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Natural History of the two Crayfish of Northwestern Iowa, *Orconectes virilis* and *Orconectes immunis*

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Abstract. The only two crayfish inhabiting northwestern Iowa, *O. immunis* and *O. virilis,* are ecologically isolated to pond and stream habitats respectively. The former burrows deeply to escape summer drought and winter cold, while the latter does not burrow extensively and apparently overwinters buried in stream beds. The pattern of reproductive events is basically similar in the two species, but *O. virilis* generally lags several weeks behind *O. immunis.* The pond species often matures in one summer under good conditions and may lay eggs in either fall or spring; the stream species is less flexible, not maturing until the end of its second summer and laying eggs only in the late spring.

Only two species of crayfish, the pond-dwelling *Orconectes immunis* (Hagen) and the stream-dwelling *O. virilis* (Hagen), have been collected from Dickinson County in northwestern Iowa over many years of study of the varied aquatic habitats surrounding the Iowa Lakeside Laboratory. *O. immunis* enjoys a wide distribution in the midwestern and northeastern United States, from Massachusetts to northeastern Colorado and from northwestern Tennessee into southern Ontario. The range of *O. virilis* extends somewhat farther north through much of southern Canada, covering Ohio on the south, and touching New Hampshire on the east and Montana on the west (Crocker and Barr, 1968).

Despite the similarity in their ranges, these two crayfish are ecologically isolated, occurring together only occasionally in areas with intermediate characteristics. The physiological and behavioral bases of this distribution have been experimentally defined by Bovbjerg (1961) and evidentally include the competitive exclusion of *O. immunis* from the stream habitat by the more aggressive *O. virilis.*

Extensive reports on the life history of *O. immunis* have been made by Tack (1941) in New York and Goellner (1943) in Michigan. The most complete information on *O. virilis* is contained in Momot's Michigan study of the population dynamics of this species (1967). Some life history data for *O. virilis* in Wisconsin (Threinin, 1958 a and b) are also available, and Aiken (1968) has reported specifically on the winter survival of this crayfish in Alberta. Scattered field notes on both species in other areas are found in a number of state surveys. Neither a state survey nor an extensive life history report on either species has been made specifically for Iowa. The purpose of this study is to compare the natural history of *O. immunis* and *O. virilis* in northwestern Iowa.

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The Pond Crayfish, *Orconectes Immunis* (Hagen)

Habitat

Although *O. immunis* is commonly designated a pond species, inhabiting both temporary and permanent ponds, it is also found in large shallow sloughs, small muck-bottomed lakes, and slowly-moving soft-bottomed portions of rivers and smaller streams. Habitats of all these types are occupied by this species alone in northwestern Iowa. It was collected from every one of the many ponds sampled, as well from the small shallow lake at Kettleson's Hogsback west of Spirit Lake, from Jemmerson and Garlock Sloughs north and south of Lake West Okoboji, and from the upper reaches of the Little Sioux River where it flows slowly over a mud bottom and usually becomes intermitant as a result of summer drying.

O. immunis feeds primarily upon aquatic vegetation, which is abundant in most of its habitats, and also to some extent on smaller aquatic invertebrates, dead plant and animal remains, and detritus. These observations corroborate these of Tack (1941). This crayfish is, in turn, preyed upon by a variety of large animals, including fish, salamanders, toads, frogs, turtles, snakes, birds, and racoons (Tack, 1941). Racoon predation was particularly evident in early summer, when crayfish remains were frequently found in association with tracks, and again in early fall, when they were found near the ruins of recently constructed burrows.

The occurrence of *O. immunis* in temporary ponds means that it may be subjected to complete drying of its habitat for widely variable portions of the year. This species is able to survive such conditions because of its ability to burrow extensively, and thus to follow the water table. Burrow construction characteristically anticipates complete drying, but the specific stimulus to which the animals are responding has not been defined. The extent of *O. immunis'* activities during periods when it is confined to burrows is unknown. It seems likely that it does some feeding, perhaps on the roots and seedlings of terrestrial plants as well as leaving the burrow at night to forage. Other activities, such as molting, copulation and egg-laying, are probably confined primarily to periods when open water is available.

Many of the habitats of *O. immunis* are either dry or solidly frozen during the winter months. In either of these cases deep burrows extending below the frost line to the water table are probably necessary for survival. In lakes deep enough to avoid freezing to the bottom, or streams where there is water flowing throughout the winter, at least some of the animals may spend the winter buried in the bottom mud instead. Again, burrowing or retreating to deep water precedes critical conditions; the direct stimulus for these actions is not known. It is known, however, that mortality is high during the winter, large numbers of dead crayfish having been seen after the spring thaw.

Life History

Hatching. The eggs of *O. immunis,* like those of other crayfish, are cemented to the pleopods at the time of laying and remain there for several weeks until hatching. The young are also attached through their first two larval stages, which may last a total of a week to 19 days in *O. immunis,* varying with temperature (Tack, 1941). After molting to the third stage the young still cling intermittantly for perhaps a week more before becoming independent.

The time of hatching varies widely, depending on the time of egg laying and temperature. Most of the females collected from the lake at Kettleson's Hogsback in Dickinson County on May 2 and 3, 1968 were carrying neither eggs nor young, but their pleopods bore traces of the cement substance secreted for the attachment of eggs. This suggested that their young had hatched two to three weeks previously and had recently left them. A few of the females collected at this time were carrying unhatched eggs, indicating that a small percentage of the current year's young would not hatch until mid-May. These were probably eggs which had been laid earlier the same spring and had developed without delay, while the young which were already independent at this time were probably from eggs laid the previous fall and carried over the winter, their development presumably inhibited by low temperatures until spring. Still greater variability in hatching time between different sites in the same area was demonstrated by the collection of two small *O. immunis* females with young from the upper Little Sioux River as late as June 12, 1968.

Growth and Maturation. After leaving the female, the young *O. immunis* molt frequently. The extent of their growth and development during the first summer is highly variable, depending partly on the abundance of food and whether the animals are forced into burrows by summer drying. A wide range of sizes is present even among the current year's young of a population in one pond. Only a portion of this variability can be due to differences in the times of hatching.

Goellner (1943) set a size criterion of 25 mm cephalothorax length for presumption of sexual maturity, based in females on the gross examination of ovaries and in males on attainment of the first, or copulatory form. Using this criterion, he found that in a series of temporary pools which dried in mid-summer few if any of a given year's young were mature by the end of their first summer, while in a series of state fisheries ponds which were kept filled through early fall one-third to three-quarters of the animals attained sexual maturity three to four months after hatching.

The situation in the Kettleson's Hogsback lake, and thus presumably also in the sloughs and other permanent bodies of water of Dickinson County, appears comparable to that in Goellner's fisheries ponds,; the current year's animals grow to a size which overlaps that of the few older animals which remain, and attain sexual maturity in time to constitute the bulk of the breeding population at the end of their first summer. In the temporary ponds, the proportion of the population reaching maturity by the end of its first summer probably varies with the amount of time any given pond remains filled during a particular summer. The maturation of an individual is apparently delayed when drought forces it to burrow.

Molting. The first group of animals to begin molting in the spring is that portion of the previous year's young which remained immature over the winter. These molt several times during the spring and early summer before finally reaching maturity. The adult males are the next group to molt, changing from the first, or copulatory, form to the second, or non-copulatory form. The molting of adult females is somewhat later because of the presence of eggs or young on their pleopods (Scudamore, 1948). Collections from Kettleons's Hogsback on May 2 and 3, 1968 contained very few freshly-molted animals, but many of both sexes molted in the laboratory during the next several days. This was interpreted as meaning that field temperatures were just starting to reach the threshold necessary for molting to occur.

Both Tack (1941) and Goellner (1943) point out that the spring molts are a time of heavy mortality among adults of both sexes and may account for much of the reduction in their numbers. Following completion of the spring molt by all of the adult males, there is a period of about two weeks when no first form males are present in the population. Then, early in June, the first of the adult males molt a second time, returning to the first form. Most of the population, including the juveniles left from the previous year, completed this molt by early July in both 1967 and 1968. Another group of first form males may be added later in the summer, if any of the current year's young reach maturity at that time. It should be noted that the portion of the population involved at any one molting period is largely dependent on how many mature in less than a year.

Life Span. The length of a crayfish life is evidently closely related to participation in reproductive activities, and thus upon the time of maturity. Tack (1941) reports heavy mortality of adult males in August and September after breeding and of adult females in the spring after the young have become independent. He adds that a few animals evidently survive to reproduce a second time, but he was unable to determine whether they were two year olds which had attained maturity at the end of their first summer, or three year olds which presumably had not. Goellner (1943) found, in his Michigan fisheries ponds, that many animals died in their second year, with only a few of each sex, especially those which had not matured by the end of their first summer, living two or even three years. By way of contrast, slow growth and delayed attainment of maturity in his temporary pools appeared to lengthen life expectancy, with animals generally living for a full two years there.

Again the *O. immunis* populations of Dickinson County appear to parallel those studied by Goellner as would be predicted from their times of maturation. Thus collections from the temporary ponds in late June and July of 1967 yielded large numbers of the previous year's young which were just reaching maturity. At Kettleson's Hogsback, however, adult-sized animals were very scarce from early July of 1968 until August when the current year's young reached this size.

Reproduction

Copulation. Copulation among *O. immunis* occurs from late June to the next April, with the exception of the winter months when the animals are extremely torpid. This period of copulation is determined by restrictions besides temperature. The field and laboratory data of other workers (Tack, 1941; Goellner, 1943; Scudamore, 1948) indicate that the males must be in first form and the female not carrying eggs or young. Copulation was not seen in the field during the course of this study, but it often occurred in the laboratory following collections.

Egg Laying. Because the sperm are indefinitely viable in a spermatophore which apparently remains wedged in the annulus ventralis or seminal receptacle of the female until the next molt, crayfish may successfully lay eggs as long as five or ten months after copulation. Tack (1941) states that *O. immunis,* in the Ithaca area, lays eggs only in the fall. Goellner's data (1943), however, indicate that in his Michigan fisheries ponds only a few females laid in the fall, the rest waiting until spring. The difference was evidently not due to climatic conditions, but rather to differences between the specific habitats which were studied; Goellner's ponds were generally drained at some time during the fall and sometimes left dry all winter, while Tack's ponds remained filled. If the normal time for egg laying is fall, but standing water is not available at that time, most of the females will delay until spring rather than laying in the burrows. Thus egg laying would be similarly delayed in temporary ponds. The few females found carrying eggs as late as early May probably laid them about the first week of April rather than the previous fall. These were females whose eggs were not ready to be laid in the fall, but were fully mature by spring. The time of ovarian maturation is thus an additional factor in determining when *O. immunis* lays its eggs; the portion of a population which was mature enough to lay in the fall might vary widely depending on how early cold weather started.

THE STREAM CRAYFISH, *Orconectes Virilis* (HAGEN)

Habitat

O. virilis characteristically occurs in rock-bottomed rivers and smaller streams, and in lakes with rocky shores. In Dickinson County it is found in the Little Sioux River, where it overlaps *O. immunis* to some extent but cannot exist in the headwater region where the river is intermitant for a part of the year. It also inhabits the smaller streams of the area and all of the rocky lakes, including Lake West Okoboji, Spirit Lake, and Center Lake.

Like *O. immunis,* this crayfish is a generalized feeder, utilizing in its diet a mixture of aquatic vegetation, small invertebrates, plant and animal remains, and detritus. Its predators include fish, turtles, birds, and racoons (Lagler and Lagler, 1943).

O. virilis escapes winter freezing by moving into deep water and burying itself among the rocks of the bottom where it is soon covered by silt if it remains inactive (Aiken, 1968). This winter retreat occurs early in autumn in northwestern Iowa. It does not burrow extensively and as a consequence is unable to survive either complete freezing or drying of its habitat.

Life History

Hatching. Young *O. virilis* hatch several weeks later than the majority of *O. immunis* in the same area. This occurs by early June in the Little Sioux River; on May 2 and 3, 1968 the adult females were carrying eggs which appeared to be less than a week along in their development and by mid-June they were free of young and just starting to molt.

Hatching time in this species is very consistent within a given habitat. Some variation occurs between sites, however, as illustrated by the collection on June 18 and 19, 1968 from Lake West Okobopi of two *O. virilis* females carrying young. This discrepancy was probably due to the effect of differing temperatures on the development of the eggs and young.

Growth and Maturation. Data from Dickinson County support the conclusion of Threinin (1958 a and b) and Momot (1967) that *O. virilis* do not mature until their second summer. By September 9, 1967 the currents year's young could still be distinguished from the adults as a relatively distinct size class; more overlap in size with the previous years animals would be expected if some had attained sexual maturity.

Molting. The sequence in which various classes within a population molt is the same for *O. virilis* as for other species, but the dates are generally later than for corresponding *O. immunis* groups. Since all the previous year's animals are still juveniles, the group which is the first to start molting in the spring constitutes a major portion of the population. These attain sexual maturity at some point in their second summer, after a number of molts. The spring molt of adult males from first to second form must take place between mid-May and mid-June in the Little Sioux River; adult molting did not begin immediately after the early May collections but no first form males were present by June 17. As previously noted, the adult females were just starting to molt in mid-June and their molt was completed by the first week of July. First form males started to reappear in the population at the end of June 1968. This summer molt extended to the end of August, probably because of the molting of previous year's males, some of which did not attain maturity until that time.

Reproduction

Copulation. As in other species, *O. virilis* evidentally copulates at any time when the males are first form, the females free of eggs and young, and the temperature sufficiently high to permit activity. In Dickinson County this period extends from early July until mid-April of the following year with the exception of the winter months. Again, this is supported by laboratory observations, although no copulations were seen in the field. Other workers (Momot, 1967; Threinin, 1958 a and b: Fasten, 1914), apparently from field observations, report no copulation before mid-August for *O. virilis* in Michigan and Wisconsin.

Egg Laying. Egg laying is restricted to a much more discrete period in *O. virilis* than in *O. immunis,* occurring only in the spring and being very closely timed among the females of a given population. Of 27 adult females collected on May 2 and 3, 1968, from the Little Sioux River, 26 bore eggs which appeared remarkably uniform in developmental stage and had probably been laid the previous week. This is nearly a month later than the spring egg laying by *O. immunis* at Kettleson's Hogsback, but a month earlier than two *O. immunis* collected from the Little Sioux in mid-June.

Summary Comparison

The very flexible life history of the pond crayfish, *O. immunis,*

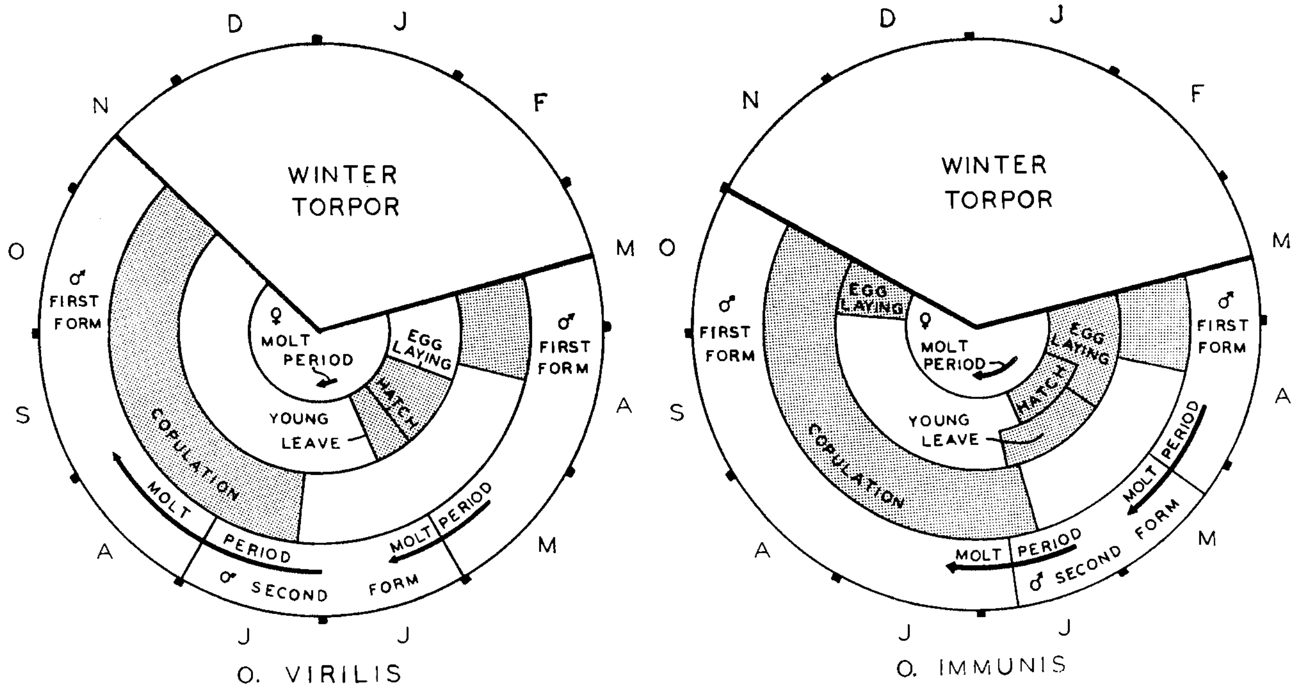

Figure 1. Diagrammatic representation of the annual cycles of *O. virilis* and *O. immunis*. Because of annual varation in seasonal temperatures and precipitation, dates indicated are representative only; the sequences of events remain constant. Outer band: sexual forms and molting periods of adult males. Second band: period of copulation, stippled. Third band: reproductive activities of adult females; period when eggs or young are carried, stippled. (In *O. virilis*, egg laying, hatching, and release of young are precisely defined as compared to more extended time ranges for these events in *O. immunis*.) Inner band: adult female molt period. Note the lag of most events in *O. virilis* as compared to *O. immunis*.

is in striking contrast to that of the stream species *O. virilis*. It is this flexibility which allows *O. immunis* to survive in the often unpredictable temporary pond habitat. Reciprocally, it is the variability of conditions among its different habitats, and from one year to another in one location, which forces this species to express its potential flexibility. The differences in annual cycles of the two species may be seen in the diagrammatic representations of Figure 1.

The flexibility of *O. immunis* occurs primarily in two aspects of its life cycle,: the length of time necessary for sexual maturation and the time of egg laying. Under favorable conditions, that is, maintainance of standing water and abundant food, *O. immunis* may mature in about four months after hatching. If drought forces burrowing at some point in the growth period, maturation is delayed until the following summer. Slowed growth and delayed maturation in the latter circumstance evidently lengthen the life expectancy of an individual.

The time of egg laying also appears to be dependent upon the presence of standing water and on the time of maturation of the ovaries. If water is present throughout the summer and fall, a majority of females can be expected to lay their eggs before the onset of winter cold, although a few whose ovaries have not become fully mature in time may still delay until spring. If the females are confined to burrows during the time when egg laying would normally occur, most or all of the population will delay its laying.

In contrast, egg laying and hatching are very closely timed within a given *O. virilis* population and occur later than in most *O. immunis* in the same area. Delayed egg laying and hatching are factors in preventing maturation at the end of the first summer in this species; maturation lags behind that of *O. immunis*. This results in a pattern similar to that displayed by *O. immunis* populations in early drying ponds where growth is retarded. The delayed egg laying in *O. virilis* could be of considerable advantage in a stream habitat, where any young which had already hatched and left the female at the time of spring floods might be more easily swept away by the rushing water than the adult.

Here, in two closely related, sympatric species with similar ranges, the basic annual cycles show striking differences. The survival value of the more flexible pattern in *O. immunis* in the rigorous and variable environment of ponded waters is as obvious as that of the more rigid pattern in *O. virilis* in the more salubrious and predictable environment of running waters.

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