Marsh. Male distribution within the site for the first week after large numbers of calling males are found is illustrated.

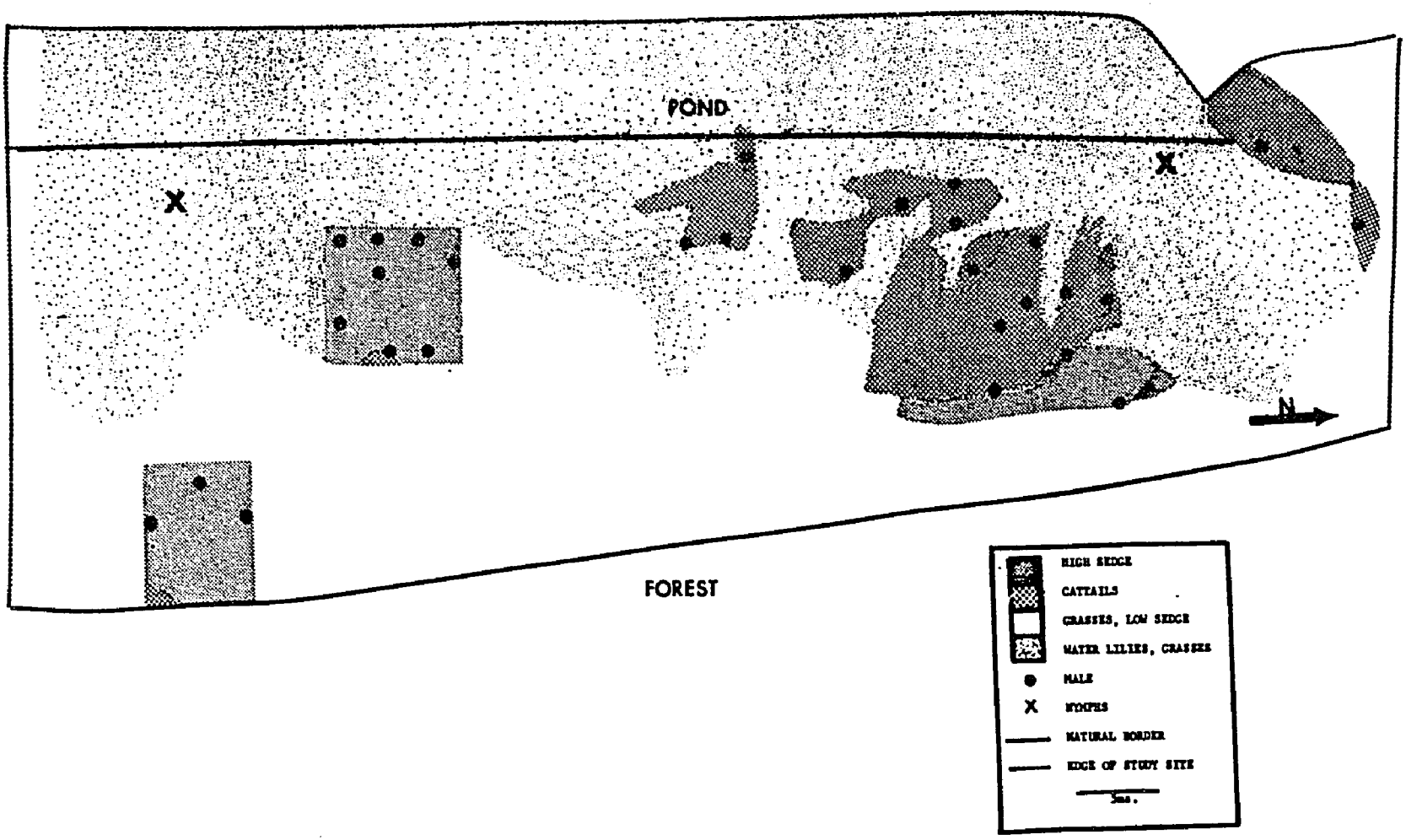

POND
FOREST
N
HIGH SEDGE
CATTAILS
GRASSES, LOW SEDGE
WATER LILIES, GRASSES
MALE
STUMPS
NATURAL BORDER
EDGE OF STUDY SITE

FIGURE 1

(Utricularia intermedia) and grasses (Poa palustris, Glyceria pallida were prevalent in these areas. The northern tip of the marsh was separated from Big Swamp by a road. The west, east, and south sides are bordered by Oak-hickory forest. On the western edge, thick thickets of meadowsweet (Spiraea sp.) separate the marsh proper from the forest. The area of the Cattail-sedge belt used for the study contained standing water in the spring (as much as 50-60 cm) but usually the edges bordering the forested areas dried by the end of summer.

Adult nigripes were usually found in patches of cattails and tall sedge. Infrequently, a male would be found calling from marginal thickets of meadowsweet. Only very young adults were commonly located in the water lily pads. All adults found in the water lily mats appeared to be transients since they were not recaptured there.

The gladiator study site was the northwest portion of Fishhook Marsh. The study site was dominated by Carex associations (mainly Carex strictor, also C. lanuginosa, C. rostrata) and meadowsweet (Spiraea alba). Ferns (Onoclea sensibilis) and forbs, including goldenrod (Solidago spp.), joe-pye weed (Eupatorium maculata), mountain mints (Pycnanthemum spp.) and buttercups (Ranunculus spp.) were common in these associations. On the west, the study site was bordered by oak-hickory forest; on the east, by a road and dry upland field. Large patches of meadowsweet occurred

on the north and south ends of the study area. These patches interdigitated into the homogeneous sedge-forb-fern associations creating two large patches joined by narrow corridors (see Figure 2). On the eastern edge of the site, two small stands of cherries and associated Cornus sp. thickets formed part of the north and south borders. Grasses (Poa palustris) were common along the borders of such stands.

Gladiator adults were usually found in the sedge-forb-fern associations. Occasionally, calling males were found on the meadowsweet bordering the Carex associations. The few adult males (3) found on the interior of the meadowsweet patches were not recaptured there.

The vulgare study site was the largest and most heterogeneous of the three sites. It was an old field dominated by Rubus, largely dewberry with some blackberry. To characterize the pattern of Rubus cover accurately, estimates of Rubus cover within a one-meter quadrat were made at 10 meter intervals throughout the field. The pattern is indicated on the map of the study area (Figure 3).

Large, distinct clumps of heavy Rubus growth (70-100% cover) were separated from each other by areas where Rubus clumps are small (< 1 m in diameter) and scattered. In areas designated as containing 40-70% Rubus cover on the map, the small Rubus clumps were separated by clumps of forbs of intermediate height. Goldenrod, tick-trefoil (Desmodium sessilifolium), blazing star (Liatris aspera),

FIGURE 2. Orchelimum gladiator study site. Male distribution within the site for the first week after large numbers of males are found is illustrated.

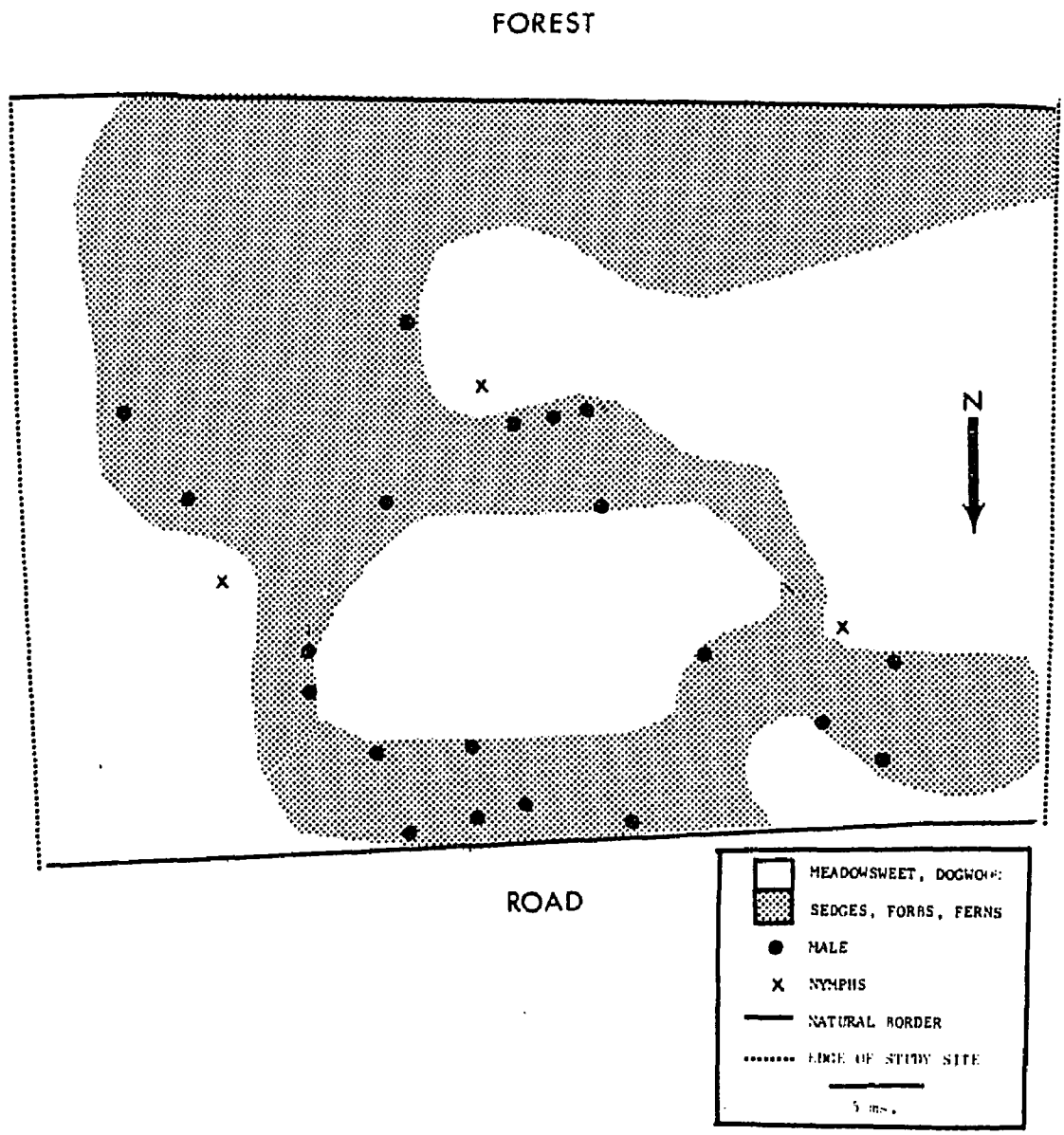

FOREST
N
ROAD
MEADOWSWEET, DOGWOOD
SEDGES, FORBS, FERNS
MALE
NYMPHS
NATURAL BORDER
EDGE OF STUDY SITE

FIGURE 2

knapweed (Centaurea maculosa), milkweed (Asclepias syriaca), bergamot (Monarda fistulosa) and bush clover (mainly Lespedeza hirta and L. capitata) were all common in these areas. Lower vegetation predominated in areas containing less than 40% Rubus cover. Antennaria spp. and grasses (Poa compressa, Panicum lanuginosum) are common in these areas. These were dry sandy areas which, in early spring, are covered with lichen.

The northern half of the field was lower and wetter than the southern half. Milkweed and butter-and-eggs (Linaria vulgaris) were more common in the northern half; blazing star, asters, tick-trefoil and bush clover were more common in the southern half. Nettle (Urtica gracilis) was found in the two low, damp depressions, one occurring on the northeastern end of the study area and the other on the southwestern end. Knapweed and bergamot were prevalent throughout the study site.

Most of the study site was bordered by oak-hickory forest. The north end faced a wetter, small woody field containing staghorn sumac and some small oak and hickory saplings. A road bisected the study area. Small stands of trees along the road interdigitated into the field. Grasses were prevalent along the borders of these stands and forest edges. (The western section of the field is illustrated in Figure 3. Ninety percent of the adult population occurs in this portion.)

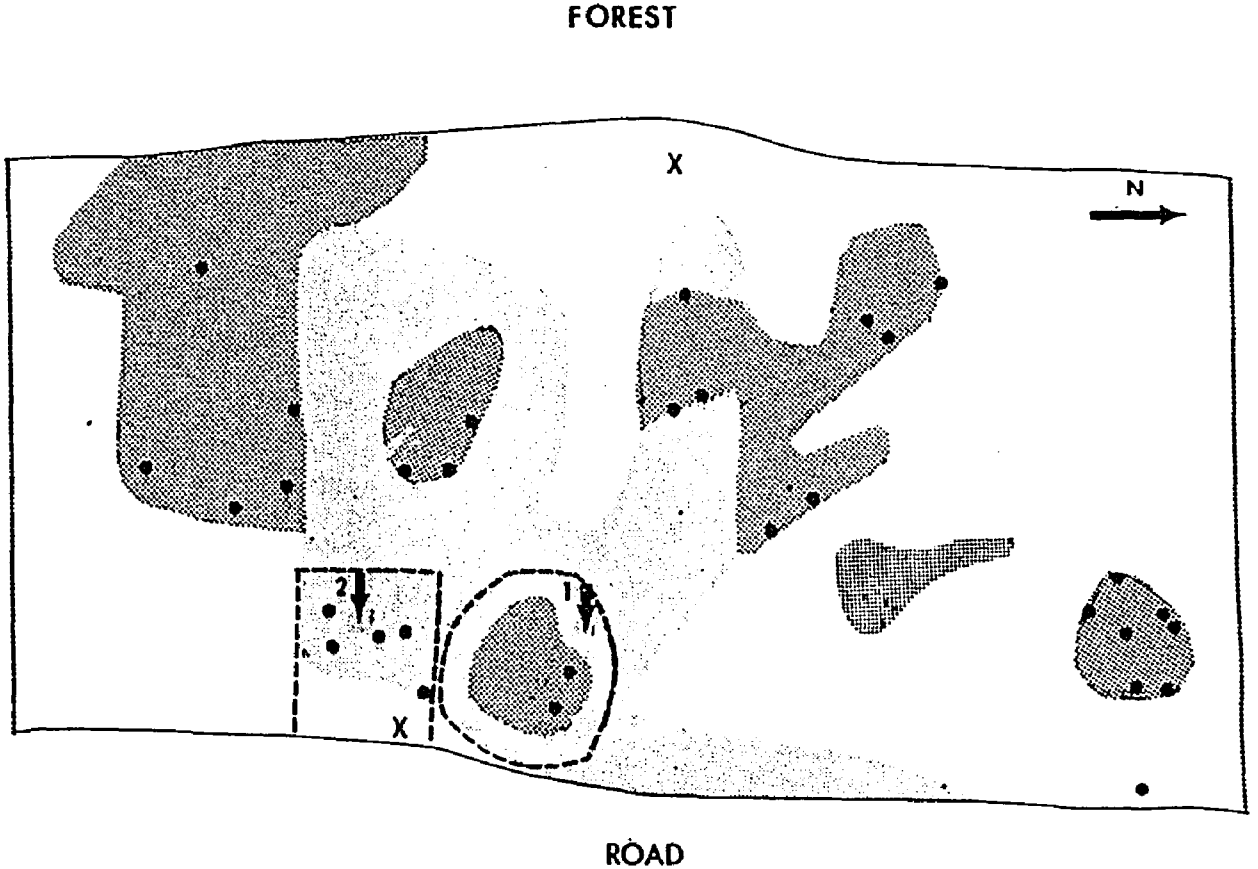


FIGURE 3A. Western portion of the study site of Orchelimum vulgare. Male distribution within the site for the week following peak recruitment is illustrated. The pattern of Rubus (berry) cover illustrated was determined by estimating the cover within one meter quadrats made at 10 meter intervals throughout the field. A. Northwestern portion of the study site. B. Southwestern portion of the study site.

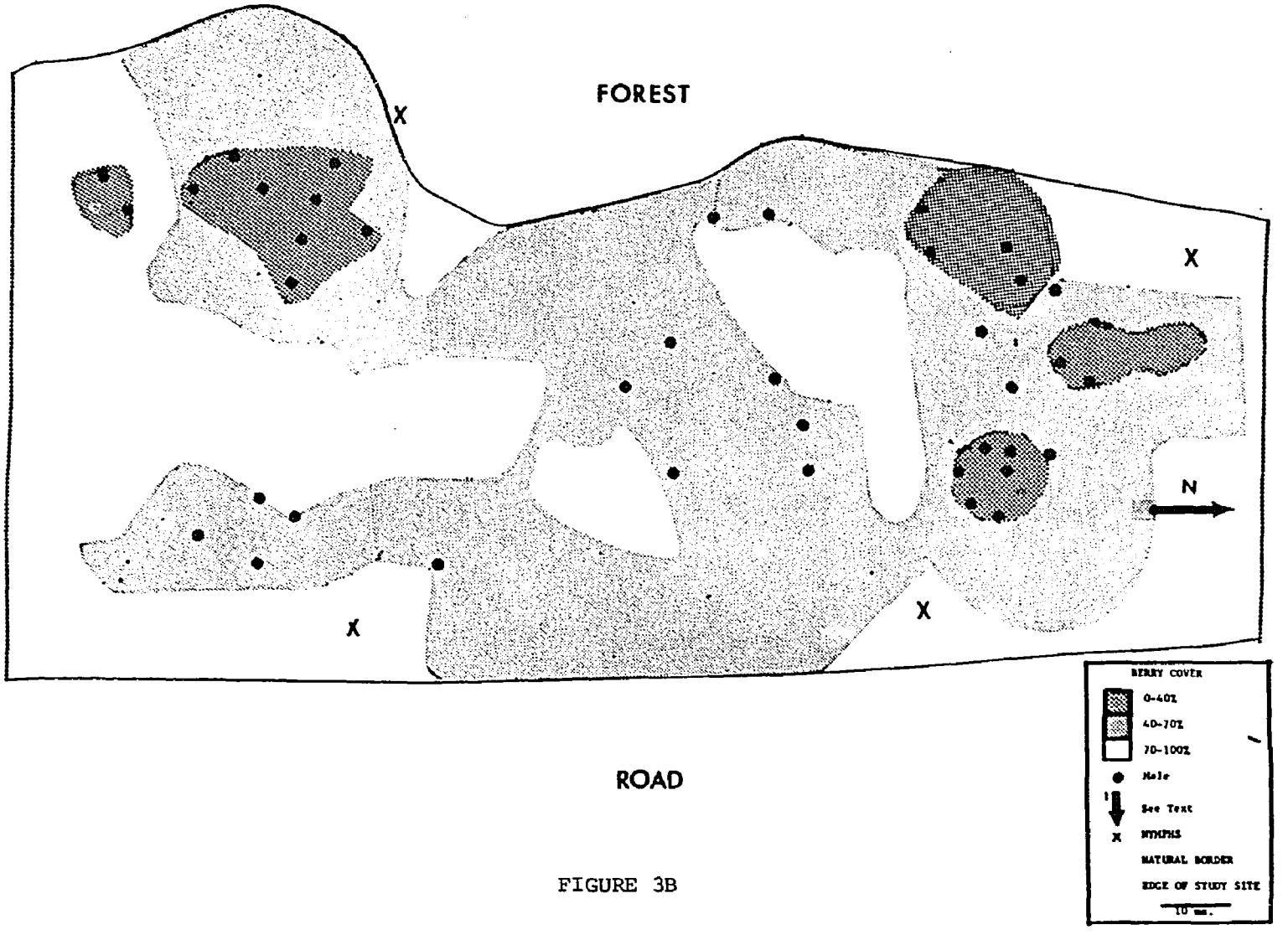

FOREST
X
X
X
X
N
ROAD
BERRY COVER
0-40%
40-70%
70-100%
Male
See Text
NYMPHS
NATURAL BORDER
EDGE OF STUDY SITE
10 mi.

FIGURE 3B

Seventy-two percent of the adults were captured in the thick Rubus clumps. Adults are also found in areas containing at least 40% cover. No tendency was noted for katydids to associate with a particular species of plant within these areas.

Over the course of the study, Rubus has become more abundant. The distribution pattern of males did not change significantly during this time. The few changes in the distribution pattern paralleled the changes in Rubus distribution. For example, in 1975, distinct, large clumps of Rubus (70-100% cover) developed in a few regions where, in the preceding years, Rubus clumps were small, scattered, and intermingled with clumps of forbs (40-70% cover). In 1975, males were concentrated in these Rubus clumps, whereas, in 1973, males were scattered throughout the larger areas defined as 40-70% cover (see Figure 4).

Resources Within Adult Male Habitats

The adult distribution patterns in the three species indicated preferences for certain areas within the study sites. Such preferences are important to any discussion of social behavior because they break up the population into smaller groups of interacting individuals. A consideration of the natural history of this group indicated that three factors may have influenced such preferences:

FIGURE 4. Changes in the distribution patterns of males from 1973-1975. The southern tip of the western portion of the study site is illustrated. In 1973, A, only one small area had Rubus (berry) cover of 70-100%. In 1975, B, a second large clump of 70-100% Rubus cover developed. Males were found in that clump in 1975. In contrast, in 1973, males were found throughout the larger area defined by 40-70% Rubus cover.

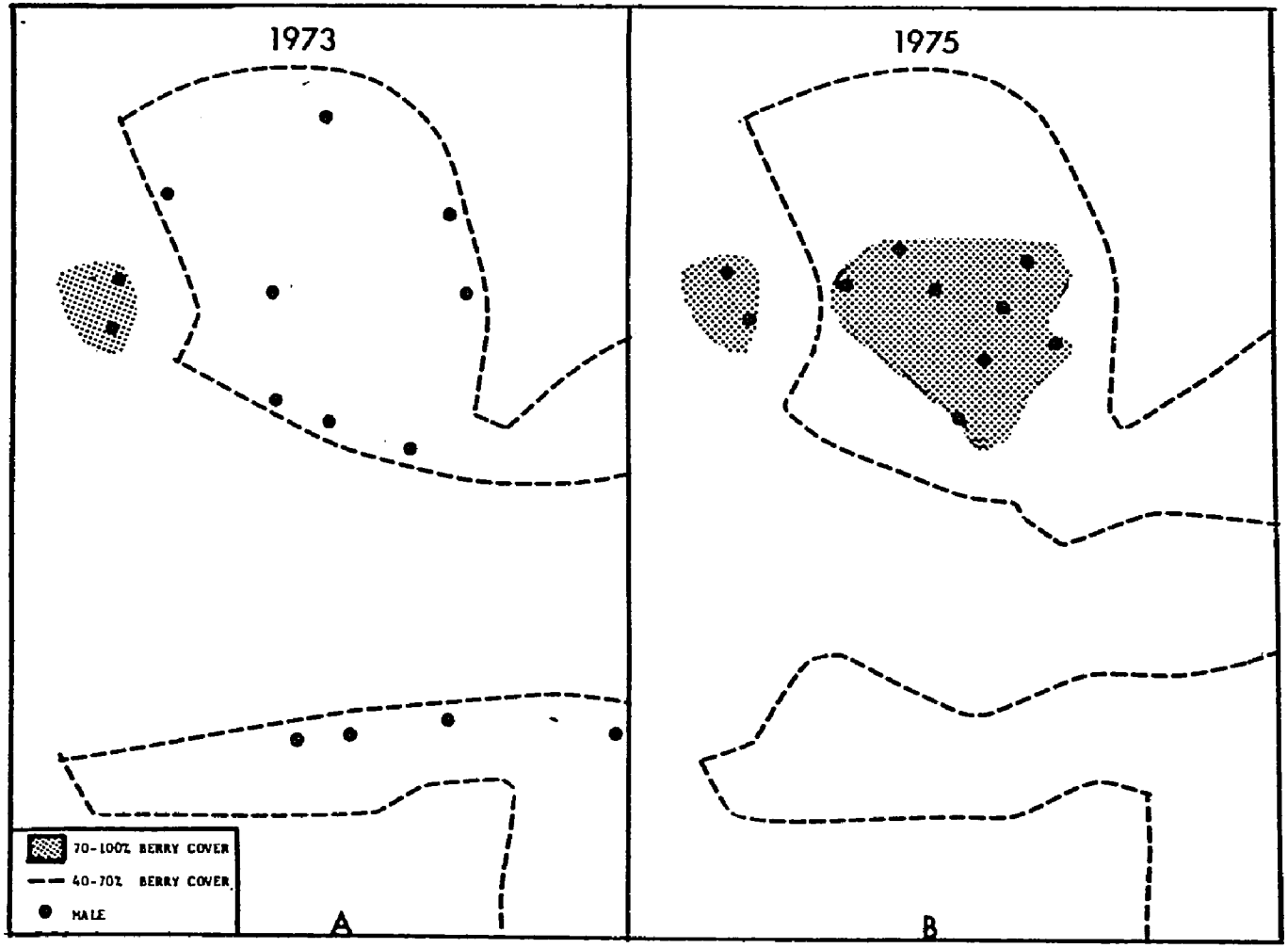


FIGURE 4

the availability of food, cover, and oviposition sites in the areas. To determine the function of territoriality in these species, data on the differences in the availability of these three factors between uninhabited and inhabited areas were collected for use in conjunction with data on the social factors influencing male-male spacing.

Food. Individuals of vulgare and gladiator fed primarily on flowers and leaves of various dicots (see Table 2). Animal matter was also eaten frequently. On two occasions gladiator males were seen to forcibly take pieces of unidentified larvae away from wasps (Polistes) that landed near them. More frequently, prey was not attacked unless it happened to land on, or move up to, the singing perches.

Orchelimum vulgare individuals were frequently seen feeding on dying plants which had seeded earlier and whose leaves were withered and covered with fungus. Much of the bergamot consumed was in this condition. Inspection of some of these plants revealed small aphids on the plants and eggs and larvae in the leaves and stems (21 observations). At first I thought that the katydids were actually after the animal matter on the plants; in the majority of the cases, however, inspection of the plants failed to reveal the presence of such items (31 observations). These observations indicate that dead, fibrous material probably constitutes a significant portion of the diet of this

TABLE 2

OBSERVED FOOD ITEMS OF THE THREE SPECIES OF *ORCHELIMUM*

(Items were not counted unless the katydid fed on it for ten minutes or until the item was completely consumed)

Species	Food Item	Number of Items
O. vulgare	flowers, leaves of bergamot, *Monarda fistulosa*; (fly, wasp larvae inside flower heads, stems and aphids on leaves consumed with the plant material	80
	flowers of goldenrod, *Solidago* spp.	54
	fruit and leaves of dewberry and blackberry, *Rubus* spp.	25
	flowers of yarrow, *Achillea millefolium*; flowers of wild carrot, *Daucus carota*; dead bare stalks; flowers of bush clover, *Lespedeza hirta* and *L. captiata*; soldier beetles, *Chauliognathus pennsylvanicus*; unidentified large beetle or Lepidoptera larvae	5-10
	flowers of blazing star, *Liatris aspera*; milkweed pods and leaves, *Asclepias syriaca*; various asters; aphids and ants	1-5
O. gladiator	leaves of goldenrod, *Solidago* spp.	40
	flowers of meadowsweet, *Spiraea alba*	25
	flowers, leaves of mint, *Pycnanthemum* spp.; leaves, flowers of ironweeds, *Eupatorium* spp.; unidentified large larvae; sedge seeds, leaves, *Carex strictor*	10-20
	ants; ferns, *Onoclea sensibilis*, *Dryopteris thelypteris*; grass seeds, *Poa palustris* and other species	1-10
O. nigripes	heads of cattails, *Typha latifolia*	200
	leaves and flowers of arrowhead, *Sagittaria latifolia*	76
	smartweed, *Polygonum amphibium*; leaves of sedge, *Carex lanuginosa*; seeds of grasses, *Poa palustris*; *Glyceria pallida*; meadowsweat, *Spiraea* spp.	5-20

species. Females of vulgare (20 observations) and gladiator (3 observations) fed voraciously on the leather straps of the tape recorder and observer's jeans, indicating that they may prefer dry, fibrous materials.

In contrast, nigripes fed on various monocots, such as heads of cattails, that are abundant in the study area, and were not observed to eat animal matter. Larvae of various Lepidoptera were present in the heads of cattails, but inspection of material being eaten failed to reveal any recognizable trace of animal matter.

Feeding was not limited exclusively to areas where males and the adults spent most of their time. In fact, most of the usual food items of vulgare were more prevalent in areas outside the berry patches. In the evening, when feeding activity was high, both sexes feed just outside the berry clumps, on goldenrod, mints and various other forbs. Adults never spent long periods outside of the berry clumps, returning to them after feeding for 20-30 minutes.

Similarly, in nigripes, 60% of the males resided in high sedge, yet sedge was only eaten occasionally. Animals found in these sedge patches fed on the few cattails found there (Figure 2) or more frequently, on the arrowhead, water lilies, and grasses adjoining the sedge clumps. Again, individuals never spent much time away from the cattails and sedges, returning to them after feeding.

Feeding activity was high in the evening after calling ceased. At this time males are nonaggressive toward one another. Often several males and females fed on the same plant. Usually, individuals in such groups behaved as if oblivious to one another's presence. Individuals, who bumped into each other while feeding, simply move 2-3 cm away and resume feeding. Rarely (10 observations in 200 hrs), males were observed to attempt genital contact with nearby females. However, once repulsed by the females, males moved away and continued feeding. The only observed exceptions to such nonaggressive feeding behavior was when individuals came upon animal prey. If the item was small, such as an ant, one male pushed another individual away from it. Such occurrences were rare and there were only six observations of this behavior.

Oviposition sites. Oviposition sites were located by scanning stems for deposition scars. The scars marked the location of incisions, made by the female's mandibles, in which the eggs were laid (see Figures 5 and 6). Locating oviposition sites was time-consuming and difficult. In vulgare, for example, only one plant exhibiting scars was located for every 200 plants examined.

Eggs of vulgare were found in goat's-beard (Tragopogon pratensis and T. major), wild carrot (Daucus carota), bergamot, and tick trefoil. In 1973, 27 oviposition plants

FIGURE 5. Oviposition sites of Orchelimum vulgare. A. Goat's-beard (Tragopogon major). B. A clump of goat's-beard at the time females are ovipositing. C. Dried goat's-beard, the typical condition of the plant when oviposition occurs. Arrows indicate positions of incisions, not visible in the picture. D. A close-up of the incisions. E. Eggs within the incisions.

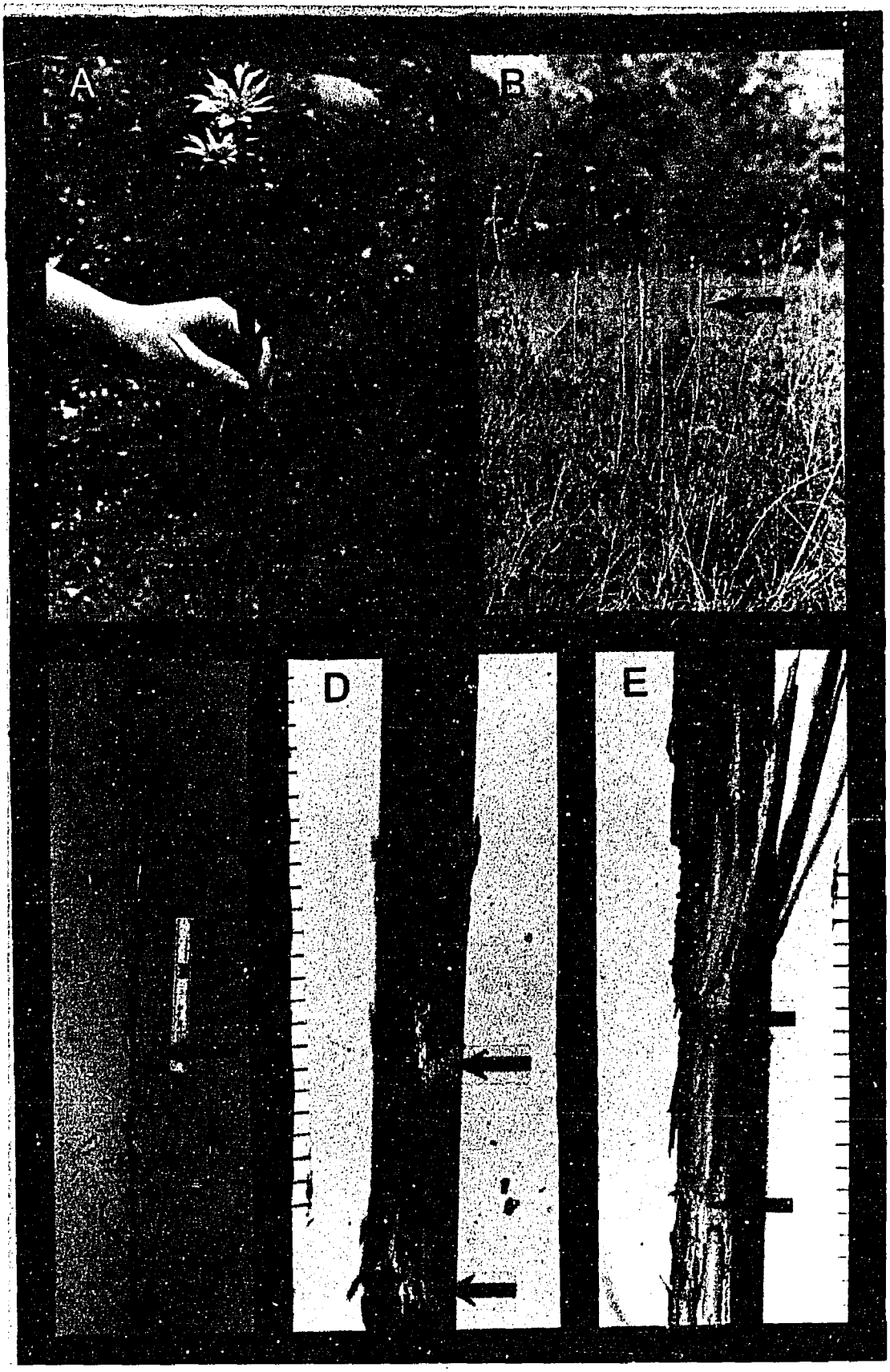


Figure 5



FIGURE 6. Oviposition sites, Orchelimum nigripes and Orchelimum gladiator. A. Cattail, one of the major oviposition plants for O. nigripes. Arrow indicates positions of incisions just above the cattail head. B. Close-up of incisions just below the head. C. Eggs in cattail head. D. Eggs of O. gladiator in sedge stem.

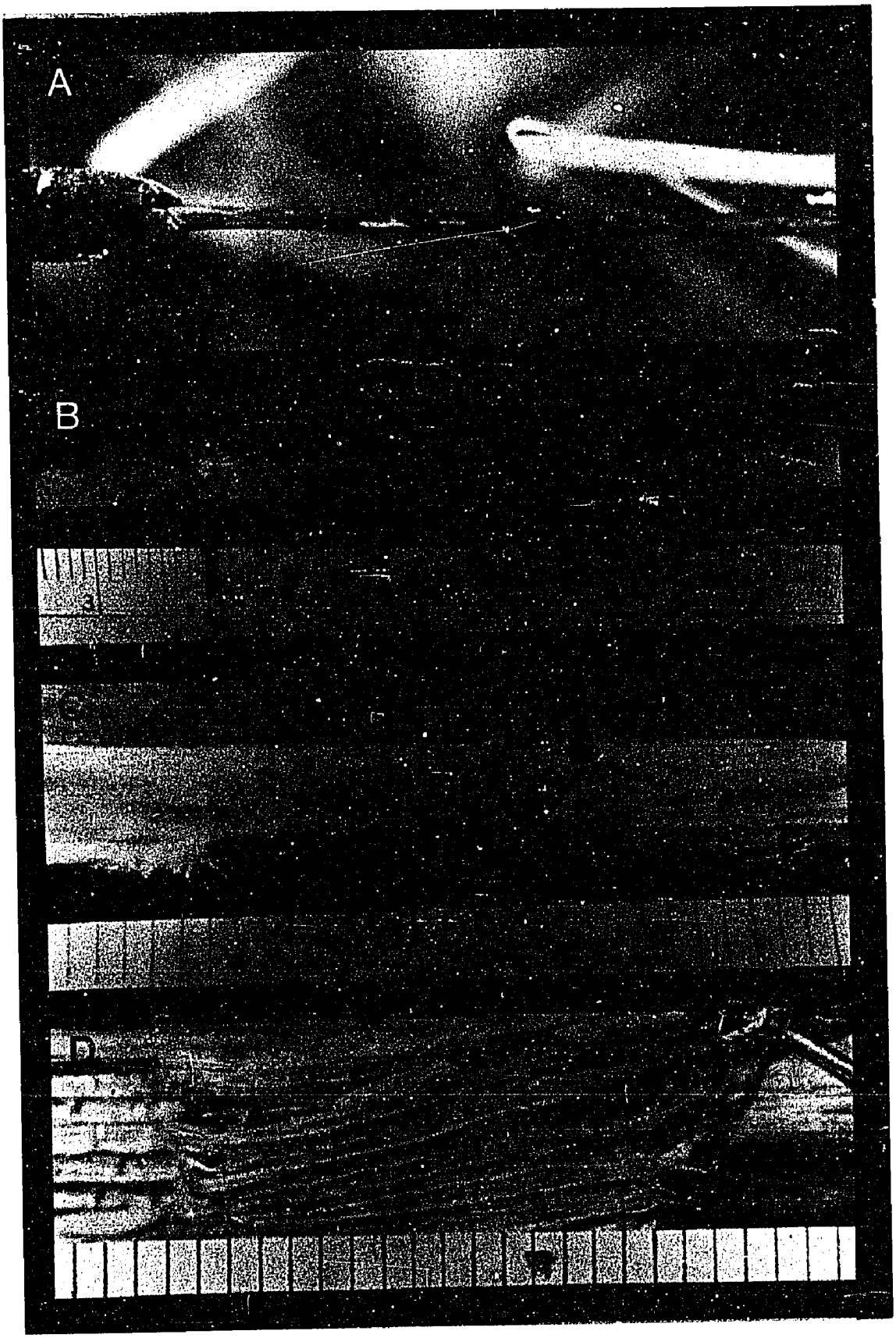


Figure 6

were located, all goat's-beard. In 1974, only five oviposition plants were located, three goat's-beard, one wild carrot, and one mint. In all, 41 plants were located in 1975; 23 goat's-beard, 12 wild carrot, four tick trefoil, and two mint. The same areas were canvassed for oviposition plants during all three years. In 1974, adult densities were low in the canvassed areas, and probably account for the few oviposition plants located.

The abundance of wild carrot on the study site increased since the study was first initiated. In 1975, in areas where wild carrot was abundant (1-3 plant/sq m), eggs were laid in both wild carrot and goat's-beard. In the same areas in 1973 before wild carrot was abundant (0-2 plants/sq m), eggs were only located in goat's-beard. Usually the same number of incisions were found in both plants but in goat's-beard two eggs are laid in each incision while five or six per incision were the usual in wild carrot. Therefore, it appears that wild carrot was preferred to goat's-beard when it was available. Tick trefoil and mints were utilized in areas where goat's-beard was sparse (~2-3 plants/sq m; see Figure 9). Only two incisions were found in mints, each containing one egg. Goat's-beard was apparently preferred over these two plants.

Rubus stems were apparently not utilized for oviposition, an unexpected finding in view of the study by Metcalf and Colby (1930). They described vulgare as a

serious raspberry pest because of the damage caused to stems by ovipositing females. Admittedly, locating oviposition sites among Rubus brambles was difficult and it is possible that some Rubus oviposition sites were overlooked, but this would not have happened if Rubus were commonly utilized for oviposition. In 1976, I removed all the Rubus stems from 15 one-meter plots from throughout the field and examined them unsuccessfully for oviposition scars. Furthermore, over the three years of the study three plants of blackberry were found with shallow incisions containing no eggs, but indicating that females occasionally test blackberry stems. No such scars were located on dewberry stems. Perhaps the berry stems on the study field were too thin to be utilized for oviposition. The eggs of vulgare are large, more than 1 mm in diameter, and all the oviposition sites located were in plant stems at least 3 mm in diameter. Metcalf and Colby (loc cit) also found that incisions in stems smaller than 3 mm in diameter did not contain eggs.

In the laboratory, vulgare females deposited eggs only in dry stems, although both green and dry stems of the three species of oviposition plants were made available. In the field, eight females oviposited and all laid in dry plants. Goat's-beard flowered in June and mint, wild carrot and tick trefoil flowered in July. The katydids did not mature until late July and most of the egg-laying

activity occurs in August, by which time the plants have set seed and died. Therefore, in the field as in the laboratory, dried material was probably utilized exclusively for oviposition. Also, living goat's-beard contains a sticky latex that may be unpalatable and thus discourages oviposition. In the laboratory, females were observed to reject green stems of this plant after some "testing" (making one or two shallow incisions).

Eggs of nigripes were found in stems of sedge and in stems and heads of cattail. Both years, 1974 and 1975, cattails were utilized for oviposition more frequently than sedge (Figure 7). In 1974, only small areas of patches 2 and 4 were surveyed for oviposition sites. 15 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 five to one (see Figure 7).

From 2-80 eggs were present per cattail and 4-20 per sedge. Older cattail stems, those with flower heads at least one year old, were usually utilized as an oviposition site by more than one female. On two occasions, two different females oviposited in the same cattail and once three different females oviposited in a single cattail. Also, indirect evidence indicates that more than one female laid in the same cattail. In the laboratory, females laid, at most, 24 eggs at one time. Yet in many older cattails

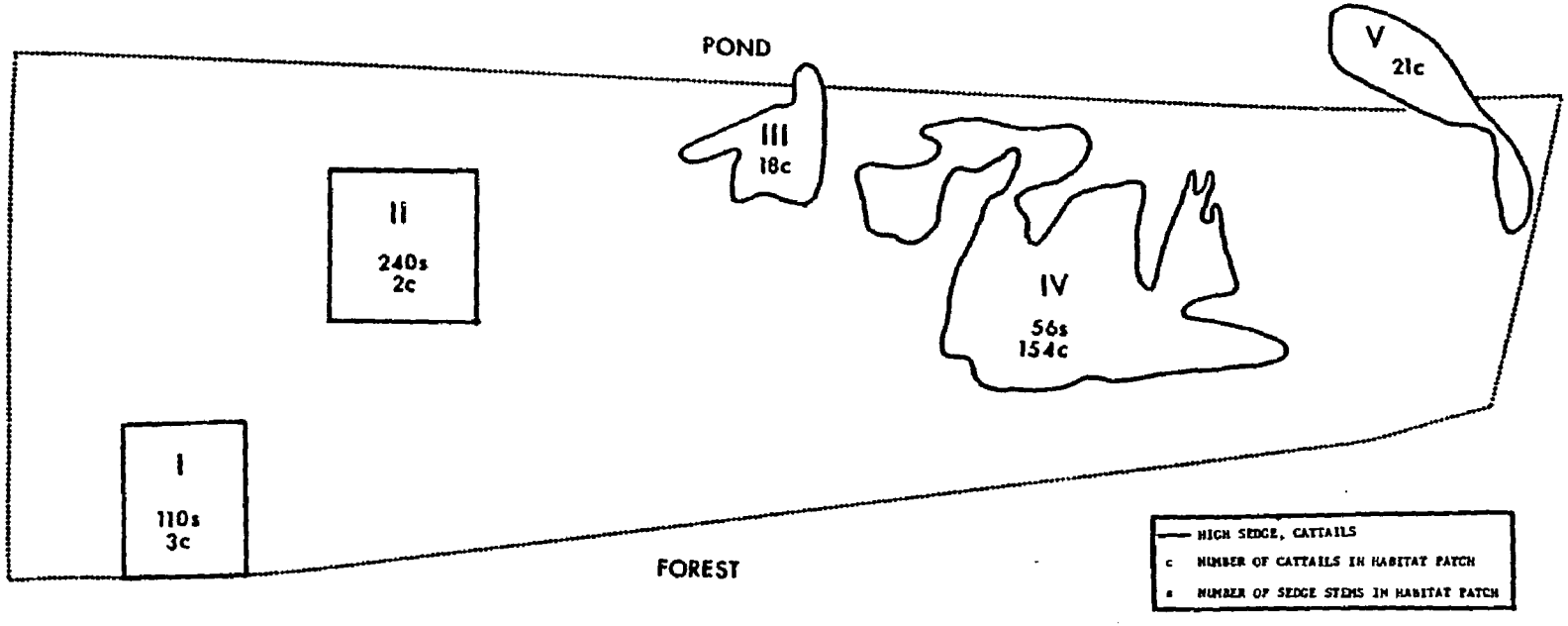


FIGURE 7A. Distribution of oviposition plants and sites, Orchelimum nigripes. A. Distribution of oviposition plants, cattails and sedges, 1975. B. Distribution of oviposition sites.

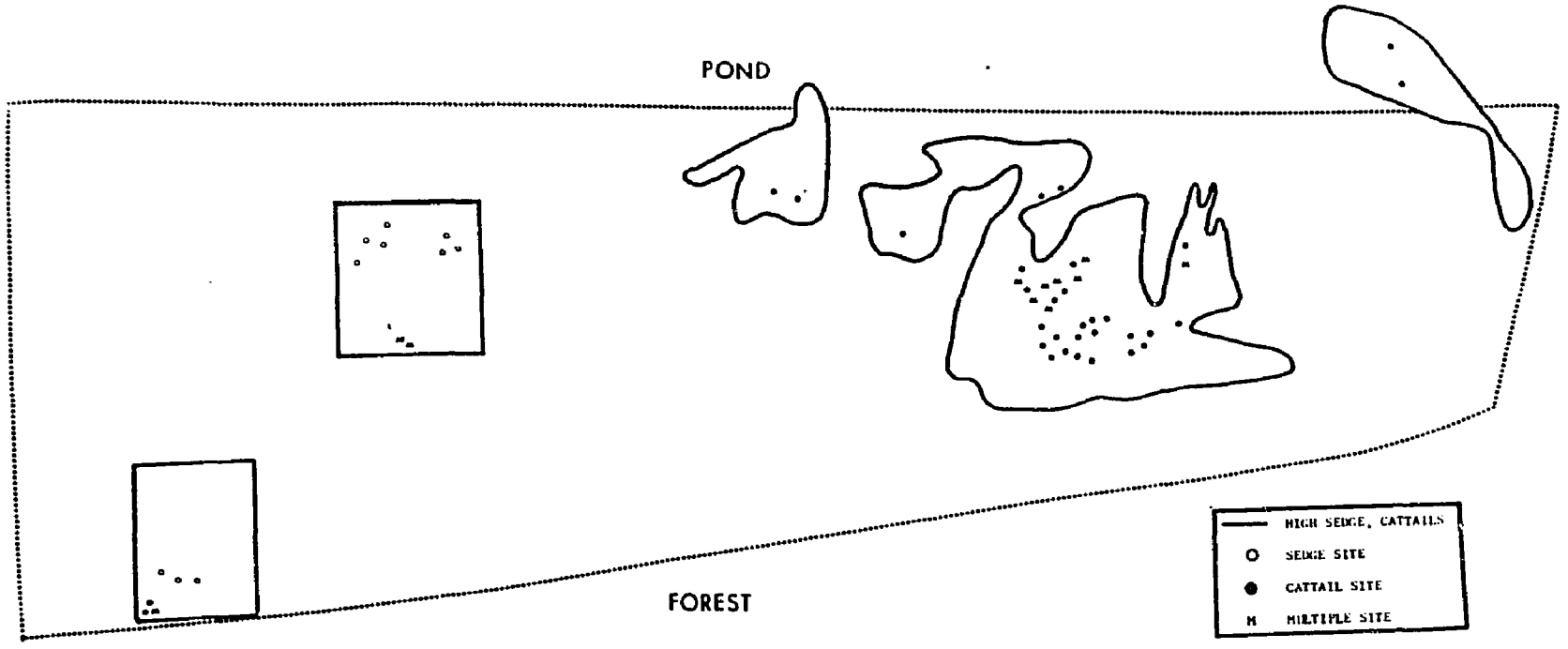

POND
FOREST
HIGH SEDGE, CATTAILS
SEDGE SITE
CATTAIL SITE
M MULTIPLE SITE

FIGURE 7B

more than 50 eggs were present and incisions were very deep indicating that a minimum of two females had oviposited in the plant. In older cattails, what remained of the head and about 25 cm of the stem below the head were utilized. In contrast, in younger cattails eggs were laid only in the tip of the head, and on the average, only eight eggs were found per head. Older cattails break apart easier than young cattails, and therefore, may be preferred by females because the stems are softer and more pliable.

Only seven oviposition plants were located for gladiator, three sedges, a mint, and three ironweeds. About 12 incisions were found per plant. In nigripes and gladiator oviposition sites were located in areas where calling males occurred and where the adults spent most of their time (Figures 2 and 9). Although there is a correlation between the distribution of males and oviposition plants, there is no indication that males specifically associate with the cattails or sedge that are later used for oviposition.

For vulgare, male distribution was not always correlated with the distribution of oviposition sites (Figure 8). In fact, calling males were never observed in the areas where oviposition occurred. Eleven females were observed ovipositing or testing plants in areas outside the Rubus clumps. Six of these females were observed moving into these areas from a Rubus patch before attempting to oviposit.

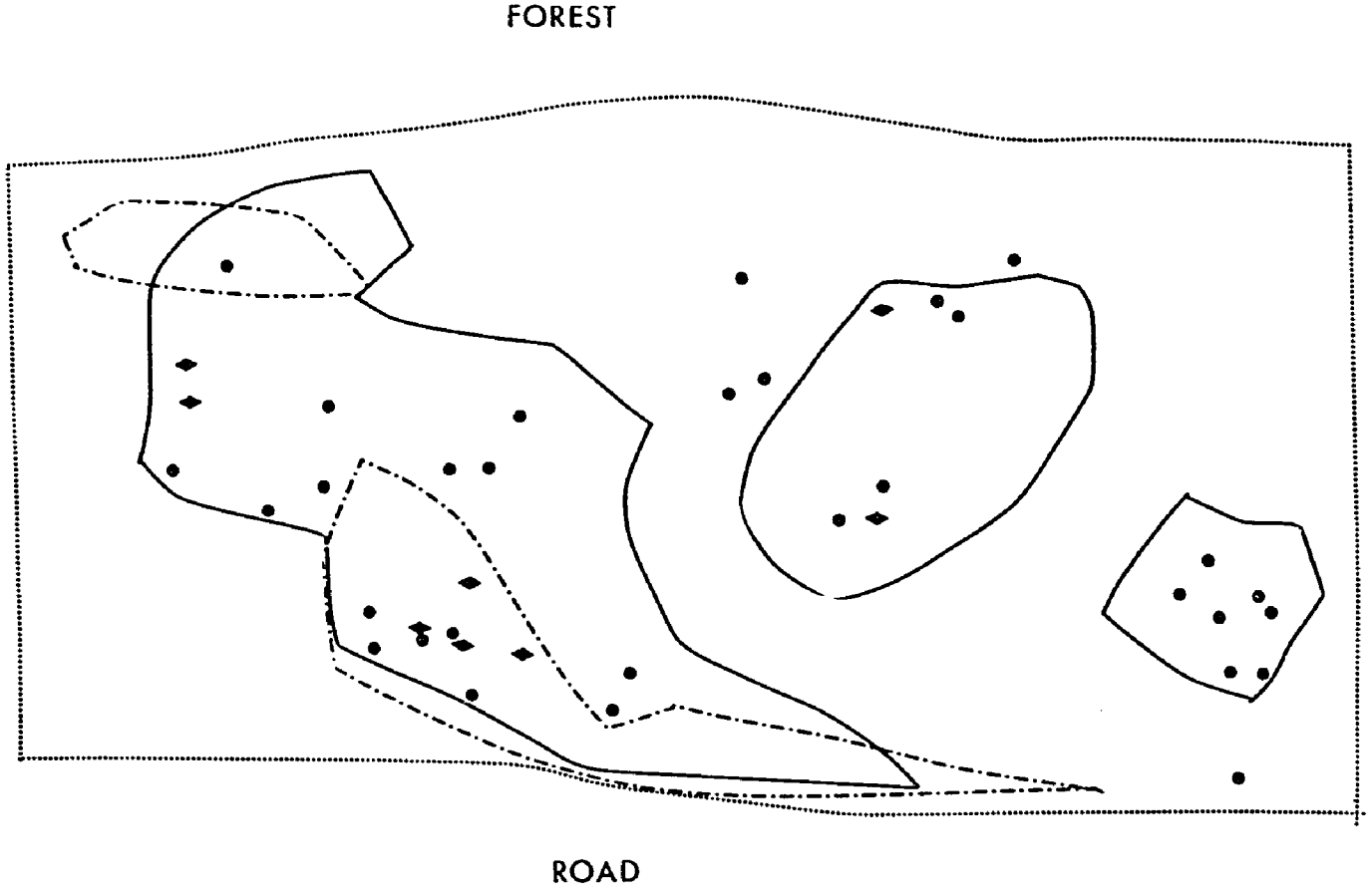


FIGURE 8A. Distribution of oviposition sites and males, Orchelimum vulgare, 1975. A. Northwestern portion of the study site. B. Southwestern portion of the study site.

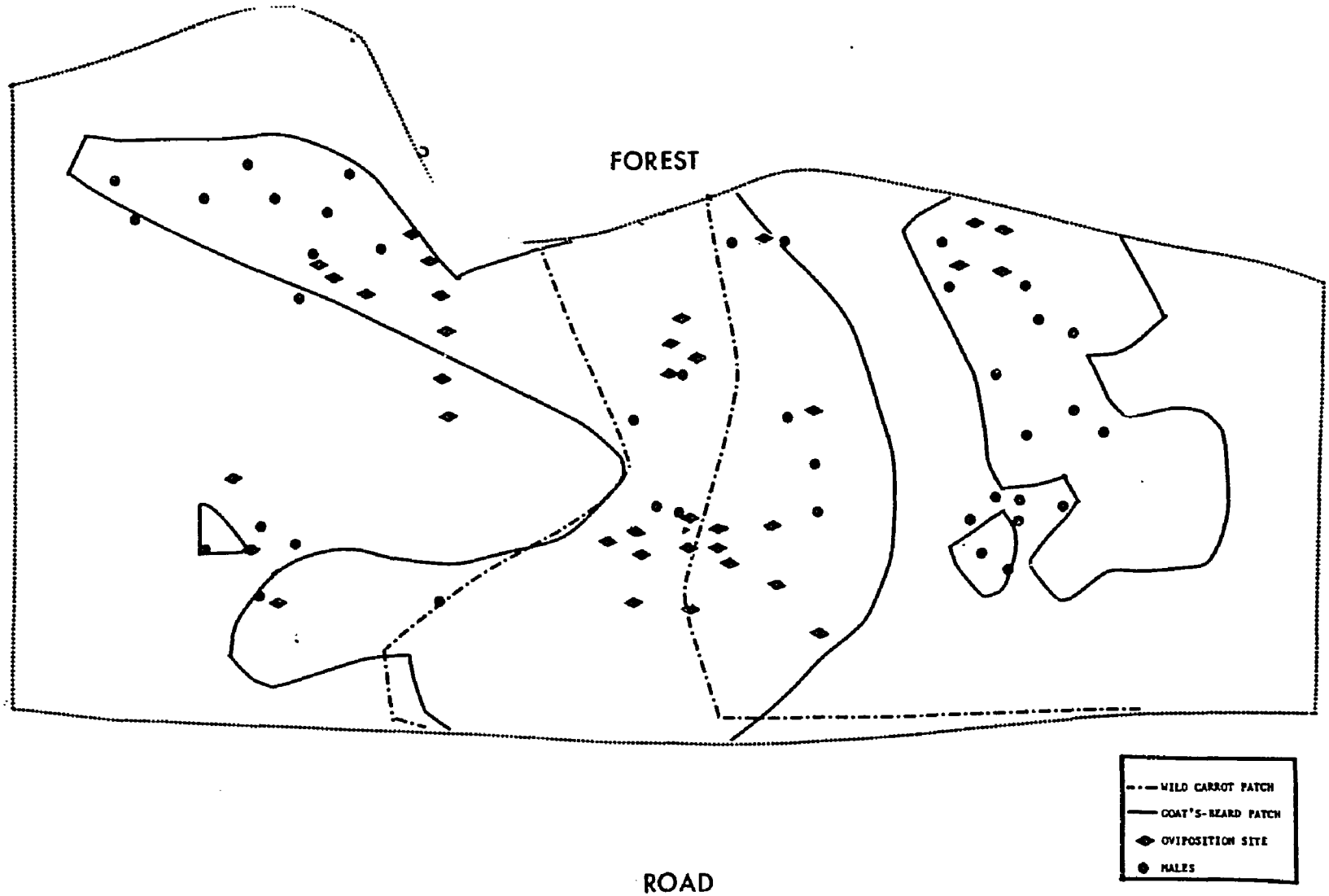
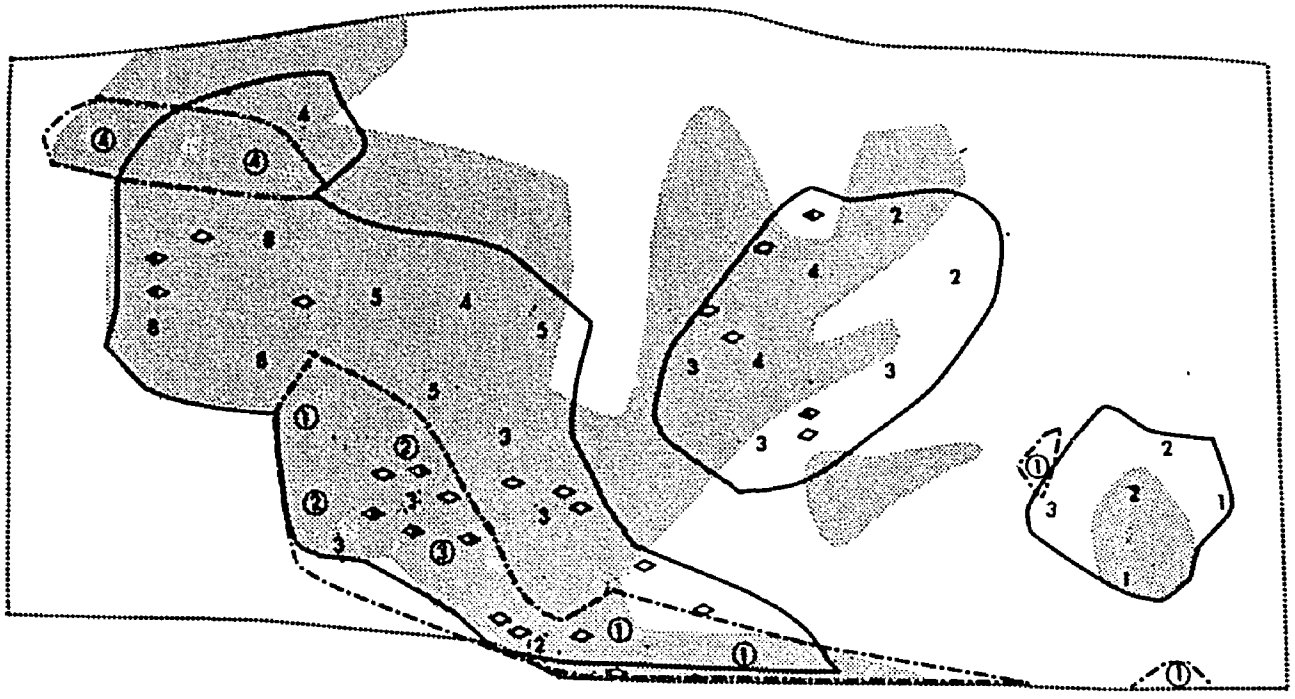

FOREST
WILD CARROT PATCH
GOAT'S-BEARD PATCH
OVIPOSITION SITE
MALES
ROAD

FIGURE 8B

All the females moved back into a Rubus patch after ovipositing although females spent as much as two days in the area of the oviposition site. As might be expected, oviposition sites were not always found in areas where the preferred plants are the most dense (Figure 8). The oviposition sites tended to be in the vicinity of the dense Rubus patches, the areas where the males commonly called and both sexes resided (Figure 9). Females appeared to be reluctant to move far from Rubus patches in search of oviposition sites. However, the availability of oviposition plants appeared to have some influence on the placement of territories. In Rubus patches not evenly surrounded by oviposition plants, the males' calling territories were shifted toward the locations closest to the oviposition plants.

In order to see if decreasing the availability of oviposition plants would influence distributions the next season, the abundance of goat's-beard was experimentally decreased in two areas following the reproductive season. Only the abundance of goat's-beard was manipulated because at that time (1973) it was the only known oviposition plant. In the area designated by arrow 1 in Figure 1, goat's-beard was removed in the area surrounding a Rubus clump for a width of three meters from the edge of the clump. In the area indicated by arrow 2, the density of goat's-beard was reduced by two-thirds. Throughout the remainder of the

FOREST



ROAD

FIGURE 9A. Distribution of oviposition plants and sites, Orchelimum vulgare. To establish plant densities, the number of plants within a one meter quadrat was determined every 10 meters throughout the study site. The pattern of distribution of goat's-beard and wild carrot, the most common oviposition plants, for 1975, is illustrated. A. Northwestern portion of the study site. B. Southwestern portion of the study site.

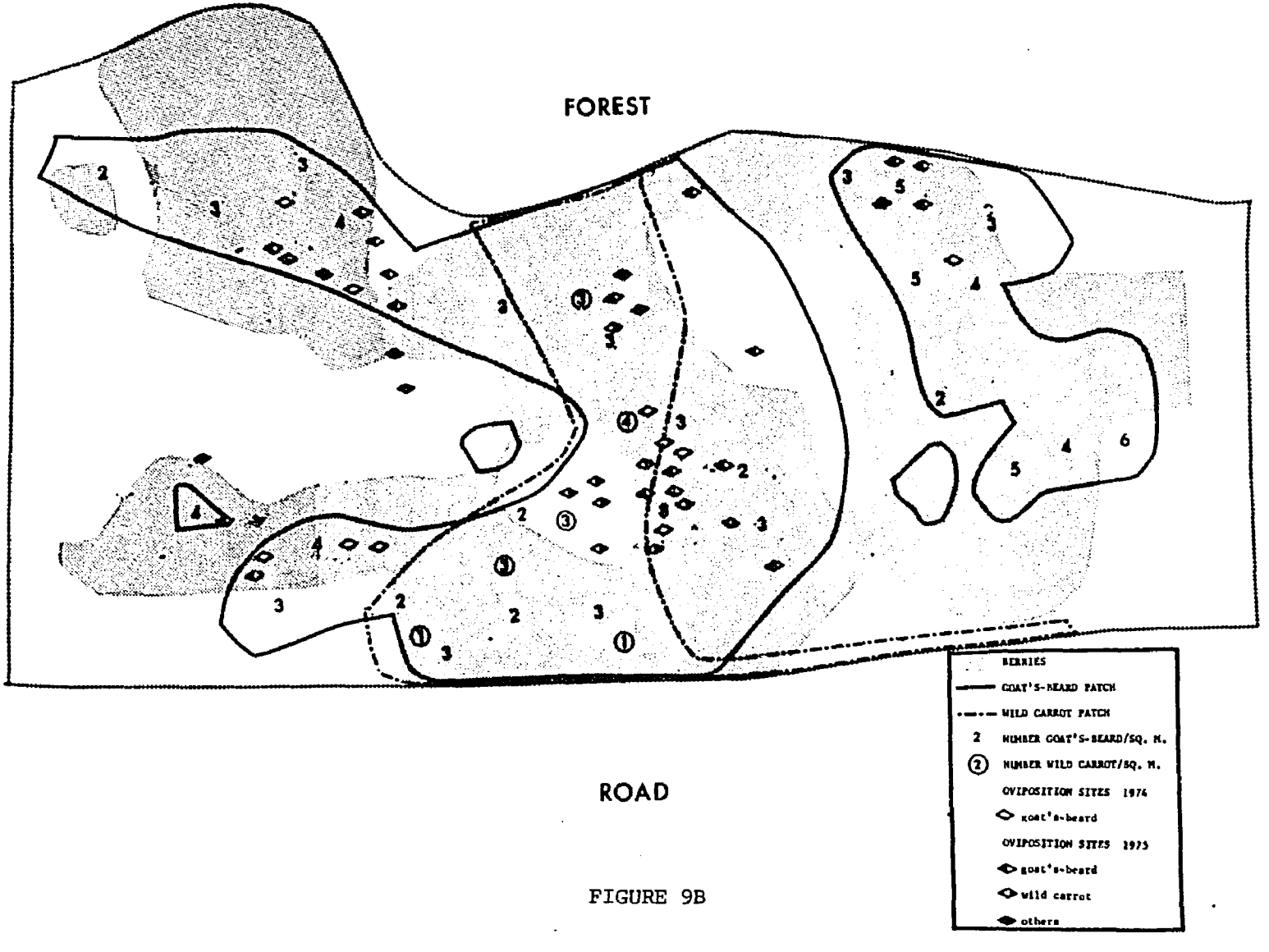

FOREST
ROAD
BERRIES
GOAT'S-BEARD PATCH
WILD CARROT PATCH
2 NUMBER GOAT'S-BEARD/SQ. M.
② NUMBER WILD CARROT/SQ. M.
OVIPOSITION SITES 1974
goat's-beard
OVIPOSITION SITES 1975
goat's-beard
wild carrot
others

FIGURE 9B

study area, the density of goat's-beard was sparse (about three plants/sq m). In Area 1 before the plants were removed the density was ten plants/sq m and in Area 2 it was eight plants/sq m. The growth the next season was spindly and the plants had few branches. In 1973, seven males resided in the two Areas. In 1974 only a single male was found in the Areas; in 1975, after wild carrot had become abundant, the Areas were repopulated. Wild carrot is more abundant in Area 2 than Area 1 and most of the males and all the oviposition sites in 1975 were found in Area 2 (Table 3).

During the study, only five males were observed residing (a stay of a week or more) in areas with little berry cover (under 40%). In all five cases, these areas contained wild carrot and goat's-beard. For example, in 1975, a patch of wild carrot developed in the grassy northeastern tip of the field (arrow 3, Figure 2). A male and female were found here for two weeks that year, although not in 1973 or 1974. These data indicate that the availability of potential oviposition plants influenced the distribution pattern of the adults in vulgare.

Cover. Males relied on concealment behavior as their first means of defense against predation. When disturbed, by a potential predator or parasitoid, males stopped calling and quickly moved to the side of the singing perch away from

TABLE 3

THE NUMBER OF MALES AND OVIPOSITION SITES IN AREAS ONE AND TWO, BEFORE AND AFTER THE REMOVAL OF GOAT'S-BEARD

	Number of Males		Oviposition Sites	
Year	Area One	Area Two	Area One	Area Two
1973 (before)	5	2	8	2
1974 (after)	1	0	0	0
1975	2	5	0	4
1976	0	4	Not censused	

the disturbance. If the disturbance persisted, males dropped off the perch into the undergrowth. In vulgare, responses of males, calling from the more barren areas, indicated that males actively seek cover when disturbed if it is not immediately available. Males were observed in areas where Rubus patches were small, scattered and separated by clumps of forbs. Among the forbs, cover may be sparse (10-30%). Males, who dropped from perches onto more barren ground, kept moving until they encountered berry cover (40 out of 42 observations). In contrast, males, in areas with heavy cover, and who dropped into the brambles, remained motionless after dropping (62 observations out of 65 observations).

In all three species, males were rarely found in areas where dense undergrowth is not prevalent. This is the best indicator that availability of cover was important to calling males. However, dense cover was available in areas of the study site uninhabited by calling males. In the gladiator and vulgare study areas, grassy areas also provided 100% cover but were not inhabited by males. In nigripes cover was abundant in the water lily mat associations and low sedge patches but neither of these was utilized by the males. Thus the availability of abundant cover was not the only factor distinguishing areas in which males occur.

Summary

It is evident that no single factor distinguished residential areas from uninhabited areas. Individuals in all three species fed both inside and outside of male territories. In vulgare, females oviposited away from the males' territories.

The areas, from which the males called, were in the proximity of oviposition plants, food and cover. Indeed, the calling territories seemed to be located in the best of "available worlds" with regard to these resources.

In vulgare, most males called from Rubus clumps. These provided ample cover and some food, and were situated within easy access to other food sources and oviposition plants. Grassy areas would have provided as much cover to calling males. However, these areas would have provided little food because many grasses had already dropped seed by the time vulgare was adult, and most other food items and oviposition plants would be located outside these areas. Forb areas, where about 30% of the males resided, provided less cover than berry patches. Since food plants were clumped, these areas would have provided as much food as did the berry patches. Oviposition plant distribution did not always correlate with the distribution of other forbs. Bergamot was more prevalent on the east side of the study site (15-20 plants/sq m) than on the west (5-10 plants/sq m), yet on the southern half of the field, goat's-beard, and wild

carrot were more prevalent in the west (Figure 7). Therefore, males in the forb area were about as far from oviposition sites as were the males in the berry patches.

If all three factors are important, the relative influence of any one on male distribution will depend upon its proximity to the others. The distribution pattern of any one factor, and so the relationship between the pattern of all three can be expected to vary from locality to locality. In different areas, then, males' territories can also be expected to be physically associated with different resources. In vulgare, male territories were located in areas offering food and cover. In nigripes, territories were located in areas where oviposition plants are abundant. Cattail patches also offered food, although cover was sparse (in some areas, less than 20%). Males in these areas, upon dropping after being disturbed, swam quickly to the nearest cattail or mat area. In contrast, in the sedge patches, males called from abundant cover and oviposition plants, but fed outside of these patches.

The significance of such variation in calling site location is that males, in these species, are not associated with and defending one resource. Perhaps katydid females do not predictably congregate at or come to any one resource, as is suggested for some other territorial insects. Some insects defend areas where females come to oviposit (Parker, 1970;

Jacobs, 1955). Male katydids, on the other hand, are probably monitoring female density directly and establishing territories in areas where females are most abundant. This will be considered further in the following section.

Establishment of Calling Territories

General Considerations

Methods of determining age of adults. Adults reached maturity at different times during the reproductive season and were not generally located until their exoskeletons had hardened. Therefore, it was necessary to develop an aging technique for adults. Such a technique enabled identification of adults either as newly moulted individuals or older transient adults.

A list of morphological changes accompanying aging was compiled on 95 nigripes, 17 vulgare and 13 gladiator that were captured with soft exoskeletons. Twenty individuals of nigripes and two of vulgare were captured in the process of moulting. The exoskeleton required two days to harden, therefore, all individuals captured with soft exoskeletons were assigned an age of two days. The following morphological changes were noted in these animals upon aging. In all three species, older adults were much darker in body color. Also the body of older adults contained streaks of brown pigment, especially about the major sutures. Body color changed from lighter to darker green over a period of three to five days. Pigment streaks became apparent about one to two weeks after moulting. The intensity of these streaks increased with age and very old individuals appeared mottled in appearance. Eye color also changed with age. Nymphs and newly moulted adults had yellow eyes which

changed over a period of days to orange (see Figure 10). This change took about 2-4 days in nigripes and gladiator, and took as long as 5-6 days in vulgare.

In nigripes, head color also changed (Figure 10). Late instar nymphs and young adults had green, or rarely, yellow heads. By the third or fourth day, the face started to show traces of beige pigment, or brown in the case of yellow heads. By the sixth or seventh 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.

In all species, older animals, at least two weeks old, could be reliably distinguished from younger adults that were lessthan one week old. In nigripes approximate ages could also 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 two 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 four days. An individual similar to the latter, but with no green on the head, was assigned an age of six days.

The basis for the eye color changes and the deposition of dark pigment streaks is unknown. Some observations

FIGURE 10. Head color changes in Orchelimum nigripes with age. A. Nymph with green head, yellow eyes. B. Nymphs and adults have green or yellow heads. A yellow headed young adult is illustrated. C. A young adult with green head, three days old, is compared with an older adult who has a beige head and is six days old. D. Older adults vary in head color from beige to brown. E. Older adult, 15 days old, with pigment streaks on head, is compared to a younger adult, eight days old, who has not as yet developed pigment streaks. F. Female from the laboratory population with a red head is compared to an adult with more typical beige head.

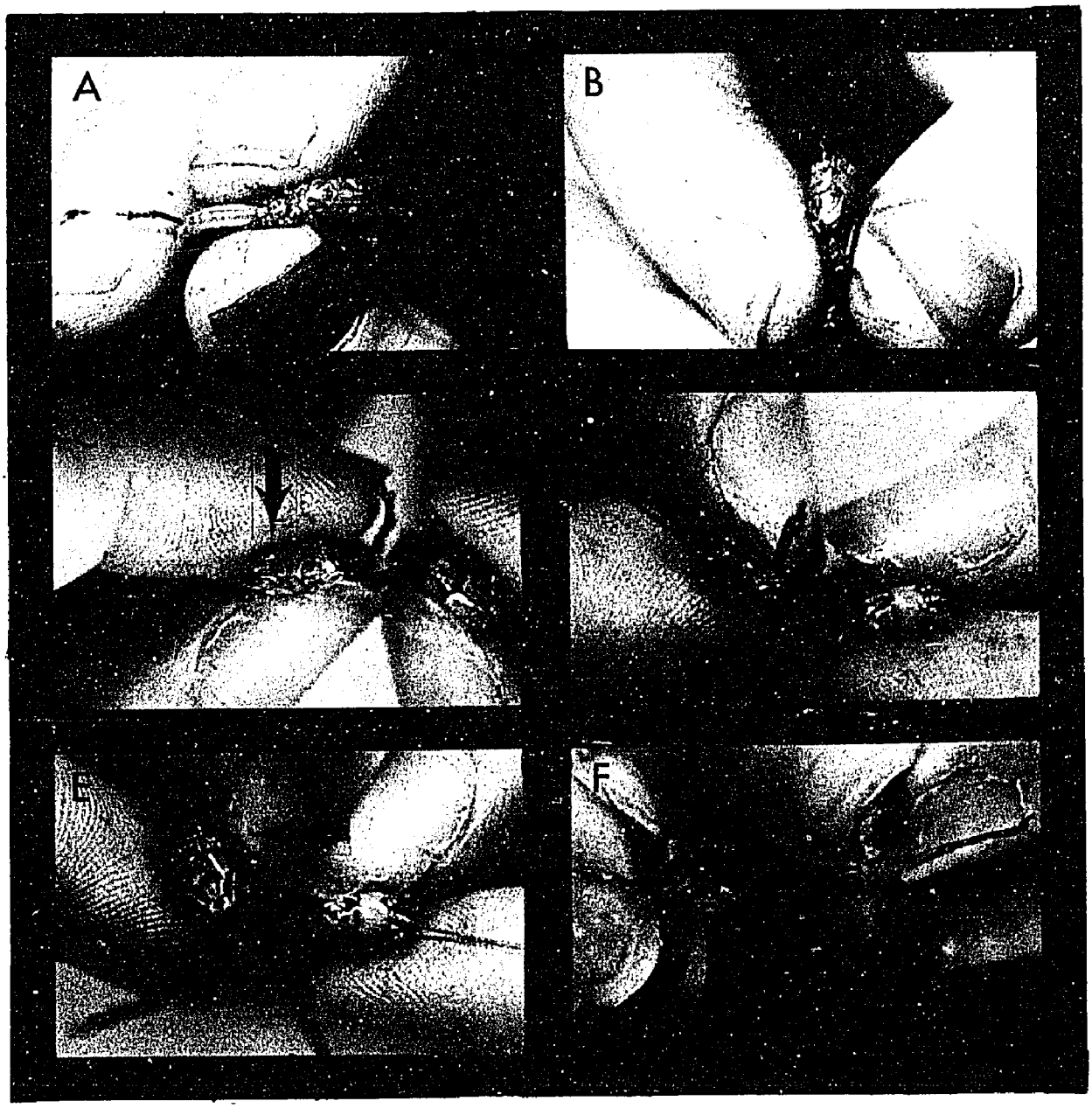


FIGURE 10

indicate that some of the variation in the head color of nigripes may be correlated with variations in diet. In the laboratory, red-faced animals were created by feeding nymphs catfood that had red pigment in it (see Figure 10). Generally, nymphs raised in the laboratory, fed a special diet of flowers and cattail heads collected on the study site, developed green heads.

A greater proportion of females than males (30% versus 5%) marked in the field developed brown heads. The diet of males did not differ from that of the females, so the color differences between the sexes could reflect physiological differences in pigment metabolism. In the laboratory, more females (ten observations out of ten) than males (three observations out of eight) fed on the catfood diet developed red heads.

Onset of calling behavior. Newly moulted individuals of all three species spent most of their time feeding on the underside of 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 moulting, nigripes adults were more likely found in the tops of lower vegetation such

as water lilies and arrowheads. Males started to call when three or four days old, and called sporadically and for short periods during the next one or two days.

New adults in vulgare and gladiator spent a long time in the undergrowth after moulting. Adults of gladiator remained in low vegetation, spending most of their time feeding, for 4-6 days after moulting. Young adults of vulgare spent 6-10 days, after moulting, feeding among thick berry brambles just above the ground.

Males in vulgare and gladiator began calling sporadically 3-6 days after moulting. Because calling was sporadic and soft, and individuals were calling from deep in the undergrowth, they were difficult to locate. In 1975, a special effort was made to locate and monitor the behavior of the sporadic callers in a small area of the gladiator site (~60 sq m) and the vulgare site (~240 sq m). As a result of this effort it was determined that, after calling was initiated, singing was sporadic for 1-2 days in the 11 gladiator males monitored and for 3-5 days in the 20 vulgare males monitored.

Changes in the number of calling males over the reproductive season. Counts of calling males were made every 3-5 days at all three study sites throughout the reproductive season. These data are summarized in Figure 11. Only consistent singers were included in the counts.

FIGURE 11. Changes in the number of calling males throughout the reproductive season. Straight line indicates the period during which newly moulted adults are found (recruitment).

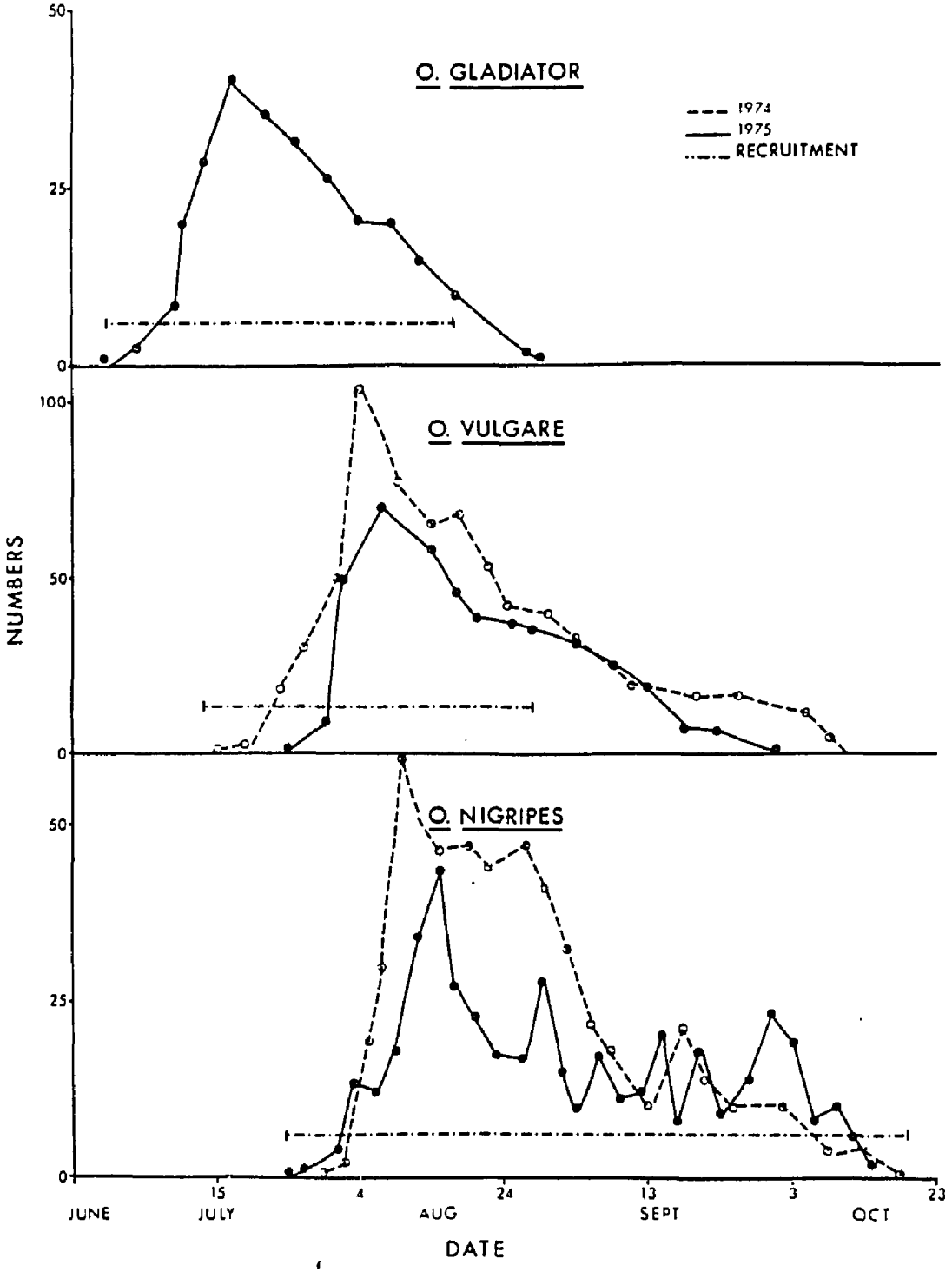

O. GLADIATOR
1974
1975
RECRUITMENT
O. VULGARE
O. NIGRIPES
NUMBERS
50
25
0
100
50
0
50
25
0
15
JUNE
4
JULY
24
AUG
13
SEPT
3
OCT
23
DATE

FIGURE 11

Sporadic callers, in most cases newly moulted males, were more difficult to locate and so their contribution to population size would be more difficult to ascertain.

In all three species, numbers peaked early in the reproductive season and then declined (Figure 11). Young males actually joined the calling population throughout the reproductive season, but later in the season, males disappeared faster than they were added (see section on survivorship).

More fluctuations in numbers of calling males were recorded for nigripes than the other two species. Nigripes was the last of the three species to hatch (Figure 1). By late August, when males in this species began to mature, night temperatures below 55°F and daytime temperatures below 70°F were not uncommon. Newly moulted adults were commonly found during warm periods, and cool weather probably inhibits moulting. In a cool period, two cohorts of nymphs that would normally moult 1 day apart in warm weather, might moult 2-3 days apart. The recruitment pattern of calling males in nigripes was punctuated by cool weather, and, therefore, more jagged than the patterns of the other two species.

A comparison of nymphal and adult distributions. Early instar nymphs (as judged by a size of less than 1 cm in length) and adults were found in different areas within the

study sites. Nymphs were usually found in low grassy areas in the vulgare and gladiator sites and in mats containing grasses, arrowheads and water lilies on the nigripes site. Areas with high nymphal densities are designated with an "X" on Figures 1, 2 and 3.

The nymphal habitats bordered those of adults and the distance an individual would have to move from one to the other could be quite small. In actuality, nymphs were found most commonly near the center of the grass patches, and therefore, located some distance away from the adult residences. During one census when early instar nymphs predominated, the average distance from each nymph encountered to the nearest adult residence of the previous year was 15.2 m for vulgare (100 observations), 10.3 m for nigripes (47 observations) and 3.5 m for gladiator (21 observations).

In nigripes and gladiator, the shift in distribution from nymphal to adult habitat areas coincided with recruitment. Newly moulted adults are found in more grassy areas, but later are recaptured in typical adult habitats. In vulgare, the shift occurs before the adult moult. Late instar nymphs (larger than 1.5 cm) were found more commonly in the berry areas and early instar nymphs (less than 1.5 cm) were usually found in the grassy areas. Males, who have just started to call, however, were frequently located in areas other than those used later when territories were

established. Therefore, some shifts in adult distribution occurred at this time in this species as well.

In all three species, early instar nymphs probably associated with the grassy areas because such areas were the only areas available that provided food and cover. In May in the vulgare site, Rubus had not yet leafed out. Most forbs had not sprouted but the grasses had flowered and were setting seed. By the end of June, when the animals were entering the later nymphal stages, forbs were starting to flower and grasses were starting to drop seed. At this time, nymphs moved into the areas that were becoming new sources of preferred food and cover.

In nigripes, water lilies and arrowheads occurred in the same areas as the grasses and all could be utilized as food by the nymphs. The nymphs stayed in these mats until they matured. As noted previously, adults also have been observed frequently feeding in these areas, but never stayed in them for long periods. By September, water lilies and arrowheads had finished flowering and were dying. At this time nymphs were often seen feeding with adults on cattails, but still associated with the lower more grassy vegetation when not feeding. Such observations indicated that the water lily-arrowhead mats were not unsuitable in any absolute sense. They still attracted nymphs, probably because they offered more cover in their dense undergrowth than some of the cattail

areas. The cattail patches were more suitable for adults, however, because the oviposition plants were there.

The circumstances were similar for gladiator. Grasses on the study site were prevalent in areas with woody vegetation, such as meadowsweet and dogwood. The grass seeds and meadowsweet were utilized as food by both nymphs and adults. Nymphs were found in the more grassy and woody areas but adults were more commonly found in the sedges and forbs that served as oviposition plants.

Social Behavior of Young Adults

This discussion will emphasize the observations made on young nigripes. More newly moulted individuals were captured and marked in this species than in the other two. Also, ages, in terms of days since final moult, could be assigned to young individuals not captured while still soft. Some data on the other two species are presented in order to evaluate the general nature of the observation on nigripes.

The relationships of young males to established calling males. Young males, not of calling age, were found in the proximity of calling males (usually within 70 cm). 24 cases were recorded of very young males near calling males in nigripes, eight in vulgare and three in gladiator. In vulgare and gladiator, these young males had yellow eyes and so were less than four and five days old, respectively.

The nigripes males had orange eyes and green heads making them less than four days old. In a few cases (5) these young males were even feeding or grooming on the calling males' perch.

Calling males acted as if oblivious to these young males, yet as pointed out earlier, the closest two calling males were ever seen without interacting aggressively was 70 cm. Calling males did not orient to the movements of the silent males and these young males were not observed to orient to or move toward them unless females were moving toward the calling male. Generally, females moved past the young males and, like the calling males, behaved as if oblivious to their presence (34 observations). Occasionally, a female would stop near one of the young males (ten observations). The young male and female would face each other momentarily; antennae were brought forward and touched. The female then left.

In nigripes, silent males of calling age were also observed frequently (108 observations) in the proximity of calling males (within 70 cm). Males of nigripes have been observed to call when four days old, yet the silent males were sometimes as old as eight days. These males stayed near the same calling male for an average of four hours. No silent, calling aged males were observed in either vulgare or gladiator.

Peak densities in nigripes were two times that of either gladiator or vulgare and calling-aged, silent males were only observed near calling males during recruitment peaks when densities were highest. Early and late in the season when densities were low, four and five day old males called. Thus, when densities were high, older males probably 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.

If the calling male was removed, the younger male began calling, indicating that the calling male inhibited singing by the young male (32 observations). In vulgare and gladiator, young males called sporadically the first few days. If a consistently calling adult was moved toward one of the sporadic callers, the young male ceased calling. The young male readjusted the distance between himself and the older male before resuming his singing. Thus it appears that in these two species, older males could inhibit the calling of younger males; but since densities were lower in these two species there was usually space for the young males to establish territories. The relationship between age and the other factors that determine dominance is considered later, but it is apparent from the above that young males were subordinate.

Interactions of males and females. During recruitment, calling males in all species were surrounded by young females. In nigripes, females were very conspicuous at this time as they rested high in the vegetation and often interacted with calling males near them. These interactions were highly variable (Figure 12). Usually, a female at a distance of 1-2 meters from a calling male, would orient toward, and move directly to him. The female stopped when 10-30 cm from the male. He oriented to her as she approached and often moved 5-15 cm toward her. At this time the female sometimes moved back 10-20 cm and then moved toward the male again. Again he oriented and moved slightly toward her at her approach. A female sometimes did this several times (moving toward and then backing away from the male) while moving in a semicircle around the male. Eventually the male and female occupied adjacent perches, or the same perch, facing each other. While the pair faced each other, antennae lay forward. At this time if the antennae made contact with the other's antennae or body, they were vibrated rapidly for a few seconds. In a few instances both individuals moved down into the undergrowth; the female leading. While in the lower vegetation, the male generally attempted genital contact. In the few cases where he was successful, the pair remained in copulo for about 20 minutes. The male generally terminated genital contact and left the vicinity. In most cases, the female

FIGURE 12. Sequence of events in typical male-female interaction. The numbers are the number of observations recorded of a particular outcome in an interaction that did not lead to mating.

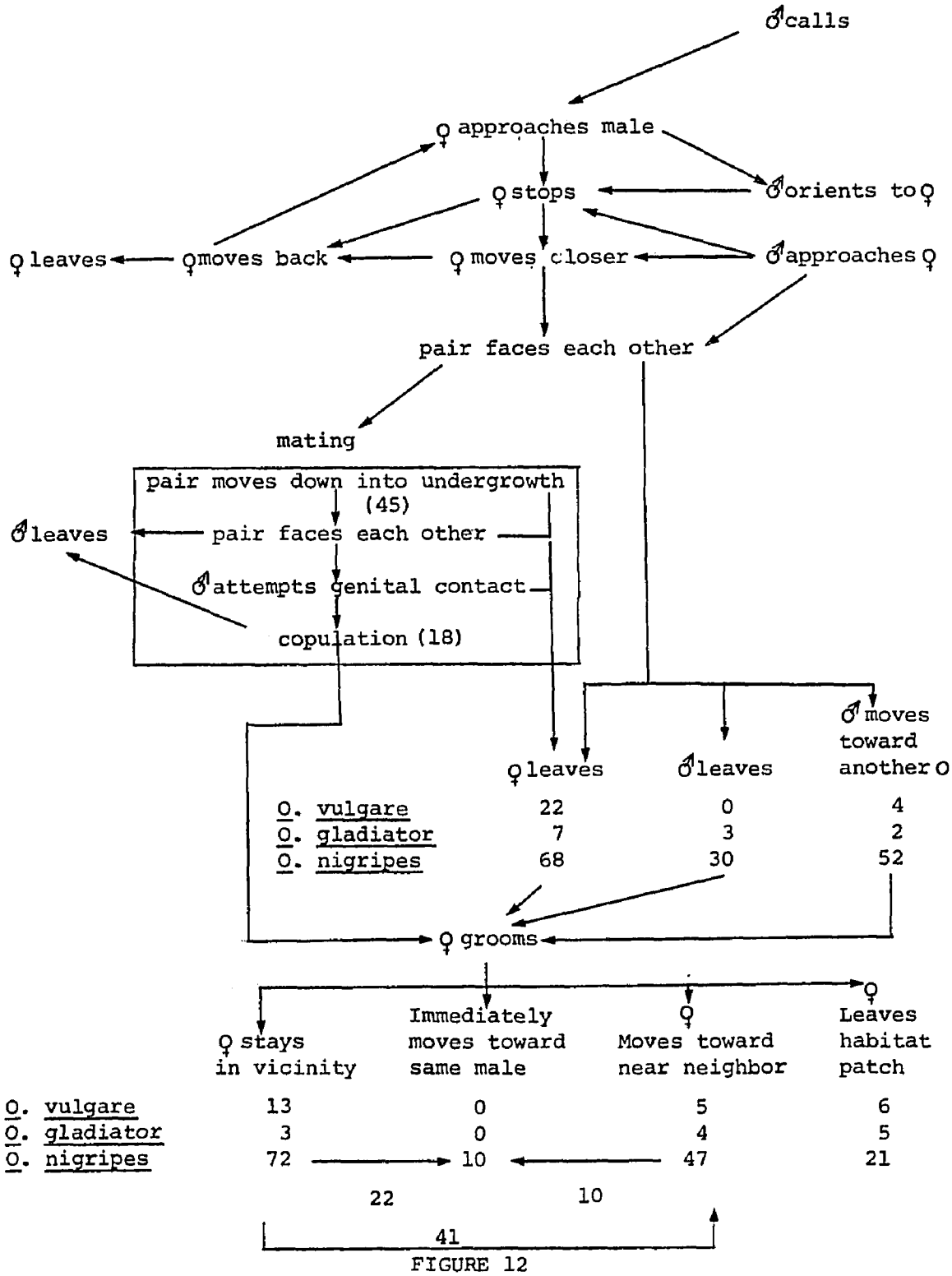

♂calls
♀approaches male
♀stops
♂orients to ♀
♀leaves
♀moves back
♀moves closer
♂approaches ♀
pair faces each other
mating
pair moves down into undergrowth (45)
♂leaves
pair faces each other
♂attempts genital contact
copulation (18)
♀leaves
♂leaves
♂moves toward another ♀
O. vulgare 22 0 4
O. gladiator 7 3 2
O. nigripes 68 30 52
♀grooms
♀stays in vicinity
Immediately moves toward same male
♀ Moves toward near neighbor
♀ Leaves habitat patch
O. vulgare 13 0 5 6
O. gladiator 3 0 4 5
O. nigripes 72 10 47 21
22
10
41

FIGURE 12

left before the male attempted contact, or after the male was not successful in his attempts.

Most interactions were terminated before the pair entered the undergrowth. After 5-40 minutes of facing one another, one of the individuals moved away. Usually, the female terminated the interaction and left the vicinity. After the termination of such an interaction, the female generally groomed for a short period. Females did not move far from the males, usually less than two meters, and spent some time feeding and resting in the male's vicinity. Females occasionally interacted again with the same male or one of his near neighbors and then with the original male. The average time a female spent in the vicinity of a single male was 47 minutes. In a cluster of three or four males, however, females spent as long as 24 hours interacting with the males in the group and usually were never more than two meters from a particular male.

Matings were observed in nigripes and gladiator. In all cases females interacted with males on the study sites from a few hours to a few days before mating. Other aspects of mate selection will be discussed later, however, it is clear that females interact with a number of males and often with the same male a number of times before mating.

Females not looking for mates, such as those looking for oviposition sites, were not conspicuous or close to males. Females in nigripes and vulgare were observed to pass calling males as they moved around in the habitat patch testing plants prior to ovipositing. They did not approach calling males unless approached by them although they paused when 1-2 m away from such males and oriented toward them before moving on. Also if approached by these males, females paused and faced them before leaving. Calling males generally did not pursue females who have interacted with them or oriented toward them.

In contrast, calling males pursued a female who moved through their territory without interacting or orienting to them. In most cases the male was able to pursue the female only for a few meters before entering another male's territory and initiating an aggressive interaction with that male. In some cases, the male was able to overtake the female in his territory; the female then turned toward the male, faced him momentarily, and then left. Once the female had interacted with the male, she was allowed to leave his territory without further pursuit. On two occasions in nigripes and four in vulgare, males pursued congeneric females until the female turned and oriented toward the male. After this interaction, the male lost interest in the female. Apparently, a male will pursue any female of approximately the right size moving through the area in order to cause her to orient toward him.

Males in the three species produce a complex spermatophore during copulation. Struggles with an unwilling female would probably interfere with the successful transfer of the spermatophore, resulting in a large loss of energy on the part of the male. Therefore, it is to the male's disadvantage to spend time trying to force an unreceptive female to mate with him. Thus it appears that males only attempted to get several females in their territories to acknowledge that they had seen him. Such acknowledgment was apparently accomplished by the female orienting to the male. Thus, if the female did not do this on her own accord, the male pursued her in his territory until she oriented toward him. The male did not carry the pursuit further nor did he attempt to mate with her if she was unreceptive.

As indicated previously, females approaching calling males ignored the silent males in the vicinity. In a few instances, silent males of calling age (nigripes) placed themselves between the calling male and the female and started calling (5 observations). They were quickly attacked by the calling male and forced out of his vicinity. In two other cases, silent males placed themselves between the male and the approaching female, raised their tegmina in a singing position and vibrated them, but remained silent. The female then approached these males but stayed in their vicinity only for a short time (less than 5 min) before proceeding to the calling male. I first thought

that the tegmina of these males were injured so that they could not sing but later when the calling male was removed, these males began singing. Thus it appears that these males were behaving as if they were the calling male while the female was approaching.

Since females ignored silent males, calling may be a prerequisite to being chosen as a mate. In fact during the course of the study, females, even in the laboratory, never mated with males who did not call. Therefore, calling males ignored silent males in their territories because silent males were not attractive to females and so not competitors for such females.

Role of Social Behavior in Territory Establishment

The following observations were compiled on the behavior of young adults as they moved into the adult habitat patches:

1) Young females moved from habitat patch to habitat patch. In nigripes 42% (46 out of 110) of all females captured more than once were recaptured in a different habitat patch. In vulgare 11% (6 out of 56) and in gladiator 29% (6 out of 21) of the females captured in one patch were recaptured in another patch. Older females, 4-8 days after becoming conspicuous, moved much less. In nigripes 13% (9 out of 69) and in vulgare and gladiator

none (0 out of 59) of these females were in a different patch when captured a second time.

2) Young males of all species followed females as they moved between patches (42 observations). All of the males who followed the females were calling-age males but had either not been seen calling or had been calling for less than three days. In nigripes, for example, silent young males in the proximity of older males followed females as they moved out of one patch and into another. If a female stopped to feed or groom for longer than a minute or two, the follower would dart one or two meters ahead of the female and start to call (13 observations). Generally, the female did not approach such males (two exceptions) and moved past such males quickly. The young males continued to follow females until they entered another habitat patch. Here the male attempted to call again and usually was forced out of the vicinity by a calling male. In only one instance was a following male observed to enter into an aggressive interaction with an established territorial male and eventually forced 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 in nigripes, four of the followers became silent males after aggressive interactions with territorial males.

The following behavior exhibited by young males was apparently an attempt to interact with a female. The end

result was that when these males began to call consistently, they established territories in habitat patches selected by the female rather than the patch they were in originally.

3) During approximately the first seven days they called, young males called from habitats that are not used by the adults later in the season, such as nymphal habitats in nigripes (42 observations) and in gladiator (18 observations) or barren areas in vulgare (16 observations). After female adults appeared in the population, males were no longer found in these "wrong" habitats and the males originally found there are later recaptured in the typical adult habitats.

4) In nigripes and gladiator, males have been observed moving from nymphal to adult habitat patches before they initiate calling (44 observations). With few exceptions, young males did not call unless they encountered a calling male. These young males first attempted to call at a distance of 1-2 meters from the other calling male and if repulsed, the young male moved away and attempted to call again. The male continued this behavior until he could call without being repulsed by the older calling male or until he entered the territory of the near neighbor. In the few exceptions in which a young male called from outside the vicinity of a calling conspecific, the young male called because he encountered a female (3 observations).

Also very young males in nigripes (less than three days old) were observed to move out of the mats and toward a calling conspecific. These young males would feed and groom in the vicinity of the calling male but did not call until they had been there for one or two days.

5) In 1974 and 1975 a special effort was made to monitor the movements of young adults of nigripes. In both years large numbers of newly moulted adults were captured in a two meter square area of the water lily-arrowhead-grass mat between two cattail patches in the northern half of the study site (Figure 13). This part of the mat is located closer to Patch 2 than Patch 1; but Patch 1 is larger than Patch 2 and so probably more suitable in terms of the amount of food and oviposition site within it. All of the males and females marked in the mat had green faces, so were less than four days old, and most had yellow eyes indicating that they were about two days old. An attempt was made to relocate these marked individuals at two, four, six, and eight days after marking (Table 4).

All except two of the individuals recaptured during the eight-day period confined their movements to the northern half of the study site. At the end of the eight days, all except three individuals were in cattail Patch 1. During the eight-day period an equal number of females went to Patch 2 as to Patch 1. However, the females that went

FIGURE 13. Patterns of movements by young adults. Adults move from nymphal habitat, X, to adult habitats, I and II. Later some adults also move from habitat II to I. Arrows indicate direction of major displacements.

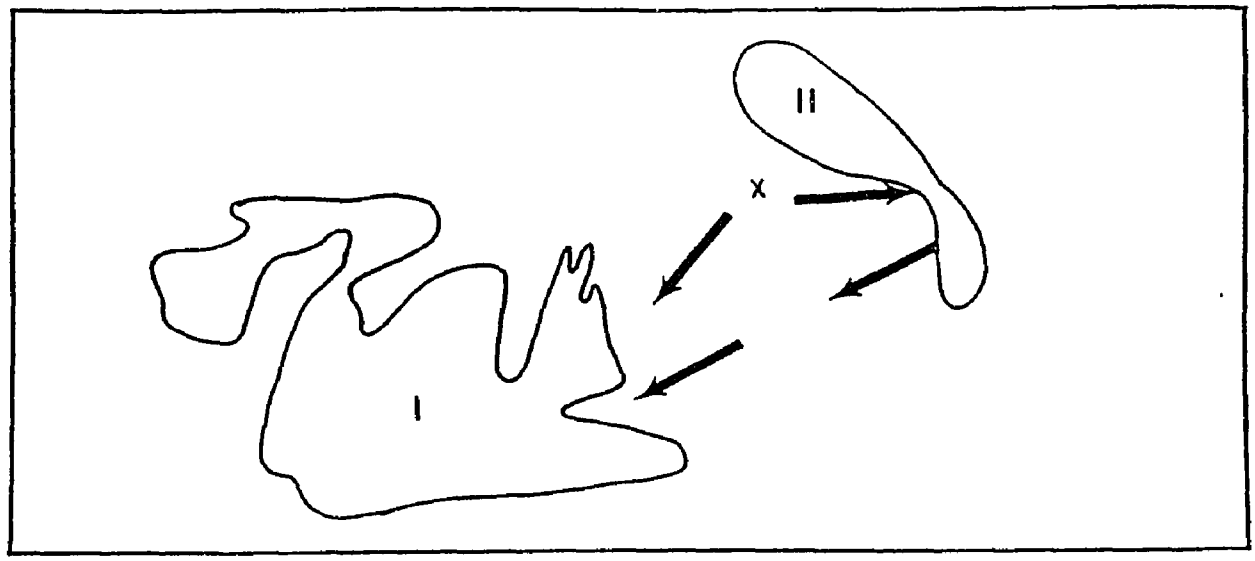


Figure 13

TABLE 4

PATTERN OF MOVEMENTS BY YOUNG ADULTS

A ♀

Days since first capture	Number recaptured in various areas			
	Mat	I	II	Other
0	70	0	0	0
2	7	17	13	0
4	0	24	8	1
6	0	16	2	1
8	0	11	1	0

B ♂

Days since first capture	Number recaptured in various areas			
	Mat	I	II	Other
0	90	0	0	0
2	22	10	17	0
4	5	20	6	0
6	0	22	3	0
8	0	19	2	1

to Patch 1 remained there; while the females that went to Patch 2 left it and were later recaptured in Patch 1. The movements of males were similar to those of females; however, proportionally more males visited Patch 2 than did females. Also, males left the water lily mat later than the females. Young 3-4 day old males remained in the mat and called for 1-2 days before moving to the cattail patches. The shift in numbers of females from nymphal to adult habitats and from one adult habitat patch to another then preceded similar shifts in the number of males.

The data on behavior of young individuals indicate that the locations of calling territories are determined in the following manner. Males in nigripes, and probably the other two species, moult and mature before the females. Early in the season, males set up territories in areas where females are most abundant at that time (the nymphal habitat where the females are moulting into adults). Later, these males, while attempting to interact with the newly moulted females, follow them into the adult habitat patches, and between patches. If females enter suitable habitat patches, they will remain in them, and so will the males that followed them there.

Males, who mature later in the season, when female density is low in the nymphal habitat, can use the calls of established males to guide them into areas where female

density may be high. If they are successful in establishing a territory and they are in a suitable area, females will approach and interact with them, and these males will stay in that area. Thus by attempting to interact with conspicuous females and sometimes utilizing calling conspecifics as clues to female presence, males eventually come to establish territories in areas of high female density.

The Effect of Density on Aggression

Relative Densities

Orchelimum vulgare was the least dense of the three species and at peak density there were 105 singing males in an area of 39,852 sq m, or 0.0026 males/sq m; nigripes was the most dense, 54 singing males in 2560 sq m, or 0.021 males/sq m.

The criticism may be made that since individuals only associated with certain types of vegetation patches, density estimates based on the number of males in the whole study area may be erroneous. Such measures include many areas indicated to be unsuitable habitat by the distribution data. However, inspection of the distribution maps (Figures 1-3) show that there is proportionally much less "unsuitable habitat" in the vulgare study area than in the nigripes study area. Therefore, the density estimates based on the entire area of the study sites are probably conservative with respect to the relative differences between the species. The vulgare density is probably a relative overestimate and that for nigripes probably an underestimate. Also, it seemed best to avoid value judgments as to the suitability of an area within the study site, in view of the shifts in distribution recorded from year to year and within a season.

Effects of Density

In the introductory section on aggression, I pointed out that males defended a circular area around their calling perch that was nearly equivalent to the nearest neighbor distance. The territories of near neighbors overlapped extensively. Usually, the territories were defended by acoustical display with only 25% of the male-male interactions ending in physical combat.

As density increased, the number of territorial interactions ending in physical combat increased proportionally. In vulgare and nigripes in 1975 when densities were low relative to 1974, fewer of the territorial interactions ended with fights between the males (Table 5). In nigripes (the densest species) proportionally more of the interactions involve combat than they did in the other two species. It appears that as the distance between males became less in this species, they were more prone to settle interactions by combat.

The number of aggressive interactions per male also increased as the density increased. In one patch in the nigripes study area, each male averaged one interaction every two hours when the density was high (10-13 males in the patch; 50 observations). Yet in the same patch when the density was 3 or 4 males, each male interacted only once every five hours (50 hours of observation). If this held true for all species then in a species like vulgare,

TABLE 5

THE RATIO OF PHYSICAL AGGRESSION/ACOUSTICAL AGGRESSION

Species	Year	Observations	% physical combat	Peak density sq m	Near neighbor distance
O. nigripes	1974	82	50	0.021	1.9 m
	1975	174	31	0.0019	2.3 m
O. gladiator	1975	31	19	0.0095	3.7 m
O. vulgare	1974	41	15	0.0026	4.8 m
	1975	61	6	0.0018	6.9 m

males that inhabited the small Rubus clumps where densities were high should have interacted more than males that occupied areas where Rubus and males were more sparsely distributed (40-70% cover). Males in small Rubus clumps (less than 50 sq m) averaged three times as many interactions as males outside these clumps. Of the 10 interactions that terminated in combat; eight occurred among males in these small Rubus patches.

Density also affected the size of male territories. For at least ten days the sizes of all the male territories in a patch in all three species were measured. The size of each male's territory within a patch decreased as the density of males within the patch increased. The results for three different habitat patches of nigripes are presented in Figure 14. The negative correlation between territory size and number of males in a habitat were significant in nigripes and gladiator over all habitat patch sizes. In vulgare there was only a significant negative correlation in the small berry patches (less than 50 sq m); in the large patches increasing density did not affect territory size. The large patches were usually so sparsely populated that when a new male entered the patch and tried to establish a territory there was space to do so. If the new neighbor was within the preferred nearest neighbor distance of an established male, aggressive interactions were used to

FIGURE 14. Effect of density on territory size. A, B, C, show the effect of varying density on territory size in different sized habitat patches in Orchelimum nigripes. The approximate shape of the habitat patch is shown in the upper right of each figure. The number within each patch is its area in square meters.

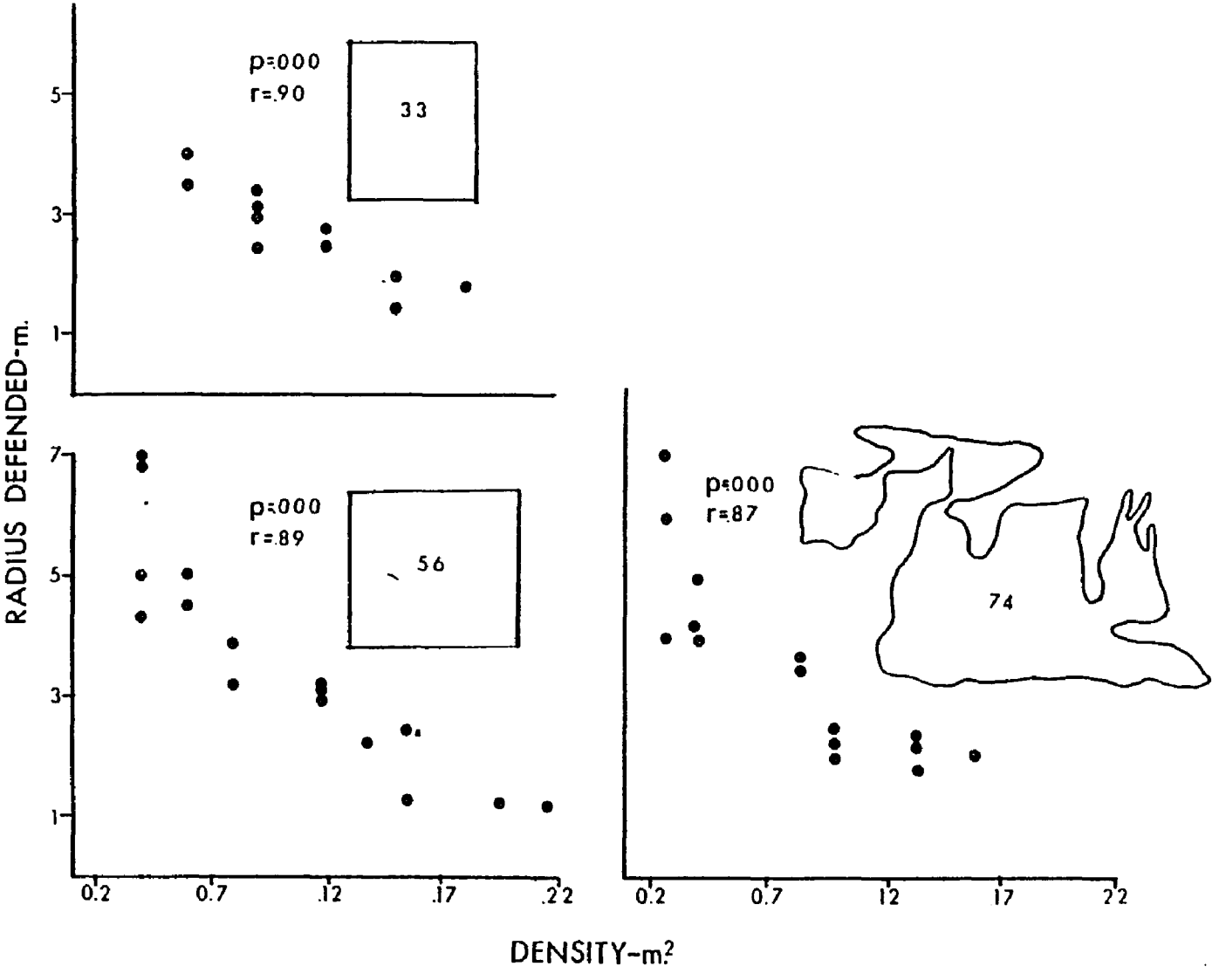

p=000
r=.90
33
p=000
r=.89
56
p=000
r=87
74
RADIUS DEFENDED-m.
DENSITY-m.²
0.2
0.7
.12
.17
.22
1
3
5
7

FIGURE 14

readjust the nearest neighbor distance to the preferred. Densities in these large patches may have been so low that there was more "suitable" area available than the established males could defend. The nearest neighbor distances in these patches averaged 6-8 meters, the largest territorial radius observed to be defended by physical combat. Thus, new males could probably be added to these habitat patches without affecting the territories already established.

Significance of Results

An Orchelimum calling territory, like the territories of many animal groups, is an elastic disk (Wilson, 1975; Brown, 1975) that can be compressed by social pressure and expands when such pressure is removed. A male, by physical combat and the threat of such, attempts to control as much as possible of the contested area within physical limits. The minimum distance a male will tolerate a near neighbor is 70 cm. Males who cannot control a territory of this size probably leave the patch or, as in nigripes, become silent males within a dominant male's territory. The maximum distance from his perch at which a male fought to control his territory was about eight meters, although males occasionally attempted to expand their control to a distance of 15 meters by the use of threats. As pointed out earlier, these animals are about two cm long and are attempting to exclude conspecifics at a distance 750 times their length.

Territories of this size were not physically defended. Most territories greater than six meters in radius were located so that some physical barrier reinforced territorial boundaries between the males. For example, the north end of the nigripes study site is separated from a larger swamp by a road. Occasionally, males were found on the edge of the swamp and study site bordering the road. Two nigripes males were situated on opposite sides of the road and were never seen to cross it. Yet each male responded to the other's movements in his direction with acoustical threats that are the prelude to physical combat.

Although territories may be envisioned as elastic disks, the habitat patches were not simply divided among the males that occur there. For example in nigripes, in the largest patch studied (Figure 14), peak density was 12 males. Each of these males defended areas that had an average radius of 2.6 m. Since the territories overlapped, only half of the available area was occupied by these 12 males. Also, at all densities, the average territory size defended in any patch varied from day to day. In a patch measuring 56 sq m, the territories' sizes varied from 1.2 m to 2.6 m on different days (Figure 14). 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 at this time. Later, when females were moving from patch to patch and, therefore, not entering the patch from a single side, males set up territories distributed around the entire patch. Usually such territories are larger than the previous ones.

Figure 15 illustrates these shifts in male distribution in one patch in 1974. (It is the same large cattail patch I, considered in Figure 14, although in 1974 it was smaller than in 1975.) In 1974 the patch was bordered by two areas of mat where high numbers of newly moulted adults were located. The mats were directly north and south of the patch. Newly moulted females were present in the south mat three days before they were present in the north mat. Male territories were first established on the south side of the patch and then the north side. Males eventually established territories on the entire border of the patch when females started moving from patch to patch. After establishing residences, females moved out of the patch for short periods to feed in the mats and returned to the patches after feeding. Females were still frequently found on the borders of the patches so the males established their territories along the border of the habitat patch. Males were, then, dividing up the suitable habitat since a preferred habitat is where the females are. Since the female distribution changed from day to day, the "suitable" areas also changed from day to day.

FIGURE 15. Changing patterns of male distribution during recruitment in an habitat patch, 1974. Arrow indicates direction of female movements. In A., females are entering habitat from the north (nymphal habitat—X). Male territories, ●, are all located on the northern border of the habitat. In B., 2 days later, females are entering from the south. Male territories are located on the southern border of the habitat. In C., 4 days later, females enter along entire border as they move in from other habitat areas. Females are also moving in and out of this area to feed.

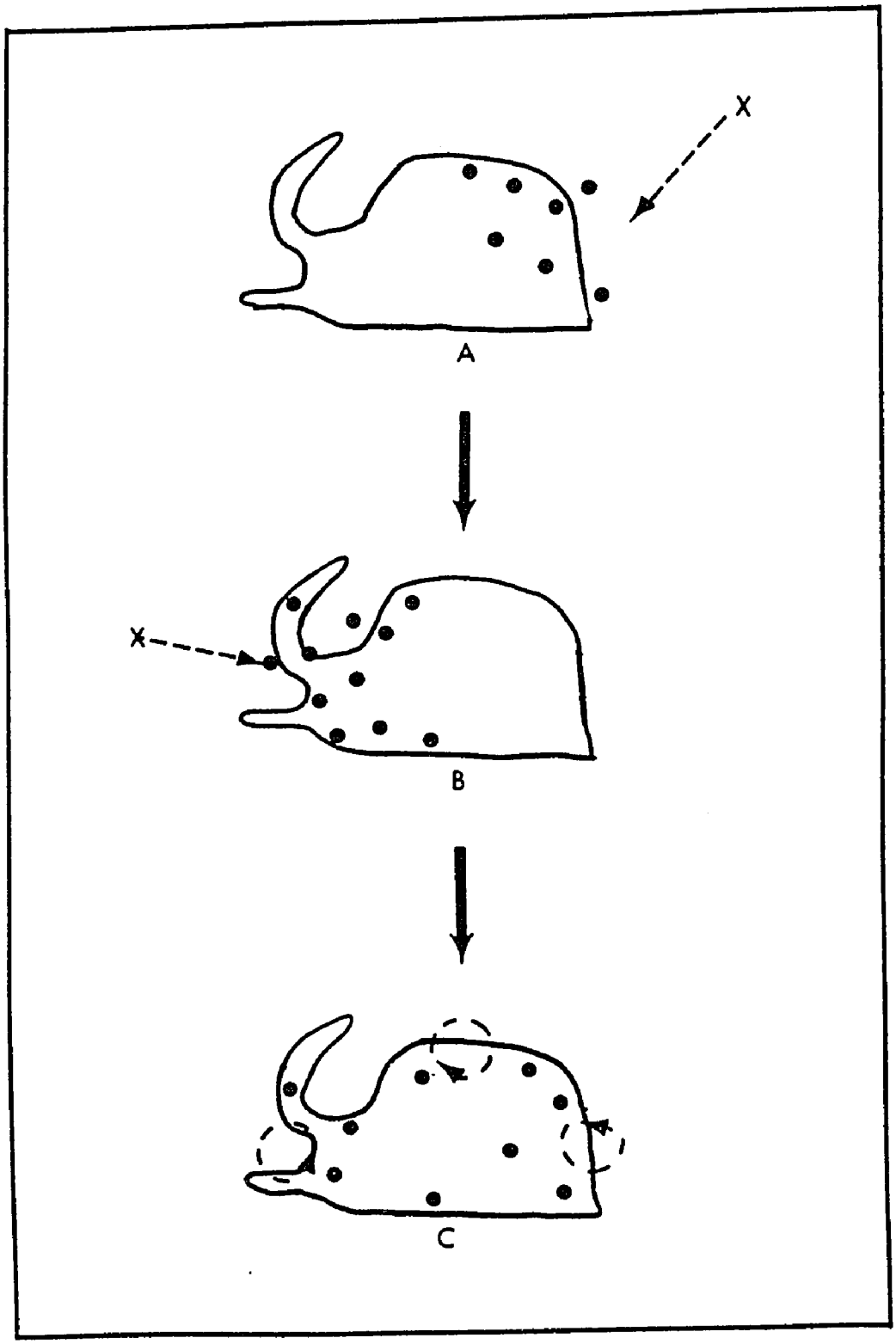


FIGURE 15

Males actively resist eviction from the patches into areas of low female density. Dominant males chase males through patches—the subordinate retreating when challenged by the dominant. After being forced from the patch, the behavior of the subordinate often changed. Subordinates were even observed to approach and physically attack the dominant (15 observations). In seven cases, the chasing behavior and the physical attacks by the subordinates, after being forced from the patch, were repeated two or three times. Each time the subordinate regained entry back into the patch he resumed the evasive behavior. It appears that subordinate males will risk physical injury from combat with dominants rather than remain outside of the patch where there are no females.

Morris (1967) investigated male-male spacing of Orchelimum in a fairly homogeneous environment, a continuous patch of sweet flag and sedge. The density of gladiator which he studied (0.15 individual/sq m) was high relative to the densities in my study. 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 often engaged in physical combat causing one of the males to leave the general vicinity. He suggested that the male

spacing patterns were the result of physical aggression and were maintained by calling, a threat of combat.

In my study, in contrast to Morris', physical aggression affected male distribution patterns only in very small adult habitat patches. In larger patches other factors, such as female distribution, seemed to have the major effect. Males are still dividing up the "suitable" habitat; but relative "suitability" is a changing parameter in an environment that is temporally and spatially heterogeneous such as the large habitat patches. Thus, the role of aggression relative to the role of other environmental factors will vary in its effect on male distribution from habitat patch to habitat patch. It was fortunate that heterogeneous study sites were selected for my study so that the role of various environmental factors were elucidated. The lower densities in my study, compared to those in Morris', enabled any differences in suitability from one area to another to be manifested in the male distribution pattern.

Sexual Differences in Life History

Maturation, Mating

In nigripes, large numbers of newly moulted females appeared 1-2 days after large numbers of newly moulted males. Females, 1-2 days after their exoskeleton hardened, began to interact with males. Males, in contrast, did not begin to interact with conspecifics until they started to sing consistently, or about 1-2 days after similar aged females began to interact socially.

In vulgare, females became conspicuous 5-6 days after males began calling and in gladiator this occurred 3-4 days after initiation of calling by the males. Since few soft individuals were located in these two species, I do not know whether females moult several days later than males, or simply spend more time than males in the dense undergrowth. Calling in males was sporadic for a few days after initiation. Sporadically calling males did not interact much with conspecifics. Females began to interact with males as soon as they became conspicuous and so, in these two species as in nigripes, probably at a younger age than males. Morris et al. (1975b) recently found that females of gladiator respond phonotaxically to the conspecific calling song when only 4-5 days old in the laboratory.

The ages of 14 female nigripes that mated were known. In these females, mating occurred when they were 7-22 days old (average 12 days). In gladiator, one female mated when she was 10 days old and another when she was 17 days old. No matings were observed in vulgare, but two females 21 days old and 27 days old, were found carrying spermatophores. Females ate the external portion of the spermatophore generally within two hours after mating, so these females mated earlier that day.

It is not known how many times a female in the field mates, but, in the laboratory, females mated only once even though males were repeatedly reintroduced into their cages.

In nigripes oviposition occurred a minimum of 3-4 days after mating (10 observations) and a female of vulgare oviposited 6 days after mating.

Females then mated and oviposited only after establishing residences in habitat patches. As indicated previously, females in all species appeared to establish residences within seven days after first capture. In contrast, males attempted to mate sooner, i.e., as soon as they initiated calling.

Movement

Adults of both sexes moved from patch to patch during the first few days of adult life. Females moved from less suitable to more suitable patches and the adult males

followed them. The average displacement for young adults (< 8 after first capture) for a two-day period was greater than that for older adults (Table 6). The pattern of displacement for both sexes of young adults was similar (Figure 16). Over the two-day interval, females moved greater distances than did males. This resulted from the fact that once a suitable habitat patch was located, males established territories while females, in contrast, moved from calling male to calling male, interacting with them.

The differences in displacement between sexes of older adults is slight or as expected females on the average move greater distances than males. However, the patterns of displacement can be very different. For example in nigripes, males tend to undergo either large or small displacements and therefore, have a much larger variance around the mean displacement distance than do females which tend to undergo small or intermediate displacements (Figure 16). Most of the movement by females was out of the patch to feed or between different males within the patch. The long moves by the males occurred when a male was forced out of the habitat patch. All of the long moves (> 10 meters) by males occurred after the male had lost several aggressive interactions that day within the habitat patch. These displaced males moved across "unsuitable" area of the habitat until they found other calling males and then tried to establish territories in the new suitable habitat patch. The attraction of displaced males to calling males in other habitat patches

TABLE 6

MOVEMENTS OVER 2-DAY PERIODS FOR OLD AND YOUNG ADULTS

Species	Year	Young Adults						Old Adults					
		N		Mean		Var.		N		Mean		Var.	
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
O. nigripes	1974	63	42	7.2	8.4	41.2	38.2	107	31	6.2	5.4	54.9	14.9
	1975	86	65	6.7	8.1	34.4	35.5	191	54	5.2	5.4	38.6	13.2
O. vulgare	1974	80	21	6.9	7.7	54.5	75.6	253	14	4.0	5.3	27.5	15.1
	1975	84	27	5.7	7.9	49.9	65.7	295	17	3.6	5.2	17.1	18.8
O. gladiator	1975	60	32	5.7	6.0	32.4	28.7	86	22	3.4	4.8	15.1	17.1

FIGURE 16. Patterns of distances moved over 2-day periods for young and old adults of Orchelimum nigripes.

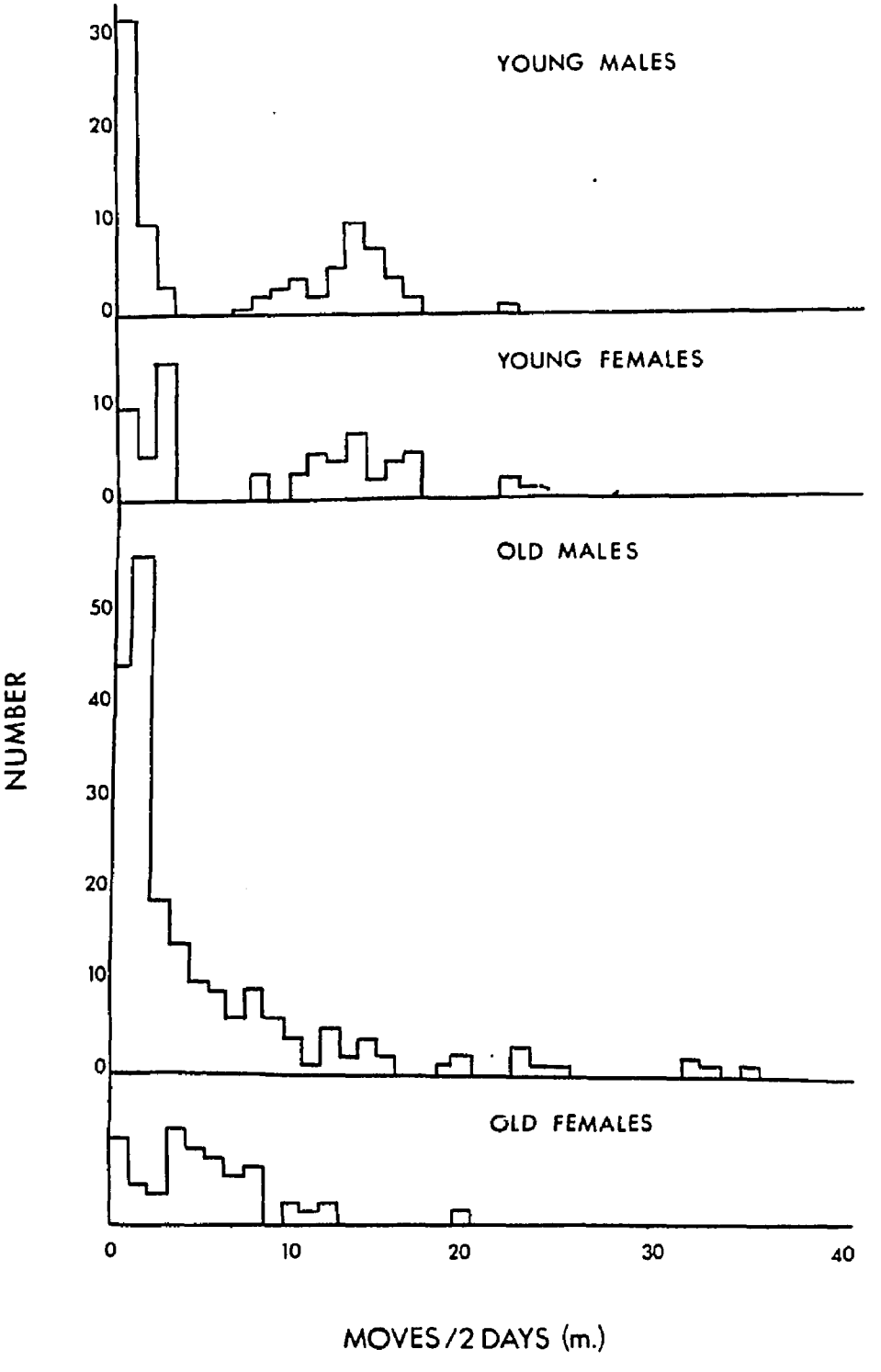

YOUNG MALES
YOUNG FEMALES
OLD MALES
OLD FEMALES
NUMBER
MOVES/2 DAYS (m.)
0
10
20
30
40
50

FIGURE 16

is apparently because the calling males are indicators of high female density. The distance displaced males moved was determined by how far away calling males and "suitable" habitat patches were located. In gladiator, for example, large habitat patches were connected by corridors of suitable habitat. Calling males were found in the corridors and large patches. Displaced males did not have to move far before encountering a calling male (see Figure 3). In this case, the variance for male moves was no larger than that for female moves.

Small displacement in old males occurred when nearest neighbors exchanged calling perches. Observations indicate that within a cluster of calling males there was a favored calling site and the males contest for this site daily. The site where a male was able to control more of the desired border of the patch was the desired one. For example in Figure 17, the most common distribution patterns for males inhabiting a small area in nigripes is 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. One male controlled most of the patch simply by virtue of his location. Females were observed more often in the proximity of this male than they were in the proximity of distal males, simply because this male controlled more of the patch border. This male was thus "central" with respect to female location within a patch and will be referred to as a "central" male.

FIGURE 17. Distribution patterns of males within a small habitat patch. Arrows denote the direction of female movement. Pattern A was commonly observed during recruitment periods. Females move into this habitat from nymphal habitats, X, along the northern border. Pattern B was common at other times, when females moved from habitat patch to habitat patch, or in and out of the habitat patch to feed. Territories are overlapping and equivalent to nearest neighbor distance. Thus, one male controls most of the habitat by virtue of his position. The dotted line indicates the boundaries of this male's territory.

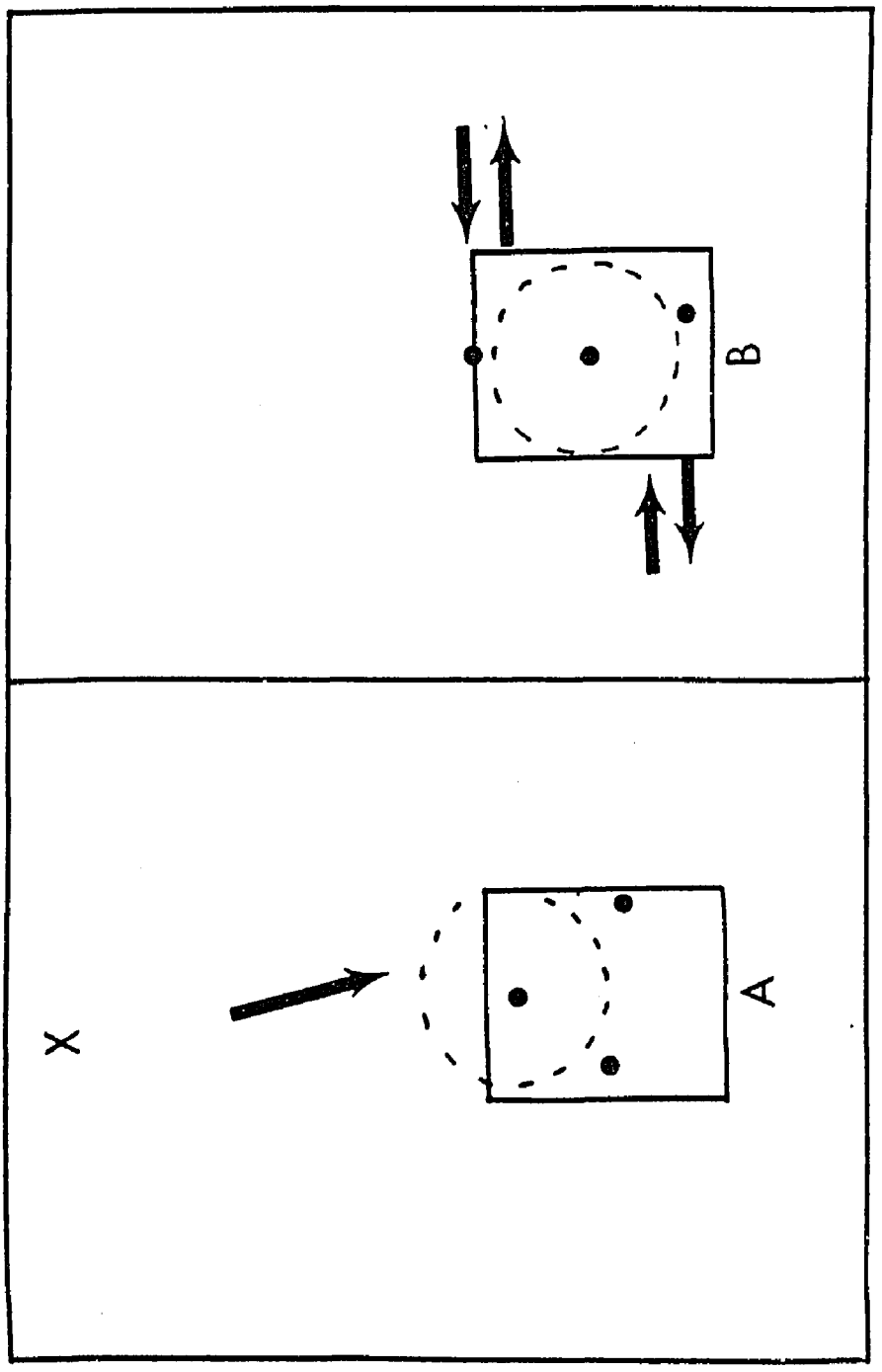


FIGURE 17

A "central" male moved continually toward one neighbor then toward the other neighbor, apparently patrolling his territory boundaries. Frequently, as the male moved toward the south neighbor, the north neighbor tried to encroach on the central male's territory, and when the central male moved toward the north neighbor, the south neighbor moved toward the center. The central males did not seem able to hold these territories for long periods of time; the average a male had continual possession of a central territory was two days.

Populations adjacent to the study sites were censused at weekly intervals to see if migration was occurring. In vulgare and gladiator, no migrants from the study area were found. In the nigripes study site seven cases of migration were noted. These males had emigrated to cattail patches that were within only 20 meters of the study site. It appears, therefore, that marked individuals did not move large distances and emigration of older individuals to adjacent populations was quite low.

Thirteen individuals thought to be immigrants were found during the study; three of vulgare, five of gladiator and five of nigripes. The five nigripes were injured, had tarsi missing or antennae broken, and were probably males from adjacent habitat areas that left after losing physical territorial encounters. The vulgare and gladiator immigrants were long-winged individuals and so were probably migrant forms from adjacent populations. The fact that the gladiator

individuals occurred in habitats that did not contain populations of this species (the vulgare and nigripes study sites) indicates that they were migratory forms from other populations.

Survivorship

Newly moulted adults. The catchability of young males varied among species (see section on Behavior of Young Adults). Most data on survivorship was obtained for nigripes but some was obtained for gladiator and vulgare.

In 1975, 142 nigripes males less than three days old were captured. Only 72 were recaptured, most of them within 2-3 days (65 out of 72), the others after four or five days (7 out of 72). At this stage males were moving throughout the habitat establishing territories. In order to make sure that the males that were not recaptured had not emigrated, areas adjacent to the study area were censused. None of the marked males were located in these areas. It appears that 50% of the newly moulted males do not survive to call since in this species males do not begin singing until they are five days old. In 1974 the results were similar; 75 two-day old males were marked and only 42 survived to age five.

Mortality was also high in young nigripes females. Eighty-five two-day old females were marked in 1975 and 45 survived to day five; in 1974, 12 of 30 two-day old females survived to age five.

In gladiator and vulgare, newly moulted adults were more difficult to find. Some data on the survivorship of young males were obtained in 1975 when a special effort was made to capture sporadically calling males. Of twenty such

vulgare males marked only eight were captured after five days or at an age of 11 days. Five of 11 gladiator males young male survived to the age of 8 days.

The causes of low survivorship in adults are unknown but there are some indications that parasite infections and poor moulting contribute heavily to the mortality at this stage.

Late instar nymphs were frequently collected from adjacent populations for laboratory use. 40-60% of the individuals collected died from infestations of horsehair worms (Nematomorpha, Gordioda) and/or nematodes (Nematoda, Mermithida). These worms feed on the internal organs of the late instar nymphs and exit from the host 2-3 days after the nymphs moult to adulthood. When the parasites exit they leave a large hole in the abdomen of the host. Some newly moulted adults from the study area died from these infections overnight while they were being held for measuring and marking.

Twenty-seven newly moulted adults were seen in the study area that apparently moulted poorly, having misshapen bodies. A high incidence of such individuals follows extended periods of cool weather. These individuals were never recaptured and it was assumed that mortality resulted from the deformities. (Such individuals were not used in the survivorship estimates; therefore, the actual mortality in newly moulted adults was probably higher than that indicated.)

Interacting individuals. Once males start singing consistently, they were easy to locate. Figure 18 gives the survivorship curves of singing adults for all three species. In order to compare these curves between species and between years, percent surviving was transformed to the log of percent surviving and the lines compared using Analysis of Covariance (ANCOVA). Table 7 gives the statistics of this analysis.

The survivorship curves for all the species and between years are similar in shape. Survivorship was low for the first few days after singing becomes consistent, then it increased. Thus the probability of a male dying soon after he establishes a territory was higher than after he had been a territorial male for a few days. Nigripes had the lowest survivorship, 50% of the males dying within 6 days after initiation of calling, and vulgare had the highest, requiring 12 days for a 50% reduction. Within a species, there was year-to-year variation; survivorship was lower in 1974 than it was in 1975.

Females were very secretive, observed only early in adult life when they were found high in the vegetation and interacting with calling males. Even at this time relatively few females were captured compared to adult males. In 1975, 45 six-day-old females were captured and marked; six days later only 50% of these survived. In this species it is possible to compare the adult survivorship curves

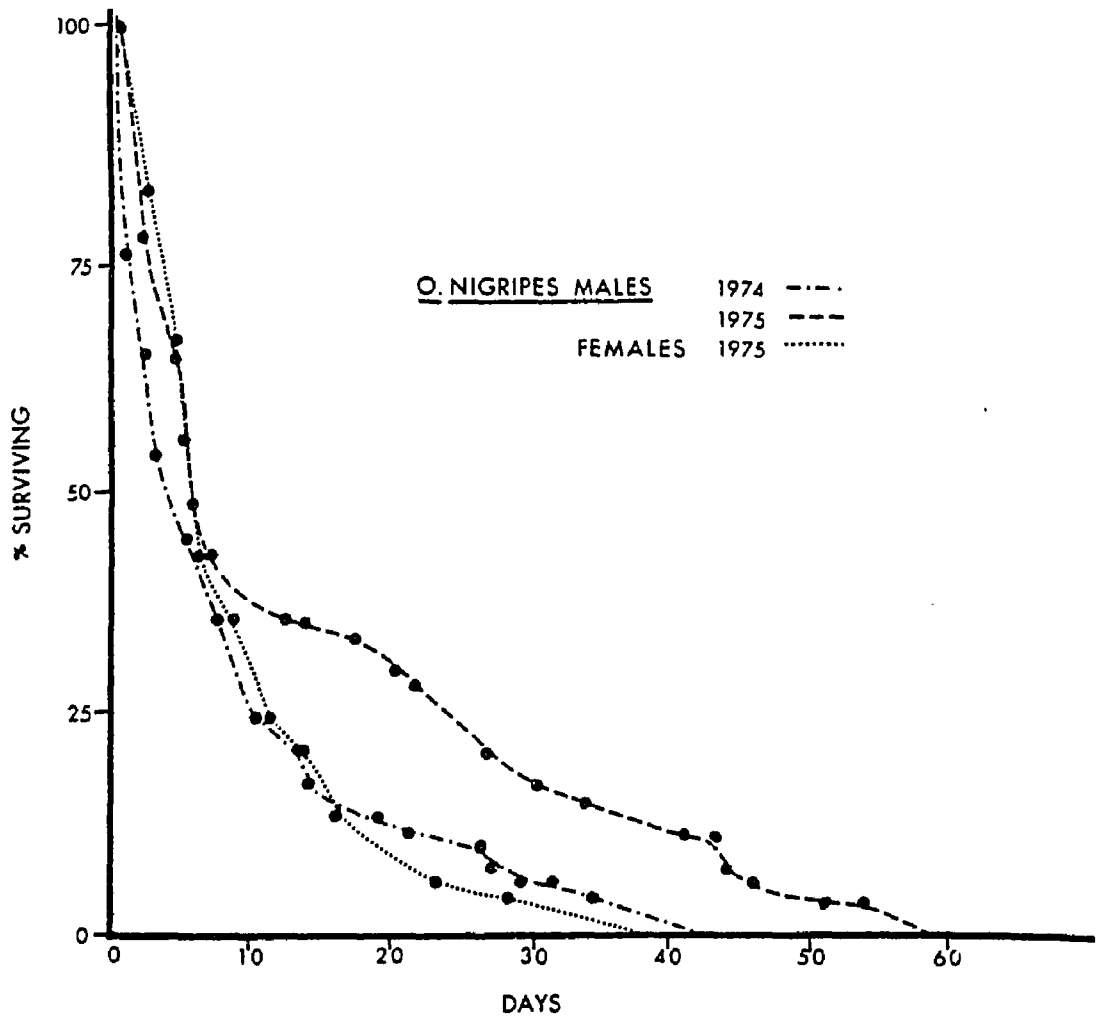


FIGURE 18A. Survivorship curves. A. Survivorship curves for Orchelimum nigripes calling males, 1974 and 1975; females greater than six days old, 1975. B. Survivorship curves for Orchelimum vulgare calling males, 1974 and 1975; for Orchelimum gladiator males, 1975.

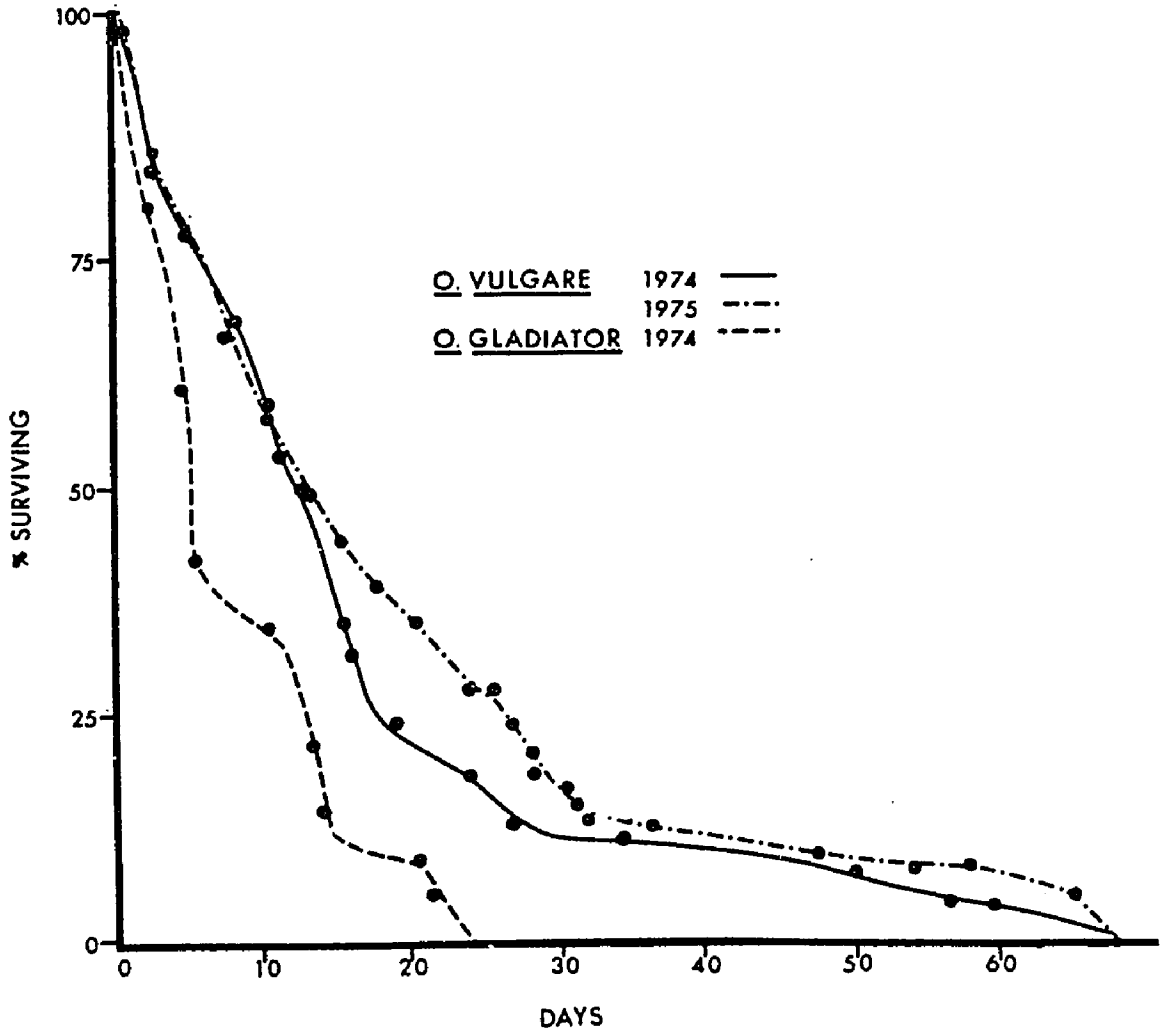

100
75
50
25
0
% SURVIVING
O. VULGARE 1974
1975
O. GLADIATOR 1974
0
10
20
30
40
50
60
DAYS

FIGURE 18B

TABLE 7

SURVIVORSHIP STATISTICS

Statistics for the regressions describing the survivorship curves for the three species of Orchelimum are given in the upper half of the table. The general form of the regression used to describe the curves is: log survivorship = a + b(days). The second half of the table gives the results of selected analysis of covariance (ANCOVA) comparisons of pairs of survivorship regressions. The numbers under the comparison column refer to "species/year" groups in the upper part of the table.

REGRESSION STATISTICS

	Species/Year	n	a	b	r^2	p
1	O. vulgare/74	17	-0.021	-0.067	0.976	0.0000
2	O. vulgare/75	24	-0.079	-0.056	0.980	0.0000
3	O. nigripes/74	16	-0.269	-0.104	0.975	0.0000
4	O. nigripes/75	21	-0.126	-0.065	0.921	0.0000
5	O. gladiator/75	9	0.069	-0.147	0.963	0.0000
6	Female O. nigripes/75	10	0.069	-0.141	0.994	0.0000

ANCOVA STATISTICS

Comparison	F-statistic slope	p	F-statistic regression	p
1 x 2	14.4	0.0005	16.7	0.0000
3 x 4	26.5	0.0000	44.5	0.0000
4 x 6	41.7	0.0000	39.2	0.0000
1 x 3	50.4	0.0000	98.5	0.0000
2 x 4	4.7	0.0367	10.1	0.0003
2 x 5	127.7	0.0000	127.7	0.0000
4 x 5	27.7	0.0000	25.9	0.0000

because males start singing consistently at age five or six. Therefore, in 1975 the survivorship curves for the two sexes start at the same age. In both sexes by the end of the next six days 50% of the marked animals are dead, but there are significant differences between the two curves. Females had a higher survivorship than males during the first six days after marking but males appeared to survive better than females after this period. The survivorship for both sexes during the first six days was probably real but because after that time males were still easily located and females were very difficult to locate, apparent differences in survivorship might have resulted from the differences in catchability.

In the other two species only a few females were captured and so the sexes could not be compared statistically. In these species there is also an indication that females survived better than males (Table 8).

As in most field studies, few instances of mortality were actually seen. A few individuals in all three species were seen in the webs of orb-weaving spiders (12 in vulgare, 2 in gladiator and 2 in nigripes). However, all animals that fall into these webs were not captured; two adult vulgare were seen to fall into webs but escaped by tearing them apart. Praying mantids were seen near singing vulgare but the males were not captured. Only one case of praying

TABLE 8

SURVIVORSHIP OF THE THREE SPECIES OF ORCHELIMUM

	O. vulgare '74		O. vulgare '75		O. nigripes '74		O. nigripes '75		O. gladiator '75	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Sample Size	84	19	76	26	68	29	103	45	30	11
% Recaptured	Days Since First Capture									
75	4	8	6	9	1	3	2	4	8	7
50	12	11	13	15	3	5	6	6	10	10
25	19	13	25	19	10	9	22	18	18	13

mantid predation was observed and that was on a female vulgare.

Small wasps and flies, possibly parasitoids, flying near singing males caused the males to stop calling and move to the opposite side of the perch. Two individuals of nigripes, taken from adjacent populations, were parasitized by tachinid flies. A few of the older adult katydids were also killed by horsehair and nematode infections, a major source of mortality in young adults. Five old adult nigripes and one vulgare died in the laboratory from such infections.

Some older katydids were found with badly mangled bodies, usually some distance from the main population. These were probably the victims of vertebrate predators such as insectivorous birds, shrews, or field mice. Most of these injured individuals did not live. Turtles were seen taking nigripes adults (four observations). Frogs were also potential predators in the nigripes and gladiator areas.

All instances of predation observed were on moving individuals. Two females of vulgare were seen walking into spider webs and another was captured by a mantis while walking past it. One female of nigripes was taken by a turtle as she left a habitat patch. Young adults moved around more than older adults and so were probably more susceptible to this type of predation. The high mobility

of young adults probably accounts for their lower survivorship relative to the older adults.

Males incurred injuries during some aggressive interactions. Injured males might have died from the wounds (two observations in nigripes). These interactions may have also increased their susceptibility to predation because of the commotion caused during physical combat. Also, if injured during combat, the individual may not have been able to escape predators such as spiders. One badly injured male vulgare walked into a spider web and was not able to get free. In nigripes, three males pushed off a cattail during combat were eaten by turtles as they tried to swim to another cattail.

Since most of the physical combat in these species took place early in the season, mortality resulting directly or indirectly from it could account for the lower survivorship of the males early in the season.

As was stated earlier, older females had a lower survivorship than the same-aged males. It was suggested that this may be an artifact. It may also result from a change in female behavior that occurred at this time. Females began ovipositing and, in the process, inserted their ovipositor into holes in plant stems. Females were not able to withdraw their ovipositors rapidly and, if they were conspicuous to predators during this process, they would be easy prey.

Density might have a negative effect on survivorship. In vulgare and nigripes survivorships were lower when the densities were higher than in 1975. At least in males the increase in densities could have increased the amount of physical combat that occurred and so resulted in increased mortality due to predation or injury.

RELATIONSHIP AMONG NEAR NEIGHBORS

Dominance

Factors Affecting Dominance

389 aggressive interactions were observed in entirety. All the interactions considered occurred after the males had established territories for the day and were initiated when one calling male approached another. Morning interactions, during which nearest neighbor spacing is first established, will be considered later.

Most of the interactions terminated with the clear retreat of one male, making it easy to determine which male was dominant. In a few instances (11) both males remained in the area where the interaction was initiated and continued to call. Apparently the intruder was able to establish himself as a territorial male but not able to drive off the former territorial owner. In these cases, males were assumed to be equal in dominance.

In 202 of these interactions, both males were marked, either before or immediately after the interaction ended. Therefore, the physical characteristics of dominant and subordinate could be compared. In most cases dominants weighed more than subordinates, although they were not often distinguishable from subordinates in other measures of size, such as pronotal length, pronotal width, body length or body width.

Where the males differed by at least 15% in body weight, the largest male always forced the smaller male to retreat (76 observations). The largest males dominated in 89% of the interactions where the males differed by 5-10% in body weight (40 out of 45), and 58% of the interactions where the difference was less than 5% (47 out of 81). Since animals engage in physical combat during which males try to push, shove and kick each other off the calling perches, it is not surprising that heavier animals (all other things being equal) would dominate in such interactions. As expected, calling near neighbors generally differed by less than 5% by weight. Small nearest neighbor distances between two males who differed by 15% by weight were unstable.

Dominance is correlated with size in a variety of vertebrates and invertebrates (see general works by Wynne Edwards, 1962; Brown, 1975; Wilson, 1975; for a list of earlier references). Generally, some measure of length is used as an indication of size and a positive length-weight correlation assumed or demonstrated (Borgia for dung flies, personal communication; Alcock, 1977). In the three species of katydids studied, there is a significant correlation between length and weight, but it is poor (Figure 19). The amount of variance explained by the regression is small (r^2=0.40 and r^2=0.28). Because of this, length by itself is not a reliable predictor of weight. There are several factors that account for the lack of predictability.

FIGURE 19. Relationship between weight and length in (A) Orchelimum vulgare and (B) Orchelimum nigripes. The correlations between weight and length are significant but poor. The regression equations for the two species are:
O. vulgare, $y=235.1x-93.81$ $r^2=0.401$ $p=0.000$ $n=71$,
O. nigripes, $y=144.8x-48.1$ $r^2=0.286$ $p=0.000$ $n=67$.

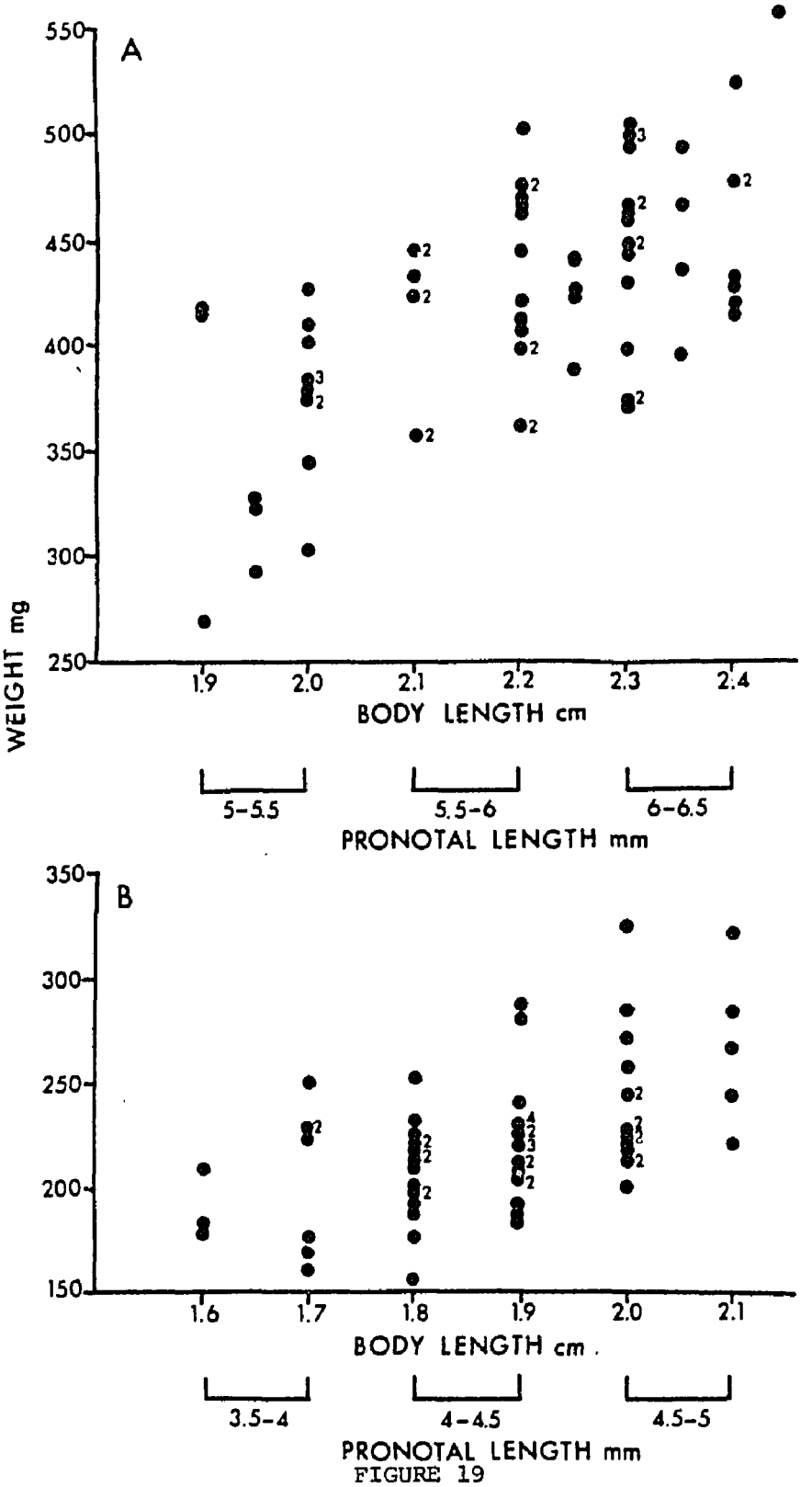

A
550
500
450
400
350
300
250
WEIGHT mg
1.9
2.0
2.1
2.2
2.3
2.4
BODY LENGTH cm
5-5.5
5.5-6
6-6.5
PRONOTAL LENGTH mm
B
350
300
250
200
150
1.6
1.7
1.8
1.9
2.0
2.1
BODY LENGTH cm
3.5-4
4-4.5
4.5-5
PRONOTAL LENGTH mm

FIGURE 19

One such factor is age. In all species, males and females gained weight after they moult (Figure 20). Two males of the same length could differ in weight, and so dominance, if one was much older than the other. Males gained approximately one-third of their adult weight after they moult. In gladiator and vulgare most of this weight gain took place before the males began to sing consistently or interact to any degree. In these species, males only increased in weight an average of 10% after they began to sing. In nigripes males started to sing soon after they moult (about 4 days), before they gained much weight. Also recruitment continued throughout the reproductive season in this species. As a result of these two factors, it was common to see two interacting males of approximately the same length but differing by 50-60 mg in weight (about a 30% difference) because a young male attempted to establish a territory near an older male. As stated previously (Section 3) when population densities were high in nigripes, young, silent males were found in the close proximity of calling males. The oldest silent male found was 8-9 days old, the age at which males attained their maximum adult weight. It appeared that if males could not set up a calling territory during these first eight days, they remained silent in the vicinity of calling males. After they reached maximum adult weight and in a sense became fully mature competitors, if they could

FIGURE 20. Gain in weight after moulting in two males and females of Orchelimum nigripes. Colors indicated are head colors.

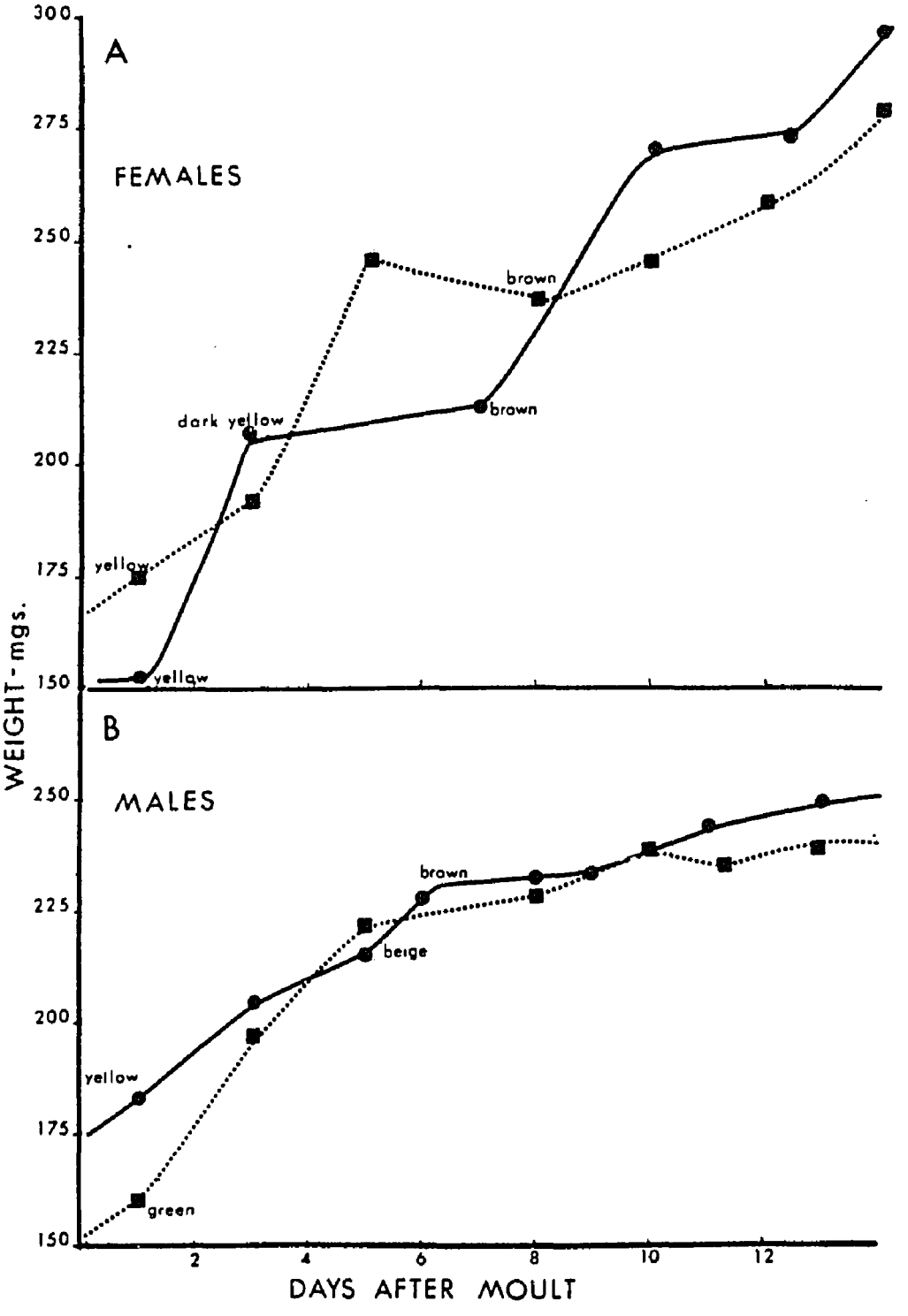

A
FEMALES
B
MALES
WEIGHT - mgs.
DAYS AFTER MOULT
300
275
250
225
200
175
150
2
4
6
8
10
12
yellow
dark yellow
brown
brown
yellow
brown
beige
green

FIGURE 20

not establish a territory in the habitat patch, they left the patch and attempted to establish a territory in another patch.

Another factor affecting male dominance status was mating. Males lost an average of 10% of their weight during mating. Much of this loss was due to the mass of the large spermatophore they transfer during mating. The external portion of the spermatophore, the spermatophylax, is the major part of the spermatophore by weight. Although it is consumed by the female following mating, its exact function has not been investigated. The production of the spermatophylax is probably very costly energetically. In the field and in the laboratory, males were silent for approximately 20 minutes after mating. For the rest of the day after mating, they sang sporadically and spent large amounts of time grooming and feeding. Indications from laboratory studies are that males did not, and appeared unable to, manufacture spermatophylaxes again the same day, although they did produce the internal portion of the spermatophore (the sperm package) in two or three more matings. Males were manipulated so that they had the opportunity to mate several times in one day. They were placed with several females and no other males but even these circumstances failed to induce the male to produce more than one spermatophylax per day. Females, when given a choice, prefer small, unmated males (two-thirds the size of the

mated males) to males that have previously mated that day (30 observations), indicating that females prefer males that can transfer a spermatophylax during mating. In the field, mated males that had occupied central positions in the habitat patch were ousted from it. During this time they would call consistently if approached by a female, but quickly retreat if approached by other males. Thus males, after mating, were low in dominance status and to avoid interacting with other males would even leave a female's vicinity.

Other factors that affect weight are parasitism and injury. Males that harbored parasites (horsehair or hookworms) were very light, approximately 50-60 mg lighter than a nonparasitized male of the same length and age. Lengthwise they were also small males (six cases for old males). Males who lost legs or parts of tegmina during aggressive interactions weighed less than males of the same length. With notable exceptions, these males were subordinate to uninjured males of the same length. One male of vulgare, missing two legs, was the dominant male in a group of normal males for the entire season. Weight appears to be a better predictor of competitive ability than length for the species under consideration. This is because weight differs with age, past injuries and mating activity, all of which are important in determining the outcome of aggressive interactions. The relative contribution of each factor affecting weight was not determined at this time, but will be considered in a future treatment of the data.

Dominance and Mating

In order to assess the success of the competitive strategy employed by males, it is necessary to determine if larger males mate more frequently than smaller males. Unfortunately only a few matings were observed in the field. In nigripes, where 18 matings were observed the average weight of the males who mated is significantly higher than the weight of the other calling males who did not mate (Figure 21). In all cases, where the past history of the males was known (15 out of 18), males who mated were the most dominant in the habitat area based on previously observed interactions among the males. However, males who mated were not always the largest male in the population or general area. A possible reason for this is that older females were somewhat residential and remained within one habitat area. These females were not censusing the entire population of males, but only the small subset within a patch. Females, as stated previously, were not observed to mate with males who were not calling (both in the field and the laboratory). Females also appeared reluctant to mate with a male if his dominance was in question. In nine of the matings observed, the female approached one male who was challenged by a nearest neighbor as soon as he oriented toward the female. In three instances, the original male quickly asserted his dominance and then

FIGURE 21. Weights of mated males, compared to that of unmated males calling at the time the matings took place, Orchelimum nigripes. Males who mated weighed significantly more (Student's T) than other males who were calling at these times but did not mate.

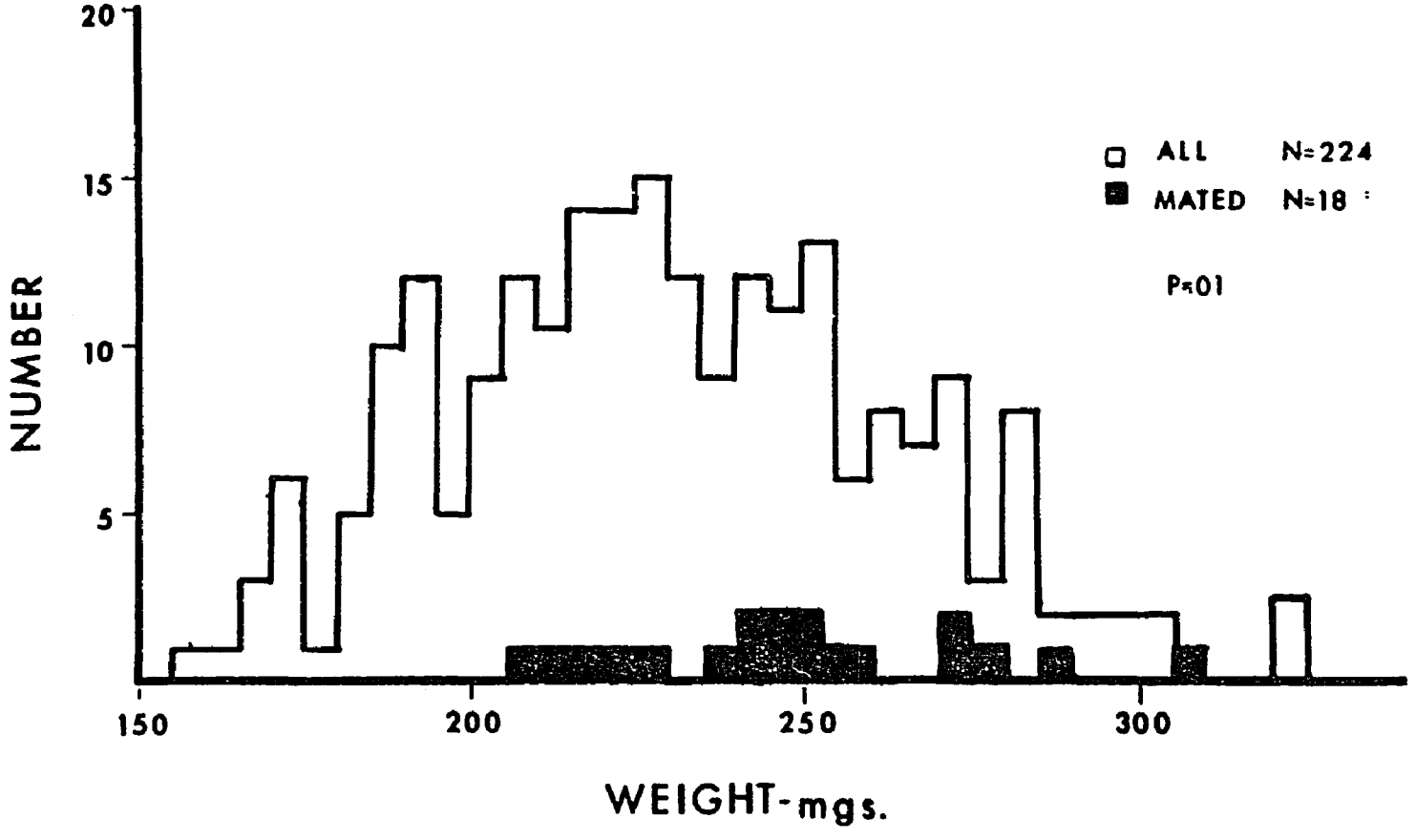

20
15
10
5
NUMBER
ALL N=224
MATED N=18
P=01
150
200
250
300
WEIGHT-mgs.

FIGURE 21

interacted with and mated with the female. In one instance the original male was successfully challenged and the female mated with the new territory holder two hours later. In the other five instances, near neighbors continued to challenge the male. Eventually (after a few hours, 1-4) the female left this group of males and interacted with another group. She mated with one of these males within 24 hours.

In one case, a female kept approaching the original central male (three times) but he was driven away each time by an intruder from another habitat area. The female then attempted to interact with the intruder, but he was repelled by a near neighbor. After four hours within this group of males, she left the area and five hours later mated with a male about two-thirds the size and weight of the males in the original habitat patch. The male with whom she finally mated had left the original habitat patch earlier, after losing several interactions with the males there. These observations indicate that females "value" the ability of males to control areas. They also suggest that it is advantageous for a subordinate male, who cannot set up a calling territory in one area, to leave and set up a calling territory elsewhere. The small male, in the above account, set up his territory in a small patch of sedge 15 cm in diameter and about 4 m from the large patch where the other males were calling. His dominance in the

small patch was clearly established since he was the only male in the patch. However it was probably rare for such small males in outlying areas to get matings because: 1) Females appeared reluctant to leave one area and will stay several hours by a contesting pair of males before doing so, and 2) Prolonged contests between males were only observed late in the season when the density of receptive females is low. Females are believed to mate only once and they do so soon after they establish residency in an area. Thus it appears that it is always more advantageous for males to stay within an area where female density is high if it is at all possible to do so.

In polygamous species, females are a limiting resource for males and thus males compete among themselves for the females. This is thought to result from the difference in preqygotic investment patterns between the two sexes. Females invest more in individual young, via the egg, than males do, via sperm. Thus, females increase their reproductive success (relative to the males) by improving the quality of the young they have, while males increase reproductive success by increasing the number of eggs they fertilize (Bateman, 1948; Trivers, 1972). Females are expected to be "choosy" and select males on the basis of phenotypic trait that may indicate genetic fitness. Female katydids are "choosy" by interacting with a number of different males prior to mating and then mating only

with the dominant territorial male. In doing so, a female mates with: 1) a male that has survived the rigors of establishing a territory and the concomitant increased susceptibility of predation associated with aggressive interactions; 2) males that are probably not diseased or parasitized; and 3) males that have not mated and, therefore, are capable of transferring complete spermatophylaxes. As a result, females mate with males who exhibit the greatest overall "vigor" or ecological fitness in the subset of males they contact.

Acoustical Aggression

Description of Acoustical Aggression

Males of all three species produce two-part calling songs: songs that are combinations of individual pulses (ticks, after Alexander, 1956) and sustained buzz of various length (Figure 22). During aggressive interactions, both parts of the song are altered; the ticks are altered more than the buzz.

The sequence of events in acoustical interactions between a clearly defined intruder and a territorial male are illustrated in Figure 23. A male challenged another by moving deep into his territory and calling. Generally, the territory holder stopped singing momentarily and turned toward the intruder. In nigripes, after a period of silence, the territorial male delivered a song in which the 1) number of ticks were increased, 2) the ticks were delivered at a more rapid rate, and 3) the length of the buzz was shortened (Figures 22 and 24). This altered song will, hereafter, be referred to as the "defense song." The increase in the number of ticks and the length of the buzz was variable; when calling, nigripes generally ticked 3-4 times prior to the buzz but the defense song had as many as 7-9 ticks preceding the buzz (Figure 22). The number of ticks increased and the buzz became progressively

FIGURE 22. Calling song, defense song of Orchelimum nigripes and calling rhythms in the three species of Orchelimum: O. vulgare, O. gladiator and O. nigripes. A calling song B Defense song C Calling rhythms in the three species (after Alexander, 1956).

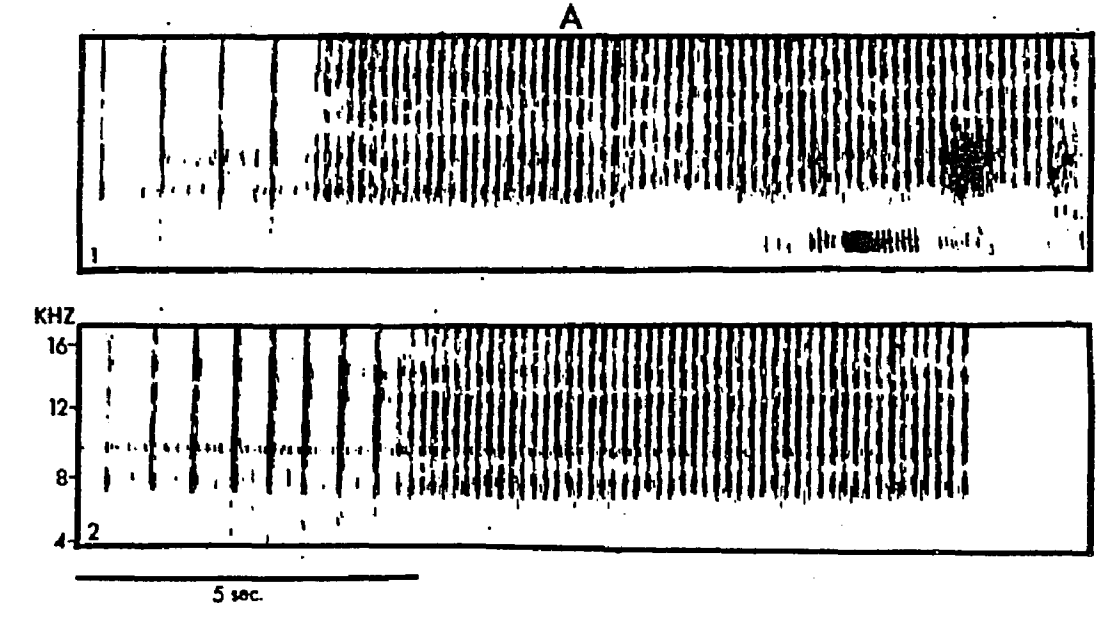


FIGURE 22

FIGURE 23. Sequence of events in a typical aggressive interaction.

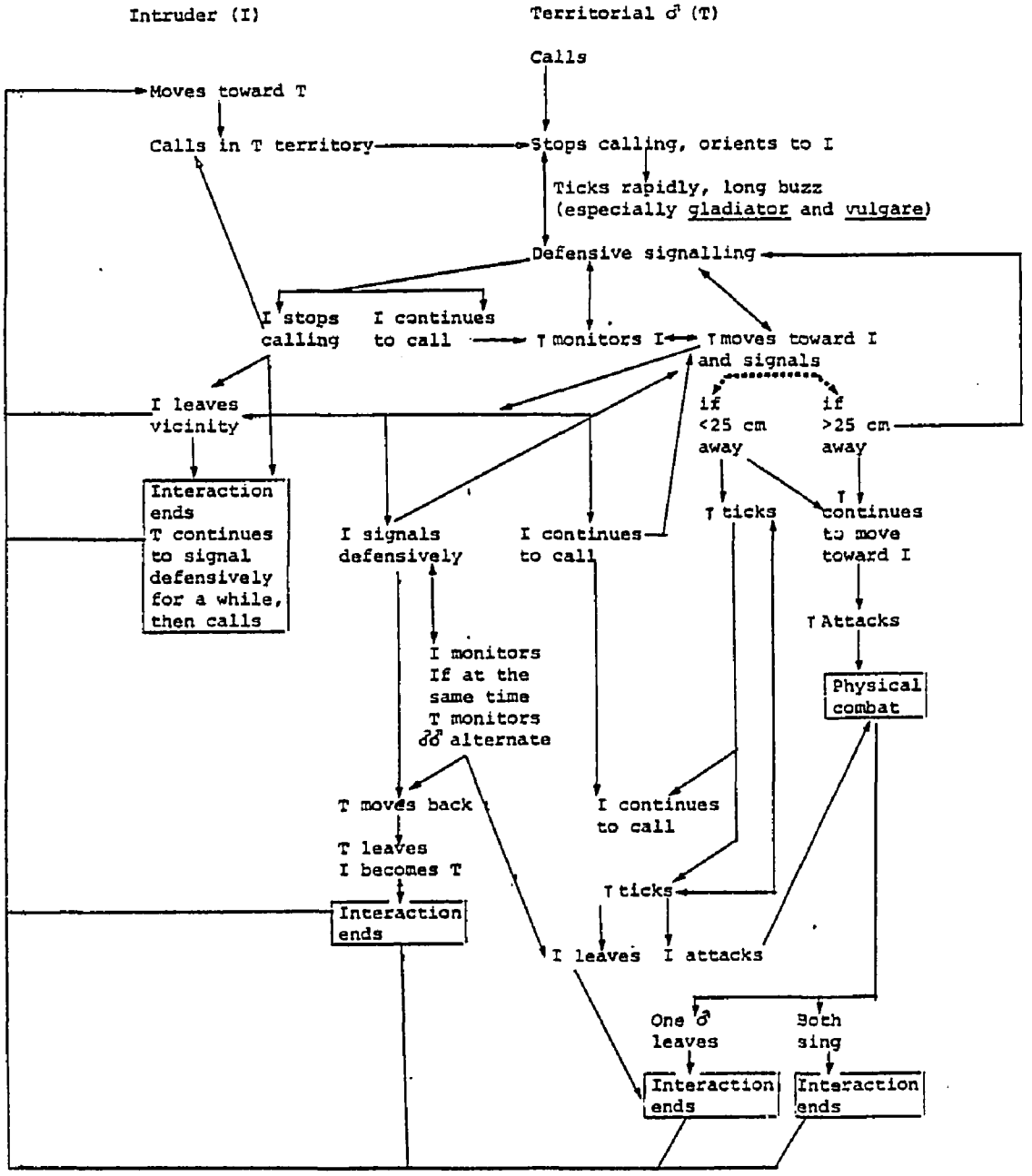

Intruder (I)
Territorial ♂ (T)
Calls
Moves toward T
Calls in T territory
Stops calling, orients to I
Ticks rapidly, long buzz
(especially gladiator and vulgare)
Defensive signalling
I stops calling
I continues to call
T monitors I
T moves toward I and signals
I leaves vicinity
if <25 cm away
if >25 cm away
Interaction ends
T continues to signal defensively for a while, then calls
I signals defensively
I continues to call
T ticks
T continues to move toward I
T Attacks
I monitors
If at the same time
T monitors ♂♂ alternate
Physical combat
T moves back
I continues to call
T leaves
I becomes T
T ticks
Interaction ends
I leaves
I attacks
One ♂ leaves
Both sing
Interaction ends
Interaction ends

FIGURE 23

FIGURE 24. Physiograph tracing of part of a morning aggressive interaction, Orchelimum nigripes. The signals of the territorial male are labeled B, those of the intruder A. B is monitoring and signalling defensively in response to A calling in his vicinity. A in response to such signalling by B stops momentarily. Since this is a morning interaction, males are just starting to space themselves. Males A and B are still within sight of one another and so tick at each other occasionally. (See text, Daily cycle, for further explanation.) The tracing was reproduced at 1/8 of the recorded speed.

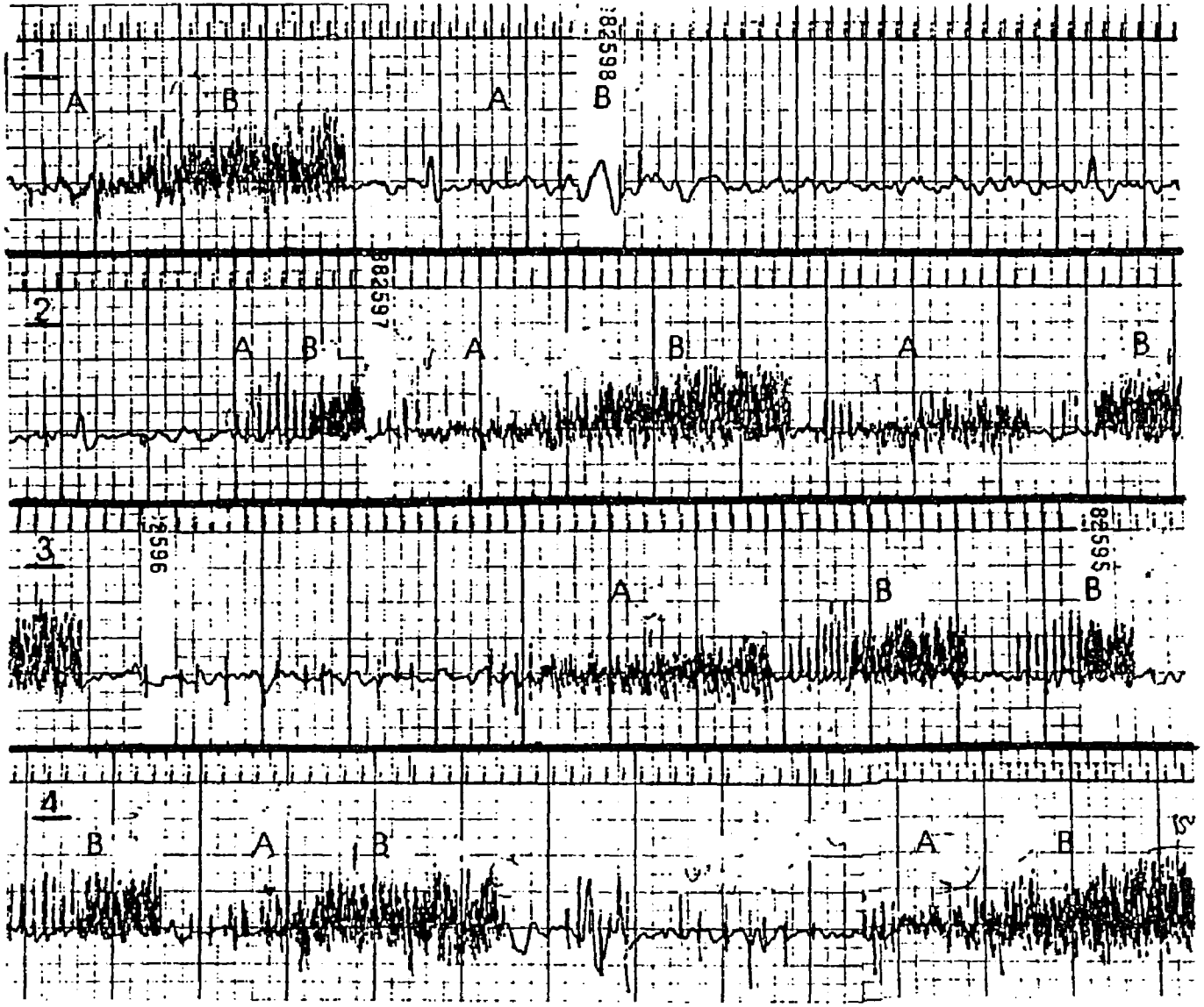


FIGURE 24

shorter as the interaction progressed. A male first added 1-2 ticks to his song then 1-2 more if the intruder continued singing. In gladiator and vulgare, most commonly the first sound, after the territorial holder oriented to the intruder, was a series of rapidly delivered ticks followed by a long buzz, about one and a half times the length of the buzz used prior to the intrusion. After this, as in nigripes, a male's songs consisted of an increased number of ticks delivered at a rapid rate and a short buzz.

The number of ticks per song in vulgare and gladiator was highly variable (Cantrall, 1943; Alexander, 1956; also see section on nearest neighbor nonaggressive acoustical interactions). During the course of the study, the modal number of ticks for calling males was for gladiator 8 (based on 52 songs) and for vulgare 16 (based on 105 songs). In calling males, the ticks were generally delivered in groups of 2-4 (Figure 22); while in interacting males, they were delivered at a very constant rate (Figure 25). As the interaction progressed, there was a tendency for the males to increase the number of ticks in the song.

Equipment was not available to monitor intensity changes, but it appeared that in all species, the territorial defense song was more intense than the calling song. This increase in intensity could be caused by males brushing the scraper across the file with more force or males could

FIGURE 25. Sonographs of part of an acoustical aggressive interaction in Orchelimum vulgare. Black lines indicate signalling by A. Other sounds recorded are B's signals. The microphone is biased toward A, so his signals appear more intense and obscure B's signals when they overlap. B is calling, A is monitoring B calls and signalling defensively. Arrows indicate ticking by A + B. B ticks more sporadically than A.

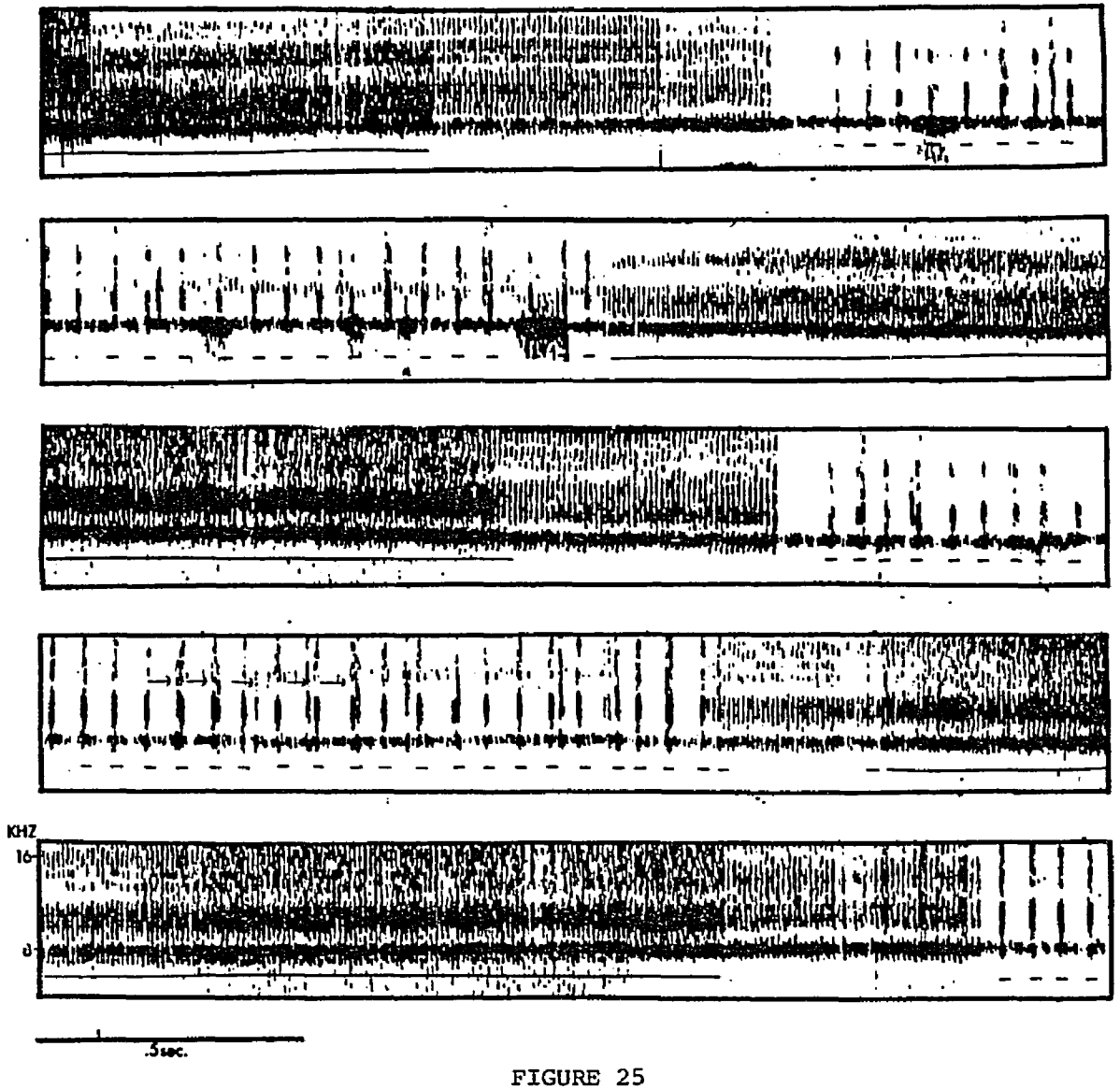


FIGURE 25

be positioning themselves so that attenuation of their song by surrounding vegetation is decreased. Generally males called from the top of the calling perches. Territorial males after orienting to the intruder, moved to the top of the calling perch, thereby placing themselves above most of the vegetation that would obstruct their song.

The reaction of the intruder was generally to turn toward the direction of the territorial male. The intruder's singing became sporadic. One common pattern observed was several acoustical bouts consisting of 1-2 songs by the intruder followed by a series of rapid songs by the territorial male. Just as commonly, the territorial male continued to deliver defense songs at a rapid rate and did not respond again by pausing and orientation to songs and silence of the intruder.

After the territorial male began his defense songs the intruder could stop singing and leave the area (Table 9). This terminated the interaction, although the territorial male would often continue to sing his defense songs for a period of a few minutes before he resumed calling songs. If the intruder continued to sing, eventually the territorial male began to "monitor" the song of the intruder (Figures 24 and 25). The territorial male placed his defense song at the end of the intruder's song. This acoustical monitoring was accompanied by antennal flicking and moving the head or the whole body from one side to another. Males also moved from

TABLE 9

THE NUMBER OF AGGRESSIVE INTERACTIONS TERMINATING WITH THE FOLLOWING BEHAVIOR PATTERN

Parentheses indicate interactions that ended in ties. Both males after interaction stayed in the area and called.

Species	Pattern			
	Defensive signalling	Monitoring	Ticking and visual contact	Fighting
O. nigripes	38	82 (2)	41	95 (6)
O. gladiator	12	13	0	6
O. vulgare	50	44 (3)	0	8
Total	100	139	41	109

one area of the perch to another and back again. A male may be proclaiming his "willingness to defend his territory by monitoring the intruder's songs. Also, he may be obtaining acoustical and visual information about the location of the intruder, since this "monitoring" was usually observed prior to movement by the territorial male in the direction of the intruder. Again the interaction could be terminated at this point by the intruder ceasing to call and leaving the vicinity. If the interaction was not terminated, the territorial male moved toward the intruder. After moving toward the intruder, the male could again deliver a series of rapid defense songs, then stop to monitor and move again. After moving into the proximity of the calling intruder (25-200 cm), a territorial male again oriented to the intruder, sang a series of defense songs and monitored the intruder's songs or moved directly toward the intruder and attacked him.

The reactions of the intruder, as a territorial male moved toward him, were highly variable: 1) he could, while the territorial male was moving toward him, cease singing and move away rapidly. Territorial males, in most cases, did not pursue retreating males, unless they have interacted with that male directly prior to this interaction. 2) The intruder could continue to call in which case the territorial male always attacked him; or 3) the intruder could start to sing a defense song. The intruder's defense song

caused the territorial male to hestiate in his move toward the intruder. The territorial male could move back a short distance (26-100 cm) and respond with a series of defense songs. In two observations, the territorial male terminated the interaction and moved out of the area at this point. More commonly, after moving back a few times, the territorial male began to monitor the intruder's song and then moved toward the intruder. The intruder could at this point: 1) move away; 2) continue to sing a defense song; 3) begin to monitor and move toward the territorial male. In the latter case, alternation of defense songs took place between the territorial male and intruder.

If the territorial male hesitated before attacking the intruder when he was less than 25 cm away from the intruder, the intruder delivered a series of ticks. The same occurred if the intruder moved toward the territorial male as soon as he approached to within approximately 25 cm. The male who was ticked at often responded with ticks. Either male could terminate the interaction at this point and leave the vicinity. Generally if the interaction had proceeded this far, the two males would eventually approach each other and engage in physical combat. The male who lost the interaction could initiate another by returning after moving away and calling in the territory of the dominant male. Also a male who retreated at any point in an interaction could initiate another by returning and calling. Eventually one male was repelled, or more rarely (11 of 389 observations;

see section on dominance) both males called, and the intruder was able to claim a portion of the calling territory of the former territorial holder for himself. In 86 of 389 interactions, the intruder was able to force the territorial male to leave his territory. Usually, interactions resulting in an intruder displacing a territorial male involved physical combat, but in 36 of the 86 interactions observed the territorial male left before fighting with the intruder. Displacements, then, can be accomplished utilizing only acoustical aggression. All 36 interactions progressed to the stage where both males monitored each other's defense songs.

The Daily Cycle of Territory Establishment (Figure 26)

Males started to call about 10-11 AM, after spending the night among the heavy low-growing vegetation. In nigripes, males, prior to calling, were heard exchanging ticks. Males, who emerged near an earlier emerging male, would be ticked at by that male. Generally, the male who was ticked at moved away. Occasionally, two males left the undergrowth at the same time; after an exchange of ticks, both adjusted their positions so that they were at least 70 cm apart (the minimum distance recorded between calling males during the course of the study). After a period ranging from 10 minutes to 45 minutes, some of the males would begin to call, a combination of ticks 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 sing a series of defense calls. Generally,

FIGURE 26. Daily cycle in Orchelimum. Relative numbers of males, females and types of activities during the period adults are active are illustrated.

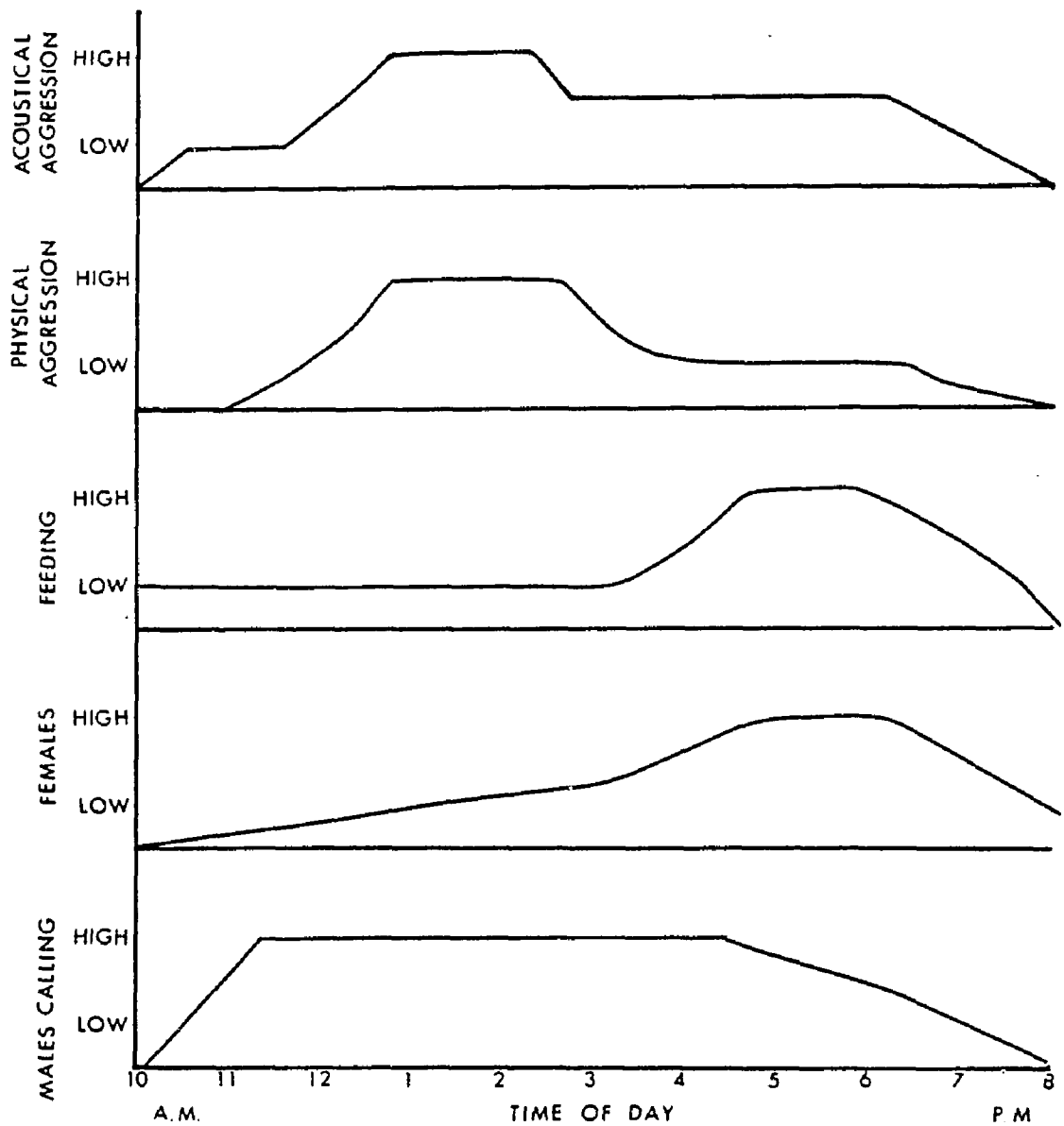

ACOUSTICAL AGGRESSION
HIGH
LOW
PHYSICAL AGGRESSION
HIGH
LOW
FEEDING
HIGH
LOW
FEMALES
HIGH
LOW
MALES CALLING
HIGH
LOW
10
11
12
1
2
3
4
5
6
7
8
A.M.
TIME OF DAY
P.M

FIGURE 26

this was sufficient to cause the new male to move further away. Males would move until their singing failed to elicit a response in the territorial male. A male, who had just initiated calling, might respond to the territorial male's song with a defense song or monitoring behavior. In this case both males moved until they failed to elicit that response in one another. Such interactions early in the morning were of short duration (1-2 minutes). However, as more males began to call, the contests became more prolonged because the new males were forced to move away from one territorial male and thus nearer another. By 11 or 12 AM in good weather, the males were evenly spaced throughout the habitat patch. This initial spacing was accomplished through acoustical aggression; no physical combat was observed at this time.

In vulgare and gladiator, the sequence of events observed during the initial spacing of males was similar; however, the males did not exchange ticks prior to calling. Ticking during aggressive interactions was observed only when males were spaced less than 70 cm from one another (see previous discussion on aggression). Therefore, as suggested by some previous investigators (Cantrall, 1943; Alexander, 1956), isolated ticking is believed to be a response to visual as well as acoustical stimulus of a competitor. Since males in vulgare and gladiator (less dense species than nigripes) tended to be spaced at least two meters apart when they emerged from the undergrowth, they were probably not in visual contact with each other

at this time. Because the visual stimulus was lacking, males did not tick prior to calling. Males in these species, like those in nigripes, first spaced themselves through the use of acoustical aggression, males bantered for positions for 1-2 hours.

Soon after the males were observed to space themselves out, interactions involving physical combats were initiated. Females left the undergrowth later than males and first became conspicuous after the males were distributed (12 to 2 PM). Males near females, generally males who held the central position in a habitat area, were challenged by their near neighbors. Females also began to interact with males at this time and aggressive interactions were initiated when one male tried to move closer to an approaching female and in doing so, moved into the territory of another male. Calling perches then were exchanged and dominance relationships between males were established through acoustical and physical combat. The period in which calling perches are exchanged and during which physical combat occurs, commonly lasted for one or two hours. 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 was readjusted through acoustical aggression; very few interactions terminated in physical combat.

(The physical interactions that did occur in the late afternoon, occurred at the end of the season, when few receptive females remained. In male groups when there was only one receptive female, neighboring males continually challenged the male with whom the female tried to interact.) Mating occurs in the late afternoon.

About 6 PM calling becomes more sporadic; males started to drop out of the chorus and begin 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 older females and probably, unreceptive. Males still moved toward such females. Males who had ceased calling were unaggressive toward each other and in nigripes, where the density was high, groups of 2-4 males and a female were observed feeding on the same cattail head. By 7 PM all calling had ceased. If the temperature continued to fall, males and females moved down into the low vegetation, but if the night temperature remained high (greater than 75°F) males would start calling again about 8 or 9 PM and continue until midnight or 1 AM. The few observations on night calling indicated that males sang more sporadically and were less aggressive than during the day.

The Effect of a Near Neighbor on a Male's Call

The calling of males with near neighbors (less than 8 meters away) was more continuous than was the calling of solitary males. There was a tendency for calling of solitary males to be punctuated by silent periods during which feeding, grooming and adjustment of their position on the perch occurred. Calling males near other calling males, tended to call while undertaking such activities.

Inclement weather, such as a thunderstorm, often interrupted calling for a period during the day. After these interruptions, calling males near one another (1-6 m apart) often re-initiated calling within minutes (<5) after one male started (74 out of 76 observations). Such behavior was not as frequently observed in males distributed further apart (40 out of 62 observations). Silencing of a male, such as when it was captured, would often cause a near male to momentarily cease singing. Again, males more sparsely distributed responded in this way less frequently (32 out of 91 observations).

Anecdotal observations suggest that near neighbors may also influence the rate at which a male in this genus calls (Fulton, 1934; Alexander, 1956). In order to investigate this further, the late afternoon songs of two near neighbors were recorded continuously for periods of 3 minutes (100 recordings), 6 minutes (23 recordings) and 15 minutes

(12 recordings) and later analyzed for any evidence that one male was adjusting his pattern of calling relative to the neighbor's.

Periods of calling by two near neighbors in which the songs of both are delivered at a fairly consistent rate (Figure 27) could be distinguished from periods in which one male's rate of calling becomes inconsistent and he appeared to be reacting to the calling songs of the other male (whose rate and consistency remain unchanged) (Figure 28). Prior to the noticeable change in rate on the part of this male, he usually oriented to the neighbor to which he is reacting. His pattern of calling was usually adjusted as follows: 1) ticking by his neighbor caused him to tick and he continued to tick as long as his neighbor did (Figure 29b & c), 2) if he was ticking at a slower rate, he adjusted his rate to match that of his neighbor's, 3) the reacting male appeared, at times, to delay his song until the song of the neighbor ended (Figure 29d). The end result of such adjustments was "synchrony" in which a male tended to start his calling song right after that of a neighbor. If males sang at perfectly consistent rates, only one such adjustment on the part of a reacting male would maintain him in "synchrony." Of course the rates were not perfectly consistent, and thus, several adjustments on the part of the "synchronizer" were usually observed during a short time period (Figure 28).

FIGURE 27. Independent calling in near neighbors of Orchelimum nigripes. Physiograph tracing of two males singing at a fairly consistent rate. The between-song intervals of male 1 are indicated by a dotted line, those of male 2 by a solid line. In a. the microphone is biased toward male 2. In b. the microphone is biased toward male 1. Tracing is reproduced at 1/8 of recorded speed.

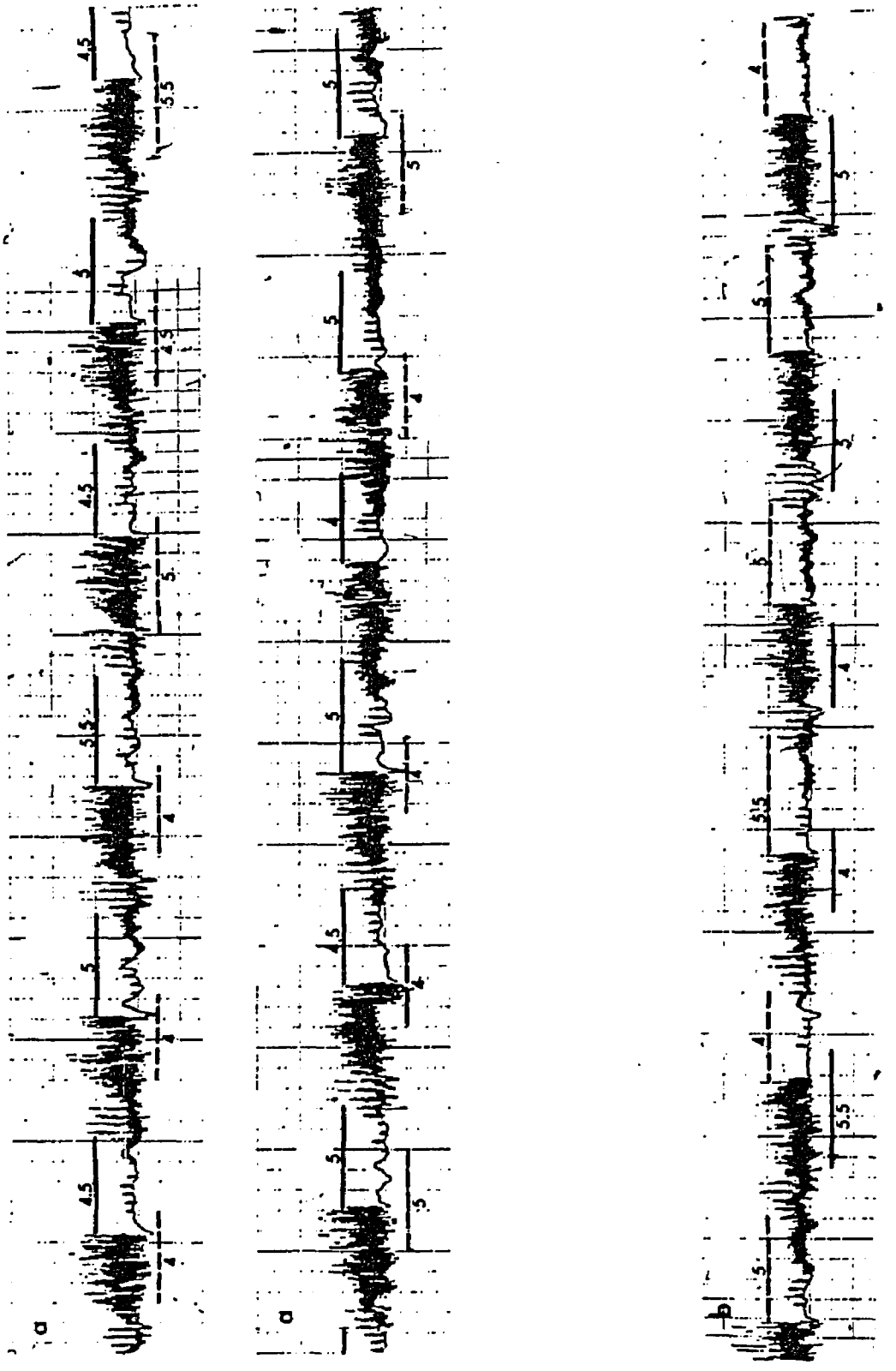


FIGURE 27

FIGURE 28. Physiograph tracing of a male's responses to the calls of his near neighbor in Orchelimum nigripes. Male 1 is synchronizing with male 2. For male 2, dotted line, between-song intervals are fairly consistent; those of male 1, solid line, vary. Numbers indicate which male is ticking. The microphone is biased toward male 2, so his signals appear more intense and sometimes obscure those of male 1. The letters indicate how male 1 is responding to male 2. See text for further explanation. Tracing is reproduced at 1/8 that of recorded speed.

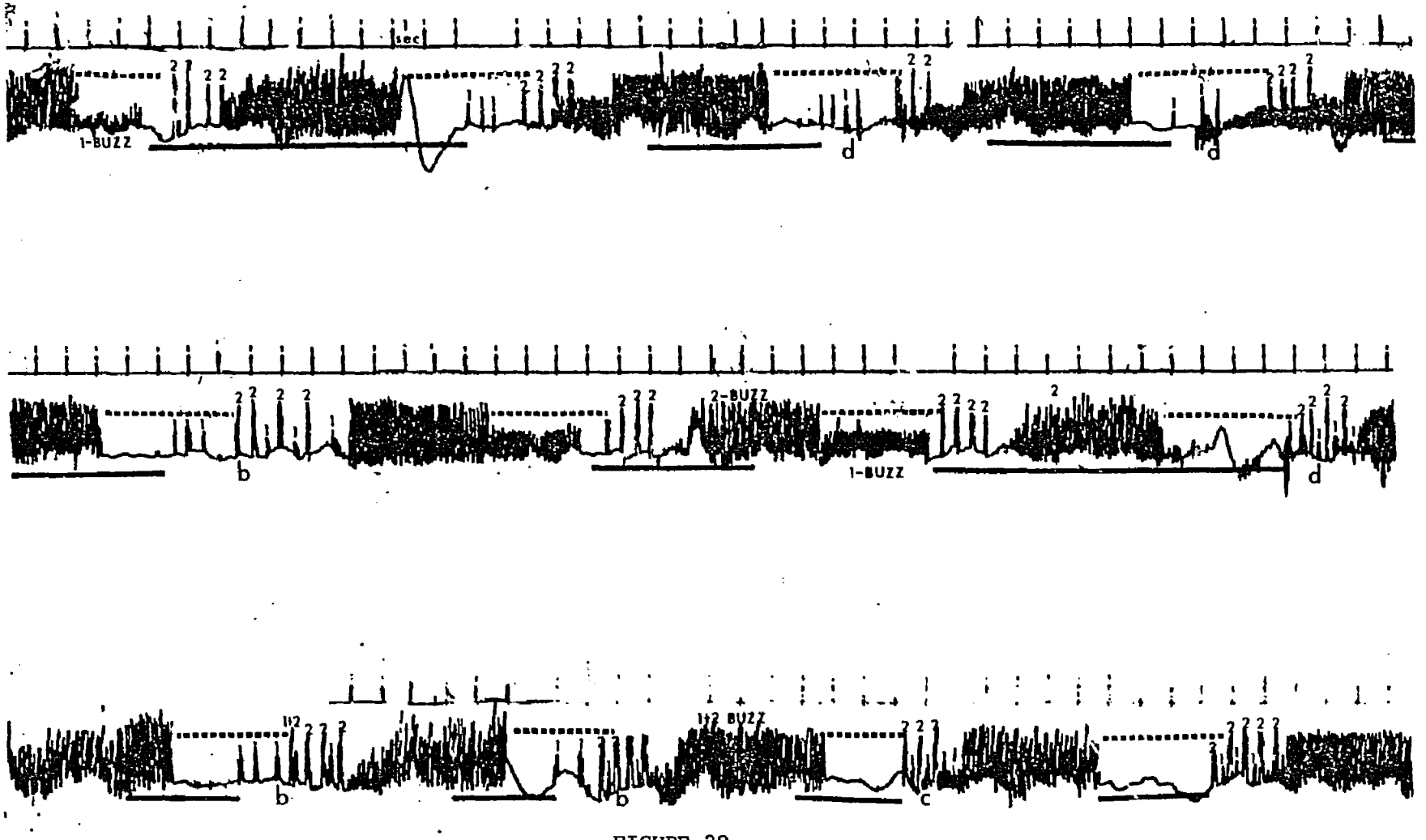


FIGURE 28

FIGURE 29. Diagram of the possible responses of a male to a near neighbor's call in Orchelimum nigripes. A. Two males call independently and at a hypothetical constant rate of 1 song per second. B, C, D. Male 2 responds to male 1. B. Male 2 ticks. Male 1 ticks after him. In response to male 1's ticks, male 2 continues to tick and adds extra ticks to his song relative to A. C. Male 1 ticks. Male 2 ticks in response to male 1's ticks, shortening his between-song interval relative to that in A. D. Male 2 waits until male 1 terminates his call before starting his call, the between-song interval of 2 is lengthened relative to A.

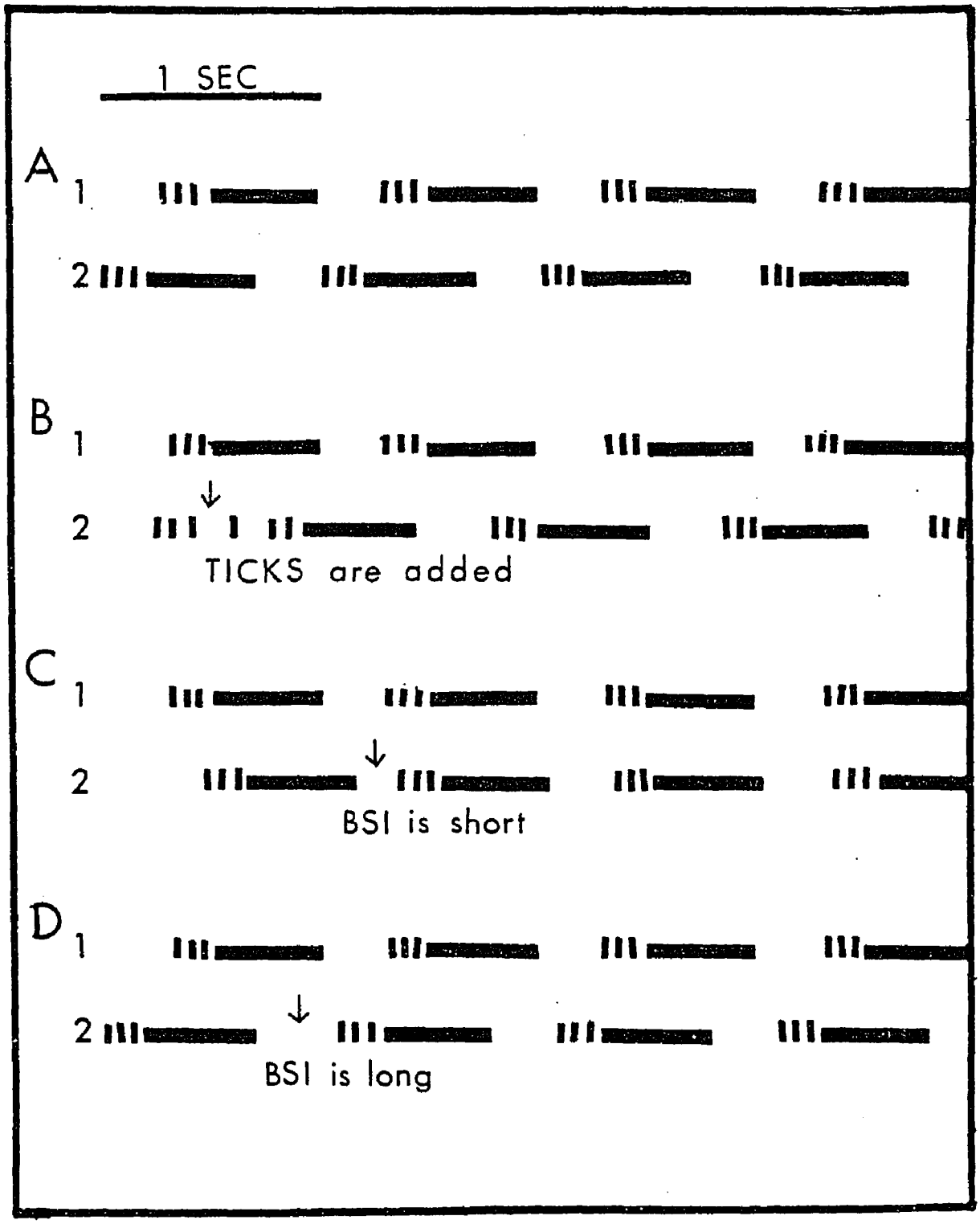


FIGURE 29

In vulgare and gladiator, the tendency for a male to continue to tick while near neighbors tick is very pronounced. Even successive songs of the reacting male differed greatly in the number of ticks they contain (Figure 30). Males of nigripes continued to tick in response to a near neighbor who has started to tick after them less frequently than vulgare or gladiator. Such occurred in only 20% (42 observations out of 205) of the instances analyzed in which the songs of the two males overlapped in that way (as in pattern A, Figure 28). In contrast in the other two species, this response occurred in 85% (86 out of 101 observations) of the cases in which the songs overlapped in that way. The number of ticks in the calling song of nigripes is few and more intimately linked to the initiation of the buzz. By contrast in vulgare and gladiator, gaps can occur not only between the end of the buzz and the initiation of ticking but also at the end of ticking and the start of the buzz. The difference between the species then is believed to result from the differences in song structure. Unfortunately to date, very little is known about how such differences may have originated. The other types of responses noted during adjustment for "synchrony," that is adjustment in tick rate and delays or acceleration of song initiation, occurred in all three species. They can be expected in about 70% (564 cases out of 804) of such situations (that is, during the period the male is

FIGURE 30. Sonographs of a male's responses to the signals of an intruder in an aggressive interaction in Orchelimum vulgare. Male A, whose signals are outlined in black, is responding to male B. The microphone is biased toward A so his song appears more intense. Male 1 continues to tick as long as male 2 ticks—song 1 and 2. When B momentarily stops singing, A ticks less—song 3. When B starts calling again, A ticks in response to B's ticking—song 4.

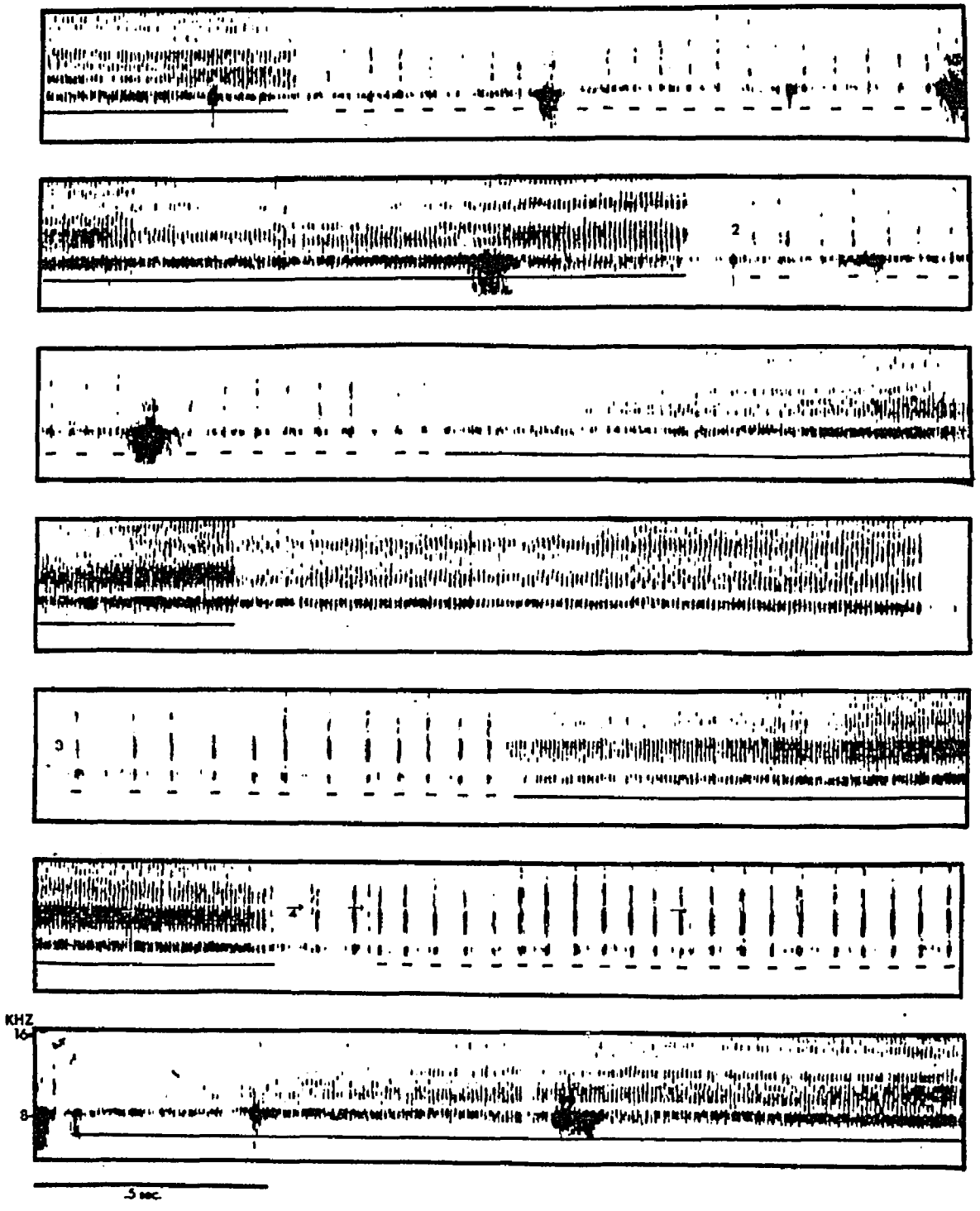


FIGURE 30

responding at all to a near neighbor's song). In all three species then, ticking by a near neighbor had a positive effect on ticking by a responding male and the buzz had a negative effect on song initiation or ticking.

The responses of one male to another during "synchrony" were similar to those observed during aggressive interactions. For example, males, while monitoring an intruder's song, waited to call until the intruder had ended his call. In the defense song the number of ticks and rate of delivery were increased. In gladiator and vulgare, territorial males tended to continue ticking as long as the intruder ticked (Figure 29).

"Central" males frequently synchronized with near neighbors. These central males were males who had interacted with, and dominated other males, although they were continually challenged by them. Such dominant males frequently synchronized with each near neighbor in turn for a few minutes while they executed a semicircle on the top of their calling perches. Synchrony was observed prior to defense signalling, especially if a calling near neighbor had sometime previously moved slightly nearer the synchronizing male. Thus, it appears that "synchrony" may be viewed as low intensity defense behavior or as a way for a dominant male to patrol and maintain the borders of his territory.

Acoustical Signals in
a Female's Presence

Males, in the presence of a female, sang more continuously than do solitary males. As mentioned previously, the calling of solitary males was often punctuated by periods of grooming, feeding and other activities. A male in the presence of a female, did not engage in such activities. In gladiator and vulgare, ticks were delivered at a consistent rate. In all three species, males did not react to near neighbors unless challenged with a defense song at a close range (< 2 m).

Females approached males and mated with males singing defense songs. The changes then, that accompanied defensive calling, such as increases in the number of ticks and increases in the rate of ticking, did not interfere with a male's being recognized as a potential mate. Perhaps, as in some crickets (Walker, 1957; Zaretsky, 1972), pulse rate of the buzz, which does not appear to change in Orchelimum, is the criteria for mate recognition. The calls of all three species contain transients or sudden changes in amplitude. These also may be important in male recognition. Busnel, Dumortier, and Busnel (1956) found that to induce a response in a female of Ephippiger ephippiger, an artificial signal had to contain at least one transient.

Comparisons with Other Studies

As stated previously, few published studies have dealt with aspects of the behavioral ecology of the Tettigoniidae. Most of the studies dealing with acoustical interactions between males are laboratory investigations of the underlying mechanisms responsible for producing rhythmical interactions, such as alternation and synchrony of successive songs, by neighboring males (Shaw, 1968; Jones, 1966a & b, Walker, 1969). Little attention has been given to the role that such interactions play in the ecology and social behavior of the species involved (Alexander, 1960). Such works and others (Lloyd, 1973a, b; Otte, 1974; and others) have suggested that such interactions are likely outcomes of competition for females. Recently, Alexander (1975) has presented a scheme for understanding the evolution of alternation and synchrony, given certain constraints on male calling pertaining to sexual selection.

Males in the three species studied sometimes "alternated" or "synchronized" successive songs. Such acoustical interactions were observed during intraspecific aggressive interactions. They result from "threatening or defense" signalling by a territorial male in response to calling by an intruder in his territory. As such they occurred in conjunction with intraspecific competition among males for females, since such threats often cause the intruder to

leave and so reduce the number of potential competitors in the territorial male's vicinity.

Social conditions can be expected to affect how regularly such interactions are observed between neighboring males. For example in nigripes during one observation period, in a densely inhabited area, no male was found that did not spend large amount of time (15-45 minutes) alternating with one near neighbor then the next. Males were spaced, on the average, 1.2 m apart and males continually interacted aggressively with one another. Any movement by one male brought him into the territory of another.

In the three species studied, however, such interactions were not automatic outcomes of near neighbor proximity. Near neighbors often sang independently of each other. Such interactions are believed to be more strenuously linked to near neighbor presence in species in which such interactions may also function to preserve the clarity of the acoustical signals for mate recognition (Alexander, 1975). For example in the snowy tree crickets, Oecanthus fultoni, Walker (1957, 1969) has demonstrated that chirp (or call) rhythms are essential to elicit a phonoresponse from females and suggested that synchronization of chirps by males allows the rhythm to remain evident to females outside the chorus. The same function has been suggested for katydids who alternate their song. Such alternation

prevents the obscurement of the pulse rhythm of the calls (Jones, 1966a; Shaw, 1968). However in Pholidiphora griseoptera, an alternator, males in groups of three or more did not sing in any ordered fashion (Jones, 1966a). If alternation is only a game played by two males (as suggested for Orchelimum by Fulton, 1932), its function in these species may be more similar to alternation in the three species of Orchelimum studied. More field work is needed on the role of such interactions in these species.

In nigripes, vulgare and gladiator, the calling song was gradually modified into the defense song, as the aggressive interaction progressed. A gradual transition from calling to aggressive signalling has been recorded for many katydids and crickets (Dumortier, 1963; Jones, 1966a; Alexander, 1967; Shaw, 1968). In most other studies, pulses of sound were added to the calling song as the males came closer. Also, the calling rate was generally increased. Similarly, in the three Orchelimum species studied, the number of ticks and the rate of ticking was increased. The buzz portion, however, was reduced in length. Because the buzz was shortened and the rate of ticking faster, the defense song was actually shorter than the calling song. Thus, ticking appears to be the major aggressive signal. Not only was the tick portion of the song altered more drastically than the buzz portion when the animals interact aggressively, but at close range, males only ticked at each

other. A visual stimulus of a competitor appeared to be required for isolated ticking. The studies of Alexander (1961, 1962), Jones (1966) and Shaw (1968) have emphasized the importance of nonacoustical stimuli in releasing high intensity aggressive signalling, although in all studies to date, acoustical stimuli could be sufficient to initiate aggressive signalling.

It is of interest to note that Shaw (1968) divided interacting males into "followers" and "leaders." It was the "follower" who adjusted his rate and who increased the number of pulses in his song relative to that of the "leader." In the present study, a follower was a territorial male; the leader was an intruder who attempted to call. "Following" behavior was a threat of attack by the territorial male. Also males, who obtained desired "central" territories, or perches, near females and so were dominant over near neighbors, "followed" their near neighbors more than their near neighbors "followed" them. It was these territorial males, of course, that near neighbors tried to encroach on by calling nearer and nearer the central male. It is these central males, then, that would be expected to constantly remind near neighbors of their presence.

The excitory and inhibitory stimuli and the way they interact to give rise to the aggressive responses observed in territorial males were not investigated in this study.

A detailed analysis of such stimuli and their underlying mechanism of interaction would require laboratory studies (like those done previously on some katydids) where: 1) environmental conditions are controlled and, therefore, reproducible, and 2) the parameters of the songs can be manipulated via playback and the use of artificial signals. Work on other species of Orthoptera indicate that excitatory stimuli are important in releasing aggressive signalling (Busnel and Loher, 1954a, b; Jones, 1966b; Heiligenberg, 1966, 1969; Shaw, 1968; Young, 1971). Excitation probably plays an important part in the species studied, since a male increased the number of ticks and the rate of ticking in response to a near neighbor's calling in his territory. Inhibitory stimuli must, however, play a part in the role of "monitoring" behavior where a male often waits to start his song just after the intruder terminates his song. The acoustical stimuli releasing aggressive signalling are probably the changes in intensity of an intruder's song as he moves closer to the territorial male. Given that a territorial male has already responded with defensive signalling, intensity changes, as the neighbor adjusts his position (moves closer or slightly back), probably also stimulate "monitoring" and so may have inhibitory effects on song initiation in highly motivated males. Changes in intensity are suspected to release aggressive signalling in other species also (Loher, 1957; Jones, 1966b; Shaw, 1968; Young, 1971).

Only three of the changes effected by neighboring male's song on the pattern of calling in a responding (synchronizing) male were described: 1) A responding male continued to tick while his neighbor does; 2) He matched the ticking rate of his neighbor; 3) He sometimes delayed the start of his song in response to the neighbor's buzz. Such responses were discussed simply to illustrate structural similarities between male responses to a neighboring male in synchrony and aggressive signalling. A detailed analysis of the mechanism maintaining synchrony, like that of the mechanism maintaining aggressive signalling, is beyond the scope of this ecological treatment. The relative role of various types of responses and stimuli involving them, however, could provide valuable insight into how such complex songs evolved.

TERRITORIALITY IN OTHER INSECTS

Circumstantial evidence suggests that "mating" territories may be widespread among several groups of insects. They have been reported in several species of dragonflies and damselflies (Kormondy, 1961[1]; Waage, 1971[1]; Campanella, 1974; Campanella and Wolf, 1974[1]), butterflies (Shields, 1964[1]; Baker, 1972), bees and wasps (Alcock, 1975, 1977; Alcock et al., 1976; Barrows, 1976a,b[1]; Raw, 1976), flies (Catts, 1964[1]; Shields, 1967[1]; Downes, 1969), and beetles (Lloyd, 1973[1]; Shields, 1967[1]). Among the Orthoptera, mating territories have been reported for a grasshopper (Otte and Joern, 1975), a few species of roaches (Ziegler, 1972; Ewing, 1972, 1973), mantids (MacKinnon, 1971) and crickets (Alexander, 1961). In the Orthoptera, mating territories are believed to be widespread among the Ensifera, katydids and crickets, because males engage in vicious fighting which involves grappling, biting and kicking, with the result that the male who wins the encounter stays in the area and the loser leaves (Jones, 1966a; Busnel, 1967; Heiligenberg, 1969; Morris, 1971[1]). Although this type of territoriality seems widespread in insects, with the

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[1]These references contain lists or summaries of older works.

exception of the Odonata, extensive field work has been limited to only a few species in each group.

Access to females and lack of interference from other males appear to be the common functions of all such territories. The physical characteristics of these territories vary but can generally be delineated. Kormondy (1961) for example characterized the territories of Tetragoneuria cynosura, a dragonfly, associated "closely with microtopographical areas delineated by overhanging shrubs that occur in the habitat." Baker (1972) noted that territories of Aglais urticae, a butterfly, were usually placed on the edge of a wall or hedge. In Ligurotettix coquilletti, a grasshopper, males associated with, and generally guarded, creosote bushes (Otte and Joern, 1975) similar to the way Orchelimum vulgare, in this study, generally associated with and guarded Rubus brambles.

The physical resources, if any, that are directly associated with insect mating territories, are apparently nest or oviposition sites. However, feeding sites or routes and cover are implicated in territory establishment in Ligurotettix coquilletti and some butterflies and bees (Shields, 1967; Otte and Joern, 1975; Barrows, 1976).

Species differ with regard to the prxoimity of the territory to resources other than females. For example, Baker (1972) reported that males of Aglais urticae defended territories at female oviposition sites whereas males of the

other species he studied (Inachis io) defended territories on the female's route to the oviposition sites. Shields (1967) reported differences among species of Vanessa in regard to distances of their hilltop territories from other resources such as food plants and roost sites. Where proximity is realized, males may control resources such that mating with a particular male may be a prerequisite for the use of these. Under such situations, the quality of the guarded resource may become increasingly important in mate selection until it is the most important criterion in mate choice (see Orians, 1969; Trivers, 1972; and Borgia, 1977 for detailed theoretical arguments about how such control of resources in general may influence mating systems and associated behavior). Tendencies toward such a regime of sexual selection are indicated for some flies (Borgia, 1971, personal communication), bees (Alcock, 1975) and dragonflies (Jacobs, 1955; Campanella, 1974; Campanella and Wolf, 1974). Jacobs (loc. cit.), for example, reported that in one species of dragonfly the males investigated potential oviposition sites before establishing territories around them; and the females continued to visit certain sites even after males were removed. Males would attempt to change sites if they did not have mating success. Males also guarded females from competing males in their territories prior to mating and during oviposition. Males not associated with sites did not mate and continually attempted to evict territorial

males. Male katydids, in contrast, did not appear to be controlling utilization of resources associated with their territories, other than females. Males were totally non-aggressive towards females and females sometimes fed, took cover, and oviposited some distance from the males with whom they mated. Sometimes these activities were carried out in territories of males other than their mates. In katydids, territories were located near resources because this is where the females occurred. As they wandered about feeding, females interacted with males they encountered. If a male could exclude other males from these areas, he increased the probability that the females would interact more often with him than with other males, and so when the females were receptive they were more likely to mate with him.

The behavioral strategy employed by male katydids is partly shaped by consideration of the type of spermatophore that is transferred and so the past history of sexual selection that has influenced its use. As suggested by the theoretical treatments, environmental considerations are probably also important (Brown, 1964; and the others cited previously).

There is no evidence from my study that, for the three species considered, resources such as food, oviposition sites or cover, were in short supply. Qualitative differences probably exist, but a variety of plants is at least indicated as suitable for food, oviposition sites and cover.

If this is the case, males cannot prevent access to these resources by females who do not mate with them. Brown (1964) points out that resources, even if limiting, must be "economically defensible." Defendability is measured in terms of time and energy required to defend a resource. For example, a moving resource is less economical to defend than a stationary one. In katydids, females were observed to lay in one stem, then after rejecting other stems along the way, lay the rest of the eggs in a different species of plant as much as 7-8 meters away. Sometime later, another female utilized some of the rejected stems. It is difficult to see how males could effectively control a resource that is so highly scattered in distribution and the quality of which is so temporally unpredictable. In some insects, males do not associate with any discernible resource, although small sites are defended where females eventually congregate or come to mate (Pajuenen, 1966; Shields, 1967; Spieth, 1970).

In most detailed studies the position of mating territories has been observed to shift (Free and Butler, 1959; Lin, 1963; Baker, 1972; Campanella and Wolf, 1974; Campanella, 1974). This is expected if, as in the present study, the contested resource or females moved from one area to the next. Also individual males did not tend to control particular sites for long periods of time, in contrast to vertebrates (reviews, birds—Hinde, 1956;

mammals—Owen-Smith, 1977; also general references as Wilson, 1975). In most of the insects studied, however, the period over which mating, and so territorial behavior, takes place coincides with the period during which adults are maturing. New competitors are constantly entering the breeding population and challenging the older males for, and sometimes gaining, their territories.

Density, in general, appears to have a negative effect on territory size (Kormondy, 1961; Moore, 1953, 1964; Pajuenen, 1964, 1966a,b; Campanella and Wolf, 1974; Campanella, 1974). Kormondy noted that, at peak density in Tetragoneuria cynosura, minimum spacing and patrolling was confined to 3-10 yards whereas in solitary individuals, the length of the "beat" was as much as 50-100 yards. Several of the works on Odanata (such as Moore, 1953; Kormandy, 1961; Pajuenen, 1966) and on katydids (this study) report some minimum size to the areas males will patrol or defend.

Subordinate, non-territorial males have been reported in most of the works on dragonflies (Waage, 1972[1]) and some bees (also see existence of alternate strategies for bees, Alcock, 1977). In the present study, subordinate, young males were non-territorial but only until they became fully mature competitors (see section on dominance). At this time, if still subordinate, they established territories in areas further displaced from females but still called and defended sites. Campanella (1974) and Campanella and Wolf

(1974) reported that conspecifics were sometimes tolerated within an area patrolled by a male although when this happened, a definite dominant-subordinate relationship was established. The subordinate was kept away from the center of the territory and had a low utilization and mating priority. In katydids, silent males were not kept away from the territory center but similarly, as a result of their subordinate behavior, had low numbers of interactions with females and thus mating priority. As density continues to increase relative to areas where females are concentrated, territorial behavior may disappear as was reported for crickets (Alexander, 1961) and a roach (Ewing, 1972).

In katydids, territories of near neighbors are highly overlapping. Calling males do not permit calling conspecifics to move closer to them and they are not permitted to move closer to the other calling male. Males in the center position control most of the suitable habitat by virtue of this position and contact more females than do the edge males.

This leads to another consideration. The term "mating territory" was used throughout this paper in order to distinguish the behavior exhibited by male katydids from that of the possible establishment of a dominance hierarchy per se, which does not imply defense of any area. Male katydids do defend and contest for certain positions in suitable areas. The most commonly used definition of

territory is that of Noble, "a defended area" (Brown and Orians, 1970). According to this definition the mating strategy utilized by male katydids is indeed a territorial one. However, most works on the topic of territoriality suggest that such areas, to some degree, should be exclusive (Emlen, 1957; Pitelka, 1959). Brown and Orians (1970) in their review, characterized three conditions to be satisfied in order for an area to be recognized as a territory: 1) a fixed area which may change slightly over time, 2) acts of territorial defense by the possessor which evoke escape and avoidance in rival, so that 3) the area becomes an exclusive area with respect to rivals. Whether the site-dependent defense behavior, displayed by male insects in general, can be considered territoriality depends on the interpretation of how slight some of the changes observed in the site location, and ownership of such sites, are (see Alexander, 1961 for discussion). In addition, it appears that, in the three studies where the exact sphere of control of near neighbors were mapped, the territories are not exclusive in any absolute sense (Campanella, 1974; Campanella and Wolf, 1974; present study). Ewing (1973) notes, for the roach, Nauphoeta cinerea, and Alexander (1961) notes for the crickets, Gryllus sp., at high densities the territorial system breaks down; site attachment is decreased and dominance hierarchies within suitable areas ensue. How "exclusive" insect territories are then may be a function of density.

A justification for the term mating territories for site-dependent defense behavior exhibited by insects is beyond the scope of this treatment. Problems associated with insect mating territories are also common to the "mating territories" of vertebrates, especially mammals (general references—Brown and Orians, 1960; Wilson, 1975; Owen-Smith, 1977; some examples—Kruijt et al., 1972; Buechner and Roth, 1974; and Lill, 1976). The term is traditionally utilized in the literature to describe "defended areas" 1) from which rivals are excluded, and 2) that increase the chances of the male, by controlling such areas, of contacting females. The term, in that sense, is appropriately used in this study, in that it is used to emphasize the functional similarities between katydid territories and other types of mating territories.

The mating territories of katydids, and some other insects, resemble, in some ways, the mating territories of lekking birds. The term lek refers traditionally to a type of breeding system in which males display communally. Each male defends a small mating territory within a larger arena, or court. Males return to the traditional courts year after year. The lek systems of birds are associated with extreme polygny and sexual dimorphism; the "central" males doing the majority of the mating. Also the term was first used in conjunction with courts that were removed from areas providing resources, such as food or nesting sites (Brown, 1964; Lack, 1968). The most "lek-like" mating

system among insects is probably found in some Hawaiian Drosophila. These species are reported to exhibit bizarre sexual dimorphic characters and with males displaying communally in areas where females come only to mate. Females feed and oviposit away from the lek. As yet the connection between mating priority, if any, and position in the lek has not been established (Spieth, 1970). Other diptera, cicadas and fireflies display communally but the relationship between near neighbors, and the court, relative to resources is largely unexplored (see Alexander, 1975).

There are problems in describing most insect mating systems as leks. For example, Campanella and Wolf (1974) used the term to describe the behavior of one of the species of dragonflies they studied, Plathemis lydia, because several males concurrently defend territories in the same area and a male's position within such an area establishes utilization and mating priorities. Campanella (1974), however, in another paper, is reluctant to call the mating system of another species, Libellula luctuosa, a lek although males are doing the same thing, because in this species an individual may also move from site to site throughout the day and may not return to the same court on consecutive days. Katydid males, also, in some sense, call or display communally and certain males, because of their position, enjoy more female contact. However in these and most other insects, the mating territories are located in areas where

females are congregating because of the resources that are found there. Males, of all species, give some indication that they monitor female presence and shift location of the courts to place themselves in a better position to contact females. Males, therefore, are coming to the females, as well as, females being attracted and coming to the clusters of males.

Alexander (1975) has recently suggested that mating aggregations, in which males actively aggregate; that is where males can be shown to attract other males (as for katydids), be included in the concept of a lek, even if males are congregating in regions where females are dense for other reasons than mating alone. If males are clustered about resources valuable to females, these leks could be distinguished from more traditional bird leks by designating them as "resource-based" leks. If the term gains wide usage, it may distinguish the type of behavior generally exhibited by katydids, and some other insects, as intermediate between highly exclusive mating territories and traditional leks. The problem still remains that environmental conditions affecting the relative abundances and location of the resources may change, causing a corresponding change in the ultimate competitive strategies of the males.

The body of predictions relating general environmental characteristics to mating strategies is growing (i.e.,

predictability, heterogeneity, temporal and spatial patterns of various resources) (see review by Orians, 1974; and theoretical works listed previously). Insects appear to be an excellent group to test such predictions because of their diversity in mating strategies; even among species living in the same area (Shields, 1967; Barrows, 1976a; Otte and Joern, 1975; personal data on katydids). The short lifespans and greater ease in manipulating large numbers of insects should provide information valuable for explaining the evolution of mating strategies that have proved somewhat troublesome in vertebrates (i.e. leks—Alexander, 1975; Borgia, 1977).

SUMMARY

Males, in the Orchelimum species studied, set up "calling" territories in areas of high female density. These territories increased the probability that a male would contact females in the general vicinity. Prior to mating, females interacted with a number of calling males in the area in which they resided. Males attempted to increase the probability that a female would interact more with them than other males by excluding male conspecifics from these areas where females were found.

Males controlled as much of the area where females were found as possible. Orchelimum territories were "elastic disks" which compressed under pressure from other males. Males, if their density was high, reduced their territory size to remain in areas where female density was high even though they could have moved to areas of lower female density and had larger territories. The smallest territory defended had a radius of about 70 cm. Silent males, with whom females did not intereact, were tolerated closer than 70 cm.

Two different types of silent males were found close to calling males. Very young males, prior to calling, approached calling males and stayed in their vicinity for some time before calling. Later they attempted to set up calling

territories as close as possible to calling conspecifics. These young males appeared to be utilizing calling con-conspecifics as clues to suitable habitats. Presumably, if males were calling from an area, females were located there. The second type of silent male occurred when population densities were high. These were older males and would call if the calling male was removed. These males were subordinate to the calling male, but reluctant to leave areas where females occurred. However, silent males would move after losing several aggressive interactions with males in the area. Females only mated with calling males, so, at some point in his life, a male had to establish a calling territory if he was to mate.

The major cause of mortality in these species is believed to be predation incurred while moving. Also, males are believed to have lower survivorship than females of the same age, while they are establishing territories, because they are more susceptible to predation as they move around during aggressive interactions. High density increases mortality rates in males, probably because they interact more.

Males did not deny conspecifics physical resources, such as food and cover, located within their territory boundaries. The calling territories were strictly mating territories.

Oviposition plant availability is thought to be a major factor influencing adult distribution in the species studied. After they matured, females were observed to move to areas where oviposition plants were located. Other factors, however, such as food and cover, also affected adult distribution. In two of the species studied, nigripes and gladiator, resources such as food and water were located in the same areas as oviposition plants. Therefore, male territories were located on the borders of patches providing cover, food, and oviposition plants and border areas where additional cover and other favored food items were found. In vulgare, food and cover were provided in and near the Rubus clump. The distribution of oviposition plants was not as localized as the distribution of Rubus patches. Also oviposition plants were not always located in the same areas as the Rubus clumps. Thus, the male territories were located on the borders of Rubus patches facing areas where oviposition plants were prevalent.

Temporal factors may also affect the female distribution. Early during recruitment, females might move into adult habitats from nymphal habitats along one of the borders of the adult habitat patch. At this time, male territories were located on the border facing the area from which the females were being recruited into the patch. Later, after females had established residences within

the adult habitat patch, males were distributed along its entire border.

Calling sites were exchanged frequently between near neighbors because males appeared to be attempting to capitalize on the differences in the number of females available from calling site to calling site, even within a small habitat area. The owner of a territory that allowed more female contact than did neighboring territories was continually challenged by his neighbors.

Males challenged other males by moving into their territories and calling. The territorial male responded to such intruders with defensive signalling. In defensive signalling the calling song is modified. The calling song consists of two parts: a series of unitary pulses, ticks, followed by a sustained train of sound pulses, the buzz. In the defense song, the number of ticks are increased, the rate of ticking increases and the buzz is shortened as the aggressive interaction progresses. Territorial males, during prolonged interactions, monitor a near neighbor's songs; they wait until an intruder finishes his call before they signal. The territorial male usually does this before moving toward the intruder. If the intruder responds likewise, alternation of signals will result. The tick portion of the calling song is modified to a greater extent than the buzz portion as males start to signal defensively.

When males were less than 25 cm from each other, they only ticked. Ticking, then, plays a more significant role in aggression than buzzing. Defensive signalling in these three species of katydids is similar to defensive signalling in crickets and other katydids in that the calling song is gradually modified into defensive signalling as the interaction progresses.

At times, males, especially dominant males who control "favored" positions, "synchronize" with near neighbors. Such synchrony consists of a male starting his song just before or after the song of his neighbor. The way males respond to the calls of their neighbor is similar to the way territorial males respond to an intruder. Synchrony on the part of a dominant may function to remind neighbors, or would-be challengers, of the dominant's continuing presence. Thus, alternation and synchrony in these species are utilized in the context of intraspecific competition among males for females. There is evidence that stimuli having inhibitory and excitatory effects function in aggressive signalling. The elucidation of such stimuli and their effects await future studies.

Where males differed by at least 15% in body weight, the larger male forced the smaller to retreat. Males who weighed less were subordinate to males their same length (body or pronotal). Males of the same length may weigh less because they are: 1) young males and

have not attained full adult weight, 2) injured and/or missing extremities, 3) have recently mated and therefore, transferred a large external spermatophore. For these reasons weight is a better predictor of competitive ability than are measurements of length.

Dominance relationships between males were usually determined by midday, prior to the time mating was observed and soon after males started calling that day. Only a few matings were observed but in most cases, females mated with the most dominant male in the habitat area. Some data indicate that females reject males whose dominance status was in question.

The mating territories of katydids are similar in function to mating territories of other insects. Other similarities, indicated by the few detailed studies of territoriality to date and the present one, are: 1) the tendency for males to monitor female presence, 2) the constant challenge provided to the male in the "favored" sites by neighbors and young males as they mature and enter the competition for sites, 3) the negative effect of density on territory size.

Territories are defined as defended, or exclusive, areas. Katydid territories, in that the territories of near neighbors overlap, do not fit the second definition. The behavior of male katydids is termed territorial behavior in this study because it involves contesting for

sites, and the competitive strategies employed by males are similar to those in other species of insects, that have been described as having mating territories.

The territories of katydids resemble the mating territories of lekking birds, in that several males are signalling in a small area and certain positions in this area, that provide greater female contact, are contested among the males. However, unlike the traditional bird leks, the territories are located in areas adjacent to resources attractive to females; males establish territories in these areas by following females into them. The mating territories of katydids appear to be an intermediate situation between a traditional, and so exclusive, permanent territory and a true lek. We need more studies that assess the influence of environmental factors, such as density pattern, abundance of resources and their predictability, so that we may eventually categorize and understand competitive mating strategies in terms of the factors that are influencing their evolution.

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