EXPERIMENTAL CROSSING OF SUBSPECIES IN NEMOBIUS

(Orthoptera: Gryllidae)1

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In 1925, in a paper on Oecanthus (1), I reported the occurrence in Iowa of three ecological races of Nemobius fasciatus (De Geer), namely, a race widely distributed in grass land, a lowland grass race and a woodland race. Each race had a distinct song. No diagnostic characters were noted except that the woodland race was lighter and more reddish in color. After moving to North Carolina, I found the three types of songs duplicated there in races segregated by habitat. The most common race which had long been considered a southern geographical race, N. fasciatus socius Scudder, sang like the lowland grass race of the north. The southern race was defined as having the ovipositor no longer than the hind femora, a character which did not hold for the other two ecological races in North Carolina. Further study revealed differences in the proportions of the male tegmina and in the shape of the tip of the ovipositor, which were correlated with the type of song wherever found. The new characters were no more clearly limited than the old but defined what seemed to be the true subdivisions of the species. These findings were reported in a general paper on the genus (2), in which I proposed that the lowland grass race of the north should be recognized as socius, and described the woodland race as a new subspecies, N. fasciatus tinnulus.

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A later publication (3) described crossing experiments using the three races as separated on the basis of song type. The fasciatus material was obtained from the mountains of North Carolina and the other two races from Raleigh. Crosses between socius and the other races gave no offspring. Crosses between fasciatus and tinnulus gave hybrid offspring from seven pairs out of eight. On maturity the hybrids proved to have an intermediate type of song which has never been detected in nature. These results indicated that the races constitute natural groups which maintain their integrity in nature.

RACE	OHIO	OHIO + N.C.	N. C.
socius	many	many many many many many pany polydinary polydinary polydinary polydinary	many many
socius + fasciatus	0 0 0 0 sq+f3 fq+s3	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	$ \begin{array}{c c} 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \end{array} $ $ fg + s\sigma \qquad sg + f\sigma$
fasciatus	0	4 5 0 4 0 0 0 \$0.+\$MC. \$MC.+\$O.	many
fasciatus + tinnulus	·	0 t 9 0.+ f & N.C.	
tinnulus	many	many 20.+ 7 8 N.C.	

Fig. 1. Crosses of three races of *Nemobius fasciatus* from two regions. Each pair is represented by a rectangle enclosing number of offspring produced.

CROSSING OF RACES FROM DIFFERENT REGIONS

The question remained whether these southern races were closely related to the northern races having the same type of song. Both socius and fasciatus show somewhat different ecological distribution in the two regions and it is not known whether this is merely a response to climatic differences and other environmental factors. The obvious procedure was to cross crickets of the same song type from the two regions. In 1935, I made a trip to Ohio about the first of August when it was still possible to obtain nymphs of all three races. Collections were made in selected areas where only one race could be heard singing and the female nymphs obtained were segregated.

Breeding stocks of the three races were taken alive to North Carolina where similar collections were made near Raleigh. As the females matured they were placed in jars on washed sand and mated with males to give various combinations of crosses. The jars with eggs in moist sand were kept in a cold place during the winter and were returned to the laboratory in early spring.

The results of the experiment are shown in the diagram (Fig. 1), in which each pair is represented by a rectangular space enclosing the number of offspring hatched. The vertical columns indicate the localities and the horizontal spaces show the races involved. The origin and race of each sex is shown by abbreviations where more than one combination is possible.

AFFECT OF FERTILIZATION ON OVIPOSITION

A few unhatched eggs were found in 8 of the jars in which no nymphs appeared and not more than 5 unhatched eggs were found in any jar in which a few nymphs appeared. At least half of the eggs in the other jars had hatched. Failure of nymphs to appear could be largely accounted for by the absence of deposited eggs. Another experiment was started to determine whether the presence or relationship of the male has any influence on the number of eggs deposited. Thirteen virgin females of socius were used. Four were mated to socius males, four to tinnulus males and five were left unmated. At the time the first nymphs appeared, the sand was washed for eggs in all jars with the following results:

Socius and socius—Eggs recovered, 41, 116, 155, 155; average, 117. Socius and tinnulus—Eggs recovered, 0, 0, 0, 0; average, 0. Socius, unmated—Eggs recovered, 15, 1, 0, 0, 0; average, 3.

One female mated to a *tinnulus* male had been observed several times drilling into the sand with the ovipositor. When no eggs were found she was killed and examined. The seminal receptacle was filled and the ovaries contained many fully developed eggs. By that time all females had been in the adult stage for over a month. Two of the unmated ones which had deposited no eggs were then given males of their own kind. In one case nymphs appeared within 14 days and the female had died, after depositing 95 eggs. The other female died after depositing four eggs.

These results possibly show only an extreme variation in the pre-oviposition period, but when considered with the previous experiments in which all crickets remained in the jars until they died, it seems probable that infertile eggs are not deposited in normal numbers.

SUMMARY OF OBSERVED EVIDENCE ON SUBSPECIFIC GROUPS

The evidence from observations bearing on the relationship of the subspecific groups of N. fasciatus is summarized below using the subspecific names as applied to a division according to song type.

- 1. Song. Each race has a characteristic and easily recognized song. Fasciatus and tinnulus use single stroke chirps differing in frequency. In socius each note is produced by rapid oscillations of short amplitude. The only intra-racial variation observed is in fasciatus. The typical song is a continuous rapid vibrato but frequently when the female is present the song will be broken into phrases of a few seconds duration. At Lakeview, N. C., Georgetown, S. C., and Camden, S. C., only the broken song was heard in the field. Caged specimens from these localities continued to sing in the same manner whether a female was present or not, except that Camden specimens sang continuously part of the time when separated from the female.
- 2. Morphology. There are slight differences in the shape of the tip of the ovipositor, male genitalia, the proportions of the male tegmina and the number of teeth in the stridulatory vein, as previously described (2). The range of variation in fasciatus overlaps that of the other two races so that none are clearly defined. The length of the ovipositor as compared to the hind femora is shorter in socius in all localities. Within each race there is slight tendency toward longer ovipositors in northern regions but the range of variation in southern and northern specimens overlaps considerably.
- 3. Color. Socius is generally nearly black or with contrasting black markings on sides of pronotum, occiput, and face. Tinnulus is tawny brown with a reddish head and with dark markings absent or inconspicuous. In fasciatus the coloration is usually intermediate and varies considerably in different localities. At Raleigh, N. C., and Camden, S. C., it is similar to tinnulus but in the other localities mentioned below it is nearly as dark as socius. The nymphs of socius have a color pattern distinct from the other two races whose patterns are similar but generally lighter in tinnulus (Fig. 2). This condition in socius is found

both in N. C. and Ohio but has not been determined in other localities.

4. Geographic Distribution. As determined by hearing the songs in the field the races are known to occur at least within the following limits. Socius and fasciatus: Fort Collins, Colorado; Ames, Iowa; Newark, Ohio; Geneva, New York; Gauley Bridge, West Virginia; Burnsville and Raleigh, North Carolina; Georgetown and Camden, South Carolina. Tinnulus: Mt. Pleasant, Iowa; Newark, Ohio; Burnsville, Plymouth, and Southern Pines, North Carolina. The race was looked for in

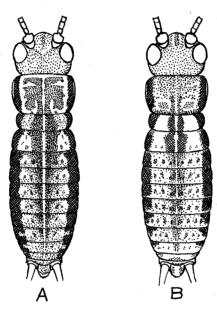


Fig. 2. Color pattern of nymphs. A, N. fasciatus socius. B, N. f. fasciatus and N. f. tinnulus.

appropriate places at Georgetown and Camden, S. C., but was not found. The whole range of the species covers the United States and parts of Southern Canada as far west as British Columbia, Utah and New Mexico and extends into Mexico.

5. Ecology. In all northern localities and in the North Carolina mountains socius is confined to a lowland grass habitat. In the Carolinas east of the mountains it is most abundant in low ground but is also common in other grass land. Tinnulus in all localities prefers an open woodland, not a dense forest, but may occur along forest borders or in shrubby areas, usually

where there is a ground cover of dead leaves. Fasciatus occurs where there is a good sod of grass either in the open or under trees. In the south it has been found only where there is a luxuriant growth of grass due to partial shade or constant moisture. Near Raleigh it has been found only on bottom lands near streams often associated with Poa pratensis and other mesic grasses. At a small lake near Vass, N. C., it was found in grass about a foot high near the shore and in partly shaded places on higher ground. Near Georgetown, S. C., it was found in grass 6 to 18 inches tall under scattered pines and in a large savannah. Near Camden, S. C., it was found in clumps of high grass in an old pasture near woods. At Camden, socius and N. griseus funeralis were found in the central parts of the pasture where the grass had been cropped short leaving small clumps of higher grass. The latter species lives in most xeric habitat of any Nemobius species. In the Georgetown savannah socius was also found, but associated with shorter grass. The habitat relations of fasciatus and socius in the south seem to vary considerably from the situation in the north, assuming under some conditions an apparent reversal of ecological distribution. Possibly each race differs physiologically in the two regions but on the other hand the apparent differences may be influenced entirely by some combination of environmental factors. Certainly the conditions affecting the growth of grasses are very different in the two regions and this seems to be in some way related to the distribution of the two races.

6. Life history. In North Carolina socius matures in June and adults may be found continuously up to December or January. In the laboratory newly emerged adults produced first offspring in about one month and these matured in a month and a half. There are probably two complete generations in a year, one beginning to mature in early June and a second beginning to mature in late August. The other two races begin to mature near the first of August both in the north and south. There is some evidence that socius matures a little earlier than the other races in the north but it probably never has more than one generation there.

DISCUSSION AND CONCLUSIONS

The one thing clearly shown by the crossing experiments is that the lowland grass race of Ohio is more closely related to socius of North Carolina than to fasciatus. Crosses of all three

song types from Ohio with the same type from the south gave some offspring, thereby showing at least close relationship. The results from crosses involving fasciatus and tinnulus however do not have any special significance since in the previous experiments mentioned, hybrid offspring were produced by crossing these two races.

The evidence from crossing experiments and observations indicates that the species *Nemobius fasciatus* is divided into three physiological or ecological races all of which occur throughout most of the geographical range of the species. The races are segregated by habitat and although some overlapping of territory occurs it is probable that they do not interbreed. As groups which maintain their integrity in nature they could properly be considered true species if they possessed good diagnostic characters, but as dead specimens they cannot be classified with any reasonable assurance that all specimens are correctly placed. This same limitation applies to geographical races from areas of intergradation.

LITERATURE CITED

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