NUMBER 253 FEBRUARY 7, 1933

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN THE UNIVERSITY OF MICHIGAN PRESS

SEASONAL CHANGES IN THE MALE POPULATION OF *FAXONIUS PROPINQUUS* (GIRARD)[1]

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HISTORICAL

THE eastern North American crayfishes and the Asiatic *Cambaroides* are peculiar in the possession of two forms of the male sexual appendage. Strangely enough the seasonal changes in the male population have never received an adequate investigation. We are aware of some of the general facts concerning these changes, but a wide diversity of opinion exists regarding their meaning.

The single character most useful in the determination of genetic relationships in all the North American crayfishes and specific relationships in three is provided by the sexual appendage of the male. A study of the fluctuation of the male population as regards the first and second form condition has consequently an important systematic bearing. Within the limits of a closely related group of species the fundamental plan of the appendage is similar, the differences occur in more trivial details. Comparisons are always drawn between males of the first form as the greatest differentiation occurs in this form. First form males are distinguishable from the second form by the corneous or horny tips found on the outer part

[1] This is Part I of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Science in the University of Michigan.

or occasionally on both the inner and outer parts of the sexual appendage. The terminology used to distinguish the two forms is poorly chosen since the second form condition is in reality the first to make its appearance and is the first condition in all young specimens. The names have become established, and to change them now would cause much confusion.

Louis Agassiz and H. J. Clark first noticed the differences between the males of a single species. These observations were communicated to H. A. Hagen, who gives a detailed discussion in his monograph of 1870. He points out that second form males are frequently larger than first form specimens and concludes that they cannot be regarded as developmental stages. He conjectures that the second form condition may be due to sterility.

Faxon (1884, pp. 147–148) wrote of a simple experiment on the two forms, which is best given in his own words:

> In the autumn of 1875 I received a lot of living *Cambarus rusticus*, Girard, from Kentucky, males of the "first form" and females, which bred freely in confinement. After pairing, three of the males moulted, and were thrown, while in the soft-shelled state, into alcohol, together with their exuviae. An examination of these specimens now reveals the fact that the soft-shelled specimens are all of the "second form," their exuviae of the "first form"! It is now clear that we are not dealing with a case of true dimorphism, such as is well known among insects and plants, but it appears probable that the two forms of crayfish are alternating periods in the life of the individual, the "first form" being assumed during the pairing season, the "second form" during the intervals between the pairing seasons. It is to be inferred that the animal is again capable of reproduction after another moult will bring it again into the "first form."
>
> The fact that large collections, made at one time and place contain only one or a great preponderance of one form of the male is now explained. . . .
>
> Such a change as this connected with the reproductive period is unparalleled, so far as I know among the Invertebrata, and even among the Vertebrata; the cases of partial atrophy of the generative organs or shedding of antlers (as in the stag) after the rut is over are hardly comparable.

It is deserving of mention, in view of the foregoing discussion, that a possible parallel does exist in the vertebrates in

the undifferentiated and differentiated gonopodia of cyprinodont fishes of the family Poeciliidae.

Mary Steele in a publication on "The Crayfish of Missouri" considers the changes of the first and second forms at length (1902, pp. 41–50). Her conclusions in her own words (p. 50) are as follows:

> My work upon the second-form males has led me to the following conclusions.
>
> 1. Normally in *C. virilis* at least, every adult male moults in the spring into second-form.
>
> 2. In the course of six weeks or two months all adult males in possession of normal chelae moult a second time and revert again to first-form.
>
> 3. Males without chelae or with imperfect ones also moult a second time during the same season, but still retain the second-form appendages.
>
> 4. Males without chelae or with imperfect ones continue to moult into second-form until the chelae have reached a size normal for the size of the animal.
>
> 5. In late fall and during winter and spring there is a noticeable difference between the reproductive organs of the first-form and second-form males, the testes and vasa deferentia of the second-form males apparently being much less developed than the same organs in the first-form males.
>
> 6. During the summer, though the reproductive organs of different individuals show great variation, there are no distinguishing characteristics by which the reproductive organs of first-form and second-form males can with certainty be distinguished.
>
> 7. Though there is some evidence in favor of regarding second-form males as sterile, there is yet no positive proof of it.

The fourth point of Steele's account is surely merely an assumption. I have seen specimens of *Faxonius nais* (*virilis* does not occur in Missouri) of the first form collected in Missouri in September and October which had imperfectly developed chelae or small stumps. First form males with imperfect chelae occur, for example, in *Faxonius propinquus*. It is conceivable, however, that the loss of the cheliped may have some influence on the time of change of the sexual appendage.

Harris in his ecological catalogue of the crayfishes summarized the knowledge regarding the two forms of the male (1903, pp. 64–65). His paper was prepared about the same time as

Steele's, and accordingly neither author cites the other's work. Harris reviews the work of Hagen and Faxon and gives the results, first published in 1901, of his own observations and experiments on *Faxonius virilis* (probably *nais*) and *Faxonius immunis*. His conclusions briefly summarized are: 1. There are some apparent exceptions to the rule of alternation of the two forms of adults. 2. No marked difference in the essential reproductive organs of the two forms is observable. 3. The adult second form males copulate and produce sperm. (From a communication of observations by W. P. Hay.) 4. The adult second form represents a period in which the regeneration of the sexual elements takes place.

The observations of W. P. Hay are certainly strange and need to be confirmed. They are not in accord with the observations of many other workers on this phase of the problem.

Such is the status of our knowledge concerning these two forms of the male sexual appendage. There seems to be a uniformity of agreement on the following three points by all recent workers on this problem.

1. Each species has two forms of the male appendage.
2. At different times during the year one or the other of the forms is the dominant type.
3. The sexual appendage undergoes a seasonal change.

Disagreement centers around the following four points:

4. The question whether or not the second form male is sterile.
5. The question whether or not the second form male breeds.
6. The question whether or not the second form male is a developmental stage.
7. The reasons for the phenomenon of occurrence of first and second forms in the male.

The first three points have a definite systematic bearing, and many of the features under each item are practically unknown. All of the detailed information has been garnered from examination of specimens of the genus *Faxonius* (a subgenus to most previous writers). *F. virilis* (probably *nais*),

F. immunis, F. rusticus, and *F. obscurus* have received all of the attention.

Method of Study

The methods used by the preceding writers have been similar. A few specimens or at most an insufficient number have been used in drawing conclusions. Most of the animals studied have been kept in confinement, and there is uncertainty as to the validity of application of data gathered from the laboratory-raised animals to those in their native haunts. The investigators have concerned themselves almost exclusively with adult material. Growth and age factors have not been adequately considered. The date of first appearance of the first form appendage has not been ascertained.

The writer has found it advisable to depart from the conventional methods of study in order to fill in the gaps of knowledge regarding the peculiar condition of two forms of the male appendage. Briefly the method employed in the present study is as follows: A single species chosen for study is collected in large numbers and at one place at stated intervals of time throughout the year. Males, females, young and old, all specimens are taken in order to give an adequate representation of the entire population. The females are separated from the males, which in turn are sorted according to their respective forms. Measurements are then made of each individual in each group. The measurement used in this study is the length of the cephalothorax. This measurement is preferable to that of the total length in that it is fixed and solid whereas the abdominal joints are flexible allowing for erroneous readings of the total length.

The measurements obtained on each form are plotted by percentages of total number of individuals for a given length. Measurements taken of specimens collected at different times of the year are plotted in sequence to show the shift of the population with advancement in age or season. First form and second form males are plotted above and below a length reference line to show graphically the size and condition of

the males at any given time. The value of this method lies in its applicability to show: 1. The percentage of change; 2. the time of change; 3. the date of first appearance of appendages of the first form; 4. the best time for collecting in order to obtain any given form; 5. the rate of growth and the age groups.

Analysis of Graph

From a consideration of the graph it can be seen that some males of the young of the year transform into the first form by the last of September, but that the great majority of them do not. A big change in the proportions of first and second form males is noted between the first of August and the last of September, indicating the approach of the breeding season, which in this species occurs in October and November (in the vicinity of Ann Arbor). There is an indication that the young of the year grow very rapidly and tend to lose their identity as regards age by attaining the size of older specimens. There is an indication that moulting is not always accompanied by an increase in size, especially if the moult involves a change of form of the appendage. The graph indicates that the older specimens of *F. propinquus* die with the approach of spring and summer towards the end of the second year and that they do not for the most part, if at all, convert back again to the second form.

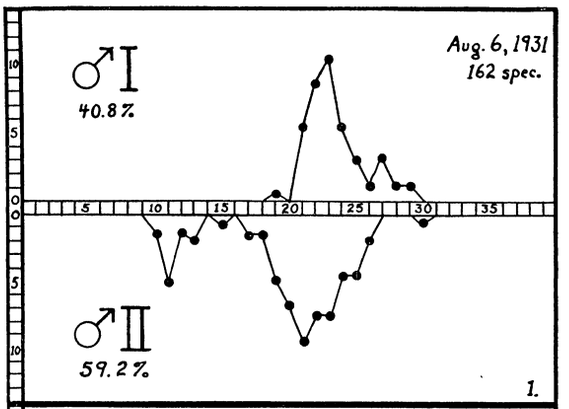
The analysis of the graph can best be considered by a study of each date separately.

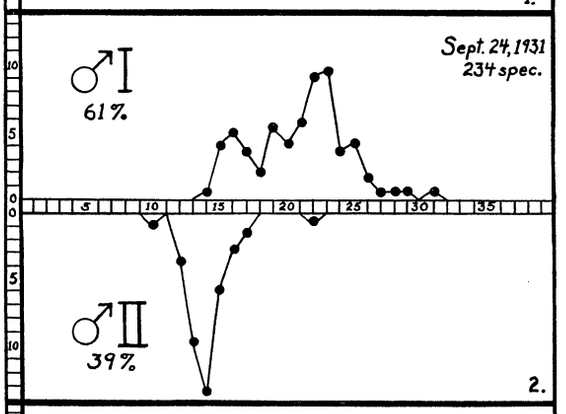
Collection of August 6, 1931

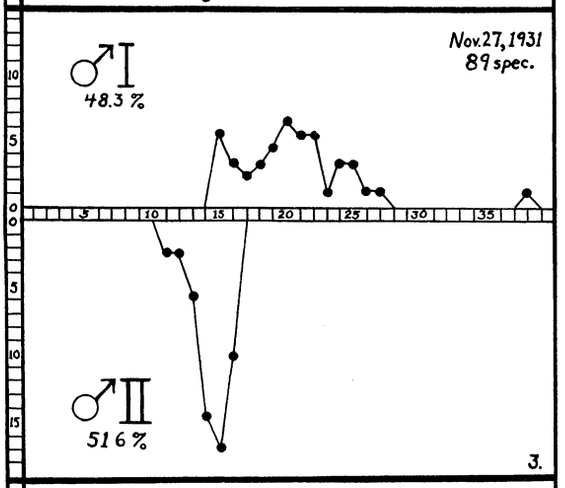
This was the first collection made. The graph clearly shows two age groups; one less than 15 mm. in cephalothoracic measurement and one more than 15 mm. The smaller group must represent the young of the year; the older specimens are in their second year. All first form males are of the older year group.

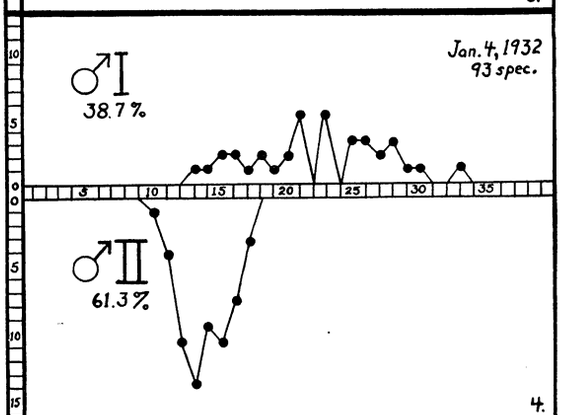
Collection of September 24, 1931

This collection obtained seven weeks later shows extraordinarily well the shift in population as regards the form of the



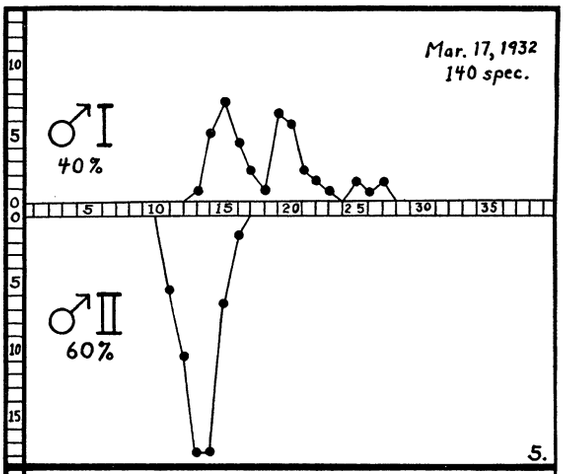


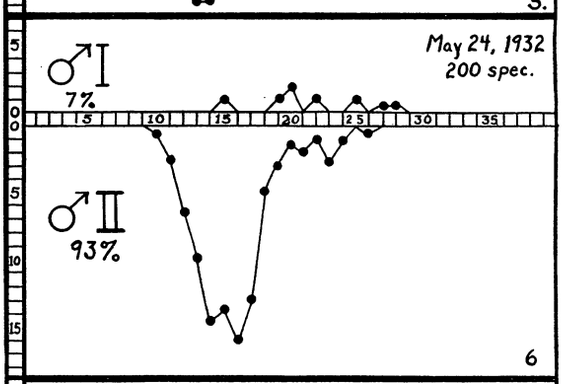


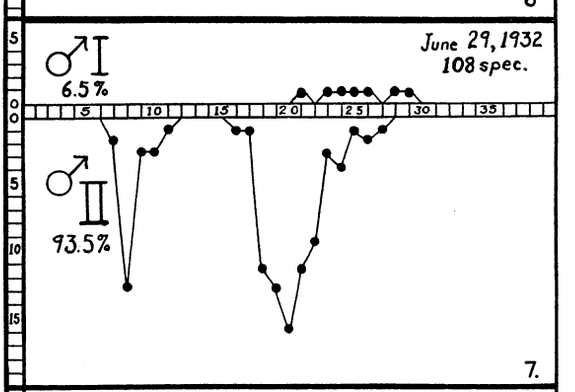


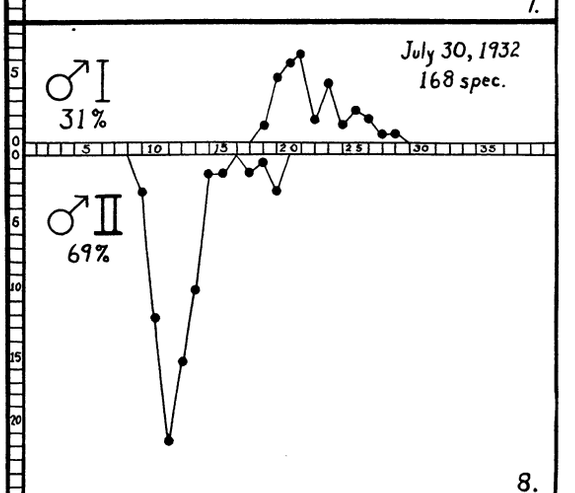
Faxonius propinquus from
Huron River
near
Dexter, Michigan

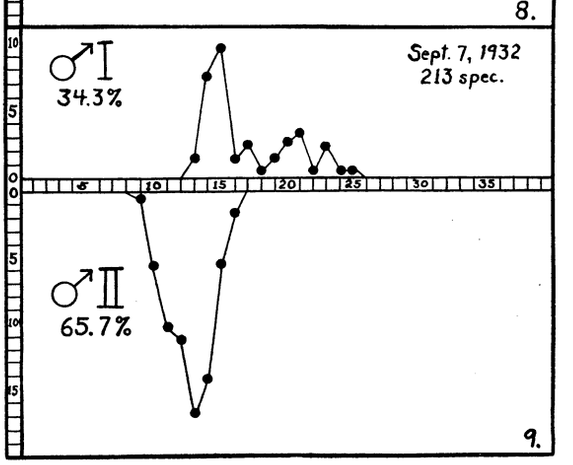
coordinates = percentage of total numbers
abscissas = length of cephalothorax in mm.











male sexual appendage. Practically all of the older second form group have changed to first form as well as some of the young of the year. The largest proportion of the young of the year are still in the second form condition.

Collection of November 27, 1931

In the interval since the preceding collection (9 weeks) there has been little change as regards the male population. The young of the year have grown to some extent. The second year group is not as abundant. One exceedingly large specimen, 38 mm. long, indicates that males may occasionally live to be older than two years.

Collection of January 4, 1932

Males were very scarce in this collection, only 93 specimens were obtained in a total catch of more than 400. Collecting was very difficult in the zero weather, and the failure to obtain data concerning year groups may be attributed to weather conditions. Crayfish are exceedingly sluggish in cold water; undoubtedly many of the older specimens were hiding away in the mud. The second form young of the year had apparently not grown any since the date of the previous collection.

Collection of March 17, 1932

This collection again demonstrates age groups. The second form young of the year and the first form young of the year together with the two-year-old group are well shown. The graph is not greatly different from the one obtained for the specimens collected on November 27, 1931.

Collection of May 24, 1932

The first form male specimens are represented by only a few individuals with no year groups shown. The second form specimens show an age group for the young of the year. From the graph it is not clear whether or not a few specimens of the second year group revert to second form. I do not believe that this occurs, but proof awaits later collections at

this critical date. Many of the females collected on this date carried eggs, indicating the approach of a new year group.

Collection of June 29, 1932

During my absence this collection was made by Wesley Clanton. First form males have almost totally disappeared; a new year group makes its appearance at this date. The young of the year and the two-year-old groups are well shown in the second form type of male.

Collection of July 30, 1932

The annual shift in population was, at this date, practically completed. The transformation occurred at an earlier date than in the previous year. The young of the year have not as yet attained a size or condition sufficient for transformation. The collection was made during my absence by S. N. Jones.

Collection of September 7, 1932

This collection made a little more than a month later shows a remarkable increase in size of the young of the year. A fair proportion of the young crayfish have transformed into the first form. The year groups of the first form male specimens are shown, and the young of the year that have attained this condition are particularly numerous. This collection should be compared with that for August 6, 1931. It will be noted that the young of the year transform into the first form condition later than the two-year-old group.

Applicability of New Method

When a sufficient number of life histories of species of different genera or species groups are worked out according to this method it may well be that type forms of curves correlated with breeding habits, ecology, or phylogeny will be established. Then it would be possible to make a single large collection of crayfish and correctly interpret facts of life history by comparison with the established key curves. The determination of the effects, if any, of altitude, latitude, and

of racial differences might well be ascertained by using this method. It would be a most valuable systematic aid. This type of work also has a very important economic utility in the determination of species suitable for rearing as food.

Summary

My conclusions regarding changes in the male population for *Faxonius propinquus* are as follows: The second form of the sexual appendage in this species may be regarded as a developmental condition. The fact that some second form males are larger than some of the first form specimens is now explained by the knowledge that some of the young of the year (but not all) transform into first form. The maximum percentage of first form males occurs during the breeding season. After breeding the older crayfish die and do not, for the most part if at all, convert into second form. Very few individuals live longer than two years. The approximate date of the breeding season can be detected by the shift in form of individuals. The change in form is independent of injuries to other appendages. The method of study employed here may later prove useful in the systematics of the groups of crayfishes and related forms.

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