Behavioral Biology of the Crayfish Orconectes virilis I. Home Range[1]

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ABSTRACT: The movements of individual crayfish, *Orconectes virilis*, were followed by hand captures of marked animals for over a year. Considerable variability was found in both the total home-range length recorded for individuals and in the capture-to-capture movement (both ranged from zero to 308 m). The average of the capture-to-capture movements was 33 m; the mode was 0-5 m (crayfish found in same grid area). Males and females did not differ in size of home-range or capture-to-capture movement, but several aspects of the data indicate that males moved more. Size was significantly correlated with movement for females but not males. Animals frequently moved farther after a molt, and many animals moved into shallow, sandy areas around the time of a molt.

INTRODUCTION

The laboratory analysis of any aspect of an organism's biology should continually be guided by knowledge of the animal in its natural environment. This is particularly true of behavior. Because of its common use as a laboratory animal both for research and teaching, and because of our own program of laboratory experiments on its behavior (Hazlett, *et al.*, in press; Heckenlively, 1970; Rubenstein and Hazlett, in press), we felt it necessary to study the field biology of *Orconectes virilis*.

Orconectes virilis is a rather well-studied animal. Roberts (1944) conducted a series of laboratory experiments on the light-related reactions of *O. virilis*, and Pearse (1909) described its sexual behavior. Some aspects of its physiology (Aiken, 1968a, 1969; Wood *et al.*, 1971) and neurophysiology (Hinkle *et al.*, 1971; Pasztor, 1969; Ringham, 1971; Taraskevich, 1971) have been investigated. This species has also been the object of a number of field observations. Pearse (1910) stated that *O. virilis* was a very abundant species in Michigan, found in lakes and larger streams. Creaser (1931) also listed it as a common species in Michigan, with a strong preference for stream bottoms with stones, under which it may hide.

Additional notes on the field biology of *O. virilis* have been supplied by a number of authors (Aiken, 1965, 1968b; Momot, 1967; Schwartz *et al.*, 1963; Threinen, 1958a, 1958b; Weagle and Ozburn, 1970). Caldwell and Bovbjerg (1969) and Bovbjerg (1970) gathered more complete data on *O. virilis* and the related *O. immunis* and, as had others, indicated that *O. virilis* was found primarily in rapidly flowing streams. Momot (1967) and co-workers (Momot and Gowing,

1972; Fast and Momot, 1973) have reported upon differential movement of male and female *O. virilis* in lakes. They found that females moved into deeper water after release of young, while males remained in shallow water until later in the season. Despite these studies, information on daily movements of individual *O. virilis* is almost completely lacking.

Several methods have been utilized to obtain information on the movements of crayfish. Merkle (1969) used radioactive tags to follow individuals of *O. juvenalis,* while Black (1963) used electroshock to collect groups of *Procambarus penni* and *P. bivittatus*. Minnow traps were used by Momot (1966) and Camougis and Hichar (1959) and by Momot (1967), Momot and Gowing (1972) and Fast and Momot (1973) to study movement in *Orconectes nais* and *O. virilis,* respectively. The above methods have an important limitation in that they do not tell the investigators exactly where the animal was in its environment prior to the treatment which resulted in its detection. This limitation does not apply to radioactive (Merkle, 1969) or sonic tags. However, the latter methods can usually be applied to only a very small sample of the total population in an area. Traps are also limited in that they provide information only on the portion of the population that is motivated to enter traps.

In the present mark-recapture study we gathered movement data on a large number of individual crayfish and at the same time characterized the exact locations within the crayfish habitat in which they were found at a given time of day or night.

MATERIALS AND METHODS

The area investigated systematically was a portion of a small stream (Fig. 1), which was below a 0.75-acre pond in the town of Pinckney in Livingston Co., southeastern Michigan. Numbers of *O. virilis* were found both in the stream and in the pond above it. The stream bottom varied in character from small stones and a few rocks to sandy or clay bottom. The section of the stream investigated was 330 m long. Markers were placed along the stream bank at 5.5-m intervals. The water entered the stream from the pond over a wooden waterfall about 1 m high. Water depth varied from 15 cm to 75 cm during the summer depending on location in the stream, but was over 2 m deep in places during spring runoff. Stream width averaged about 2 m. Several species of fish, snapping turtles and raccoons appeared to be important predators on *O. virilis* in this area.

Crayfish were caught individually by hand capture (all day captures) or with a scoop net (some night captures). The crayfish were marked individually by the pleural clip method of Goellner (1943). These clips did not appear to damage the crayfish and were clearly visible even after a molt by the animal. Pleural clips were difficult to recognize with certainty after more than two molts and thus were reaffirmed whenever an animal was recaptured after it had molted. Because of the size of the population and the rapid molting

rate of smaller size classes, only individuals over 38-mm carapace length were marked. Collecting proceeded from downstream up, thus decreasing the problems caused by turbidity from the captors walking in the stream. Usually two people worked the stream catching crayfish and a recorder on the stream bank put the information in coded form on prepared data sheets. This information was later punched on computer cards and stored in a Taxir file (Brill, 1969). A total of 4328 captures were recorded between 10 October 1971 and 27 August 1972. No collections were made between 18 November 1971 and 2 April 1972.

For each capture, the following information was recorded: date, time of day, carapace length in mm, sex, egg state if female, molt state, clip identification and location of capture. The latter data included grid marker, position in the stream (N bank, S bank, center of stream) and type of microhabitat in which the crayfish was first seen
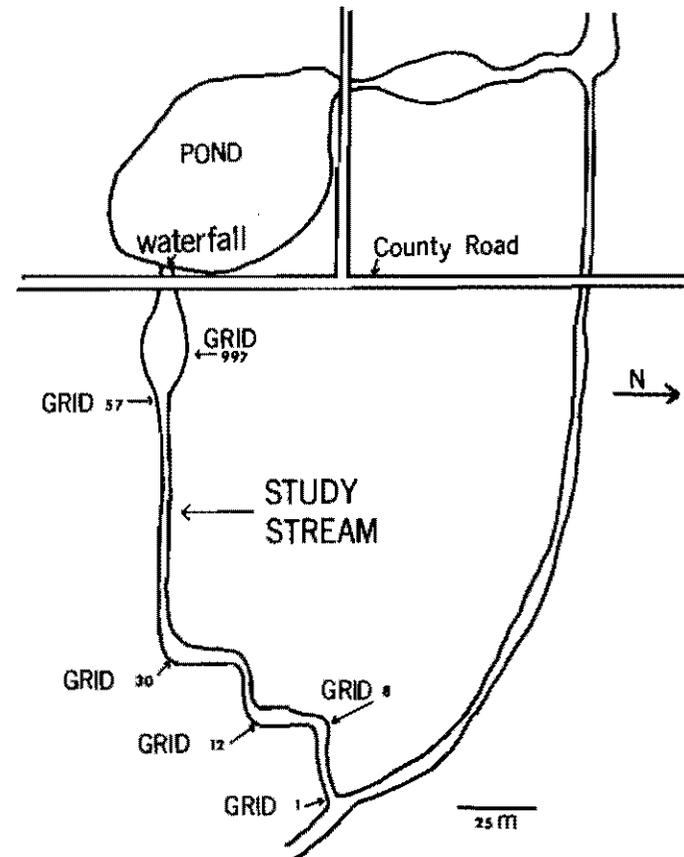

Fig. 1.—The study area in the village of Pinckney, Mich.

(and almost always captured in). The microhabitat was categorized as follows: open in stream, under bank of stream, under rock, under log, under clump of earth, in stream vegetation or in burrow. The vast majority of daytime captures were guided by touch rather than sight. The captors simply reached under rocks, logs and clumps with both hands, felt the crayfish and grabbed them. Similarly, burrows up to about 1 m long were searched with one hand, the crayfish found by touch, and removed, recorded and replaced in the burrow. The presence and capture of large snapping and musk turtles in some large burrows and overhanging bank areas made sure the reflexes of the investigators were in good form.

The majority of collections were made during the day, in the afternoon (48 out of 63 collections), but a number of collections were also made at night. Night collections were aided by headlamps and a scoop net.

By the 9th week of the summer's collections, over 90% of the animals captured on any run were previously marked and many of the unmarked crayfish had obviously recently molted into the markable size class.

Statistical analysis was aided by computer programs provided by the University of Michigan Statistical Research Laboratory. In instances where there was some question as to the equality of variance in sample being compared, Baysian probabilities were computed. The appropriate test statistics and their significance levels are presented in the Results section.

RESULTS

A feature of this population which initially brought its field biology to our attention is the large size of many individuals (Fig. 2). Crayfish of 58- to 62-mm carapace length (c.l.) were frequent in the study area, whereas the previous size record for the species was 55-mm c.l. (Pearse, 1910; Schwartz et al., 1963; Threinen, 1958a), with the exception of Creaser (1931) who said, "This species . . . frequently attains a size of over eight inches." (This equals 4 inches carapace length, or 101 mm c.l.) We found several males 64 mm c.l., one female 69 mm c.l. and a gynandromorph 62 mm c.l.

These crayfish burrowed extensively both in loose soil and in packed clay along the stream and in the pond which feeds into the stream. Laboratory observations confirmed that large individuals could burrow over 3-4 ft in heavy clay in 24 hr. A particularly interesting aspect of burrow occupation was the posture frequently assumed by these crayfish when in a burrow. With a few exceptions, these crayfish had their chelipeds blocking the burrow, often with the dactyls closed and the tips of the chelae pushed into the mud or clay bottom. Burrow captures usually involved pushing the meri of the chelipeds down in order to grasp the carapace to pull the animal out (cheliped autotomy was frequent if removal by just a cheliped was attempted). The burrow systems of O. virilis in this stream were extensive, many of them extending

beyond our reach into the banks of the stream. The burrows frequently had two entrances and interconnections, and until we had learned the systems, many individuals escaped by rapidly backing out an alternate entrance to a burrow. The conditions of such escapes suggested that the crayfish were using rheotactile cues, perhaps involving the receptor system reported by Taylor (1968). Many burrows in sod-soil areas of the stream bank had entrances opening above water level, and a surprising number of in-air captures were made. Occupation of a burrow by two crayfish was extremely rare during the period of this study.
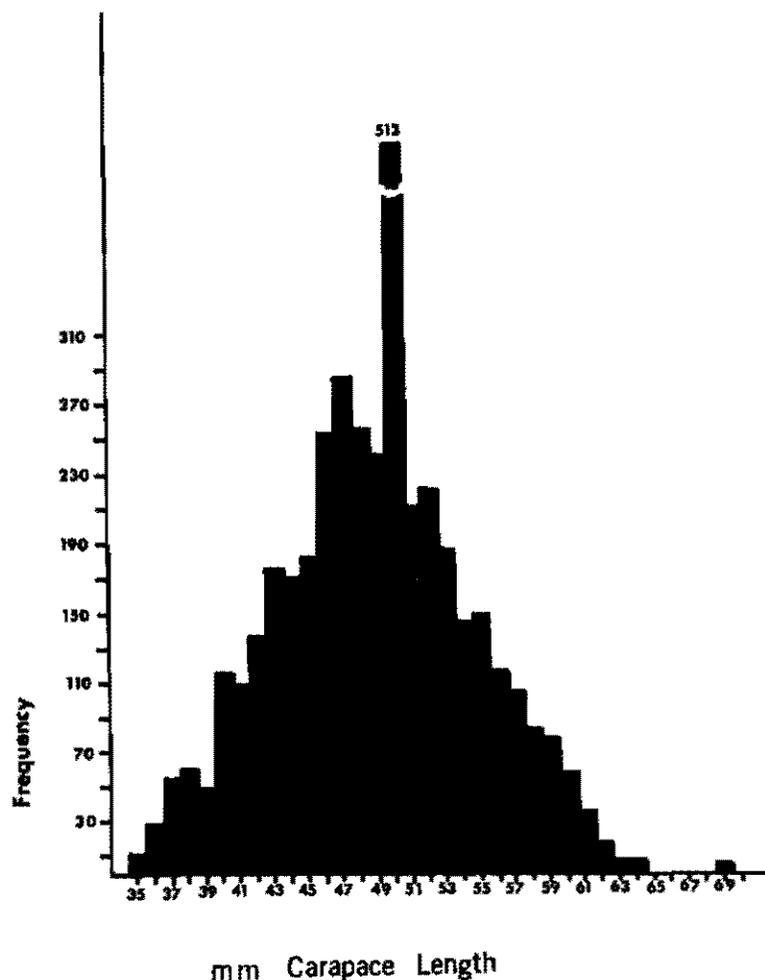

Fig. 2.—Frequency distribution of size of crayfish (carapace length) in total study sample

Copulating pairs were found occasionally, but they were under rocks or clumps of earth as frequently as in burrows.

The general behavior of these crayfish at night was particularly interesting. Whereas the majority of daytime captures were in burrows or under rocks (Fig. 3), almost all captures after 2100 hr were of animals out in the open. The crayfish were not frequent in stream
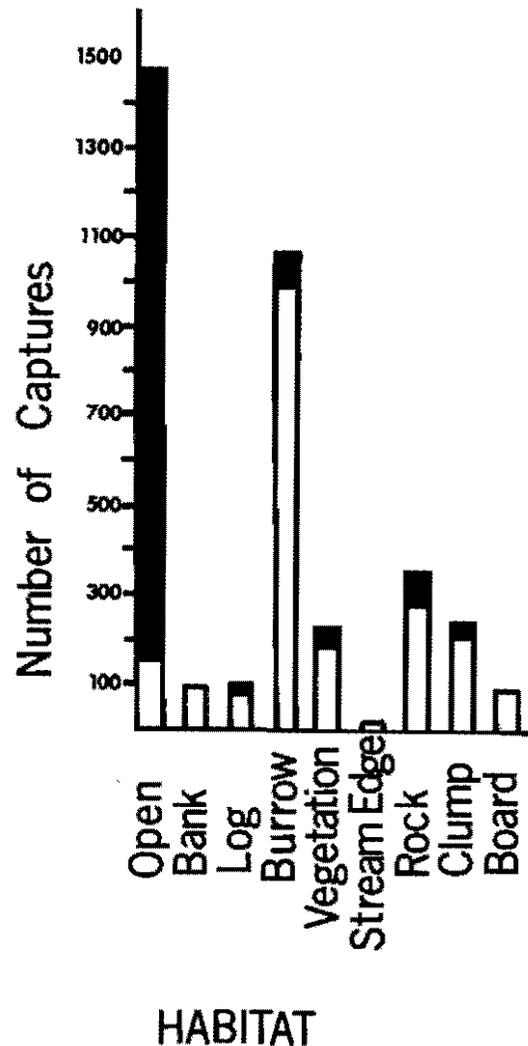

Fig. 3.—Distribution of captures by habitat. Open portions of bars refer to daytime captures, darkened portions to night captures. Stream edge refers to individuals first seen out of water, on land, near the stream edge

vegetation at night; on the contrary, most were found wandering about or, in many cases, completely motionless (until disturbed by the center beam of the headlamps) on sand bottom. Densities of 5-8 large crayfish (over 50 mm c.l.) in 1 sq m of clean sand bottom were not uncommon at night. During the early night collections (2100 to 2300 hr) we frequently found animals still covered with some clay or silt from very recent burrow occupation.

Home ranges.—The only individuals considered in analysis of home ranges were captured (1) at least four times and (2) with dates extending over at least 4 weeks. These criteria restricted us to 291 individuals (139 males and 152 females). The number of times an individual was captured varied from four to 21. They were followed for an average of 71.1 days in the case of males and 62.2 days for females ($t = 1.31$, $p > 0.10$; however, the variance was significantly higher for the males, $F = 1.51$, $p. < 0.01$). There was a significant size difference between the males (46.4 mm) and females (48.1 mm) in the "good" individuals (those fitting the above criteria) ($t = 2.44$, $p = 0.015$; no difference in variance). This is particularly interesting since in our total data sample the males (49.4 mm average) were larger than the females (48.9 mm) ($t = 2.23$, $p = 0.025$; also females were more variable in the total data sample, $F = 1.14$, $p = 0.002$). This means that the larger males tended not to be caught regularly enough to be included in the final home range analysis. We believe this is due to a tendency of large males to stay in long burrows more consistently.

The home range data for the "good" crayfish are presented in several forms. In Figure 4, the frequency distribution of the sizes of total ranges for the 291 individual crayfish is shown. Male and female data are combined since there was no difference in their means ($t = 0.51$, $p = 0.61$). The distribution of movements by individuals from one capture to the next is shown in Figure 5. Again there was no difference in male and female movements (multicell chi-square $= 1.08$, $p > 0.50$). While the average capture-to-capture movement was 33 m for females and 32 m for males, the distribution is very strongly skewed. The mode for both sexes was 0-5 m, *i.e.*, they were found in the same marker area. This suggests that crayfish frequently move very little, but when they do, it is for some distance. This general trend was apparently not the result of two clear classes (movers and
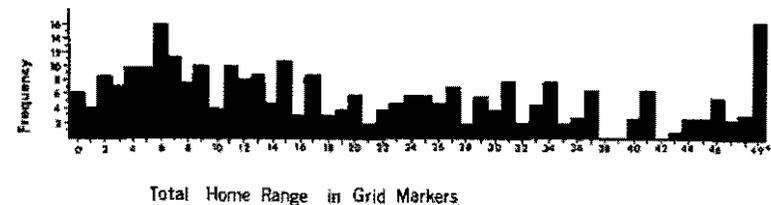

Total Home Range in Grid Markers

Fig. 4.—Frequency distribution of total home range lengths for individual crayfish in number of grid markers. Each grid area is 5.5 m long

nonmovers), since the frequency distribution of average movement per individual crayfish (Fig. 6) is not bimodal, but unimodal, skewed toward lower values.

The size of total home range did not correlate strongly with animal size (carapace length) for males (r = 0.15, p = 0.067), but was significantly correlated in the case of females (r = 0.19, p = 0.019). The relationship between size of crayfish and average capture-to-capture movement was also weak for males (r = 0.15, p = 0.083) but significant for females (r = 0.21, p = 0.011) (Figs. 7 & 8).

Since individual crayfish were followed for varying numbers of days, it is possible that some of the variance in home range size is due
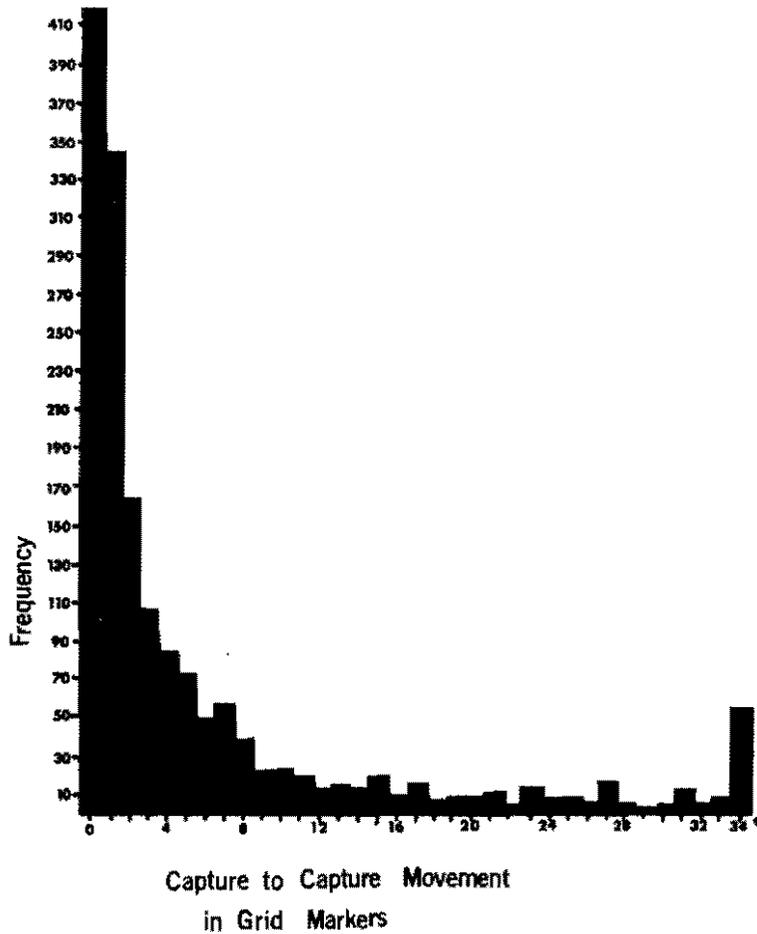

Capture to Capture Movement
in Grid Markers

Fig. 5.—Frequency distribution of capture-to-capture movement for individual crayfish

to how the data were gathered. The correlation between size of home range and how long the crayfish happened to be followed is significant (r = 0.18, p = 0.002). When analyzed by sex, however, there was no relationship apparent for females (r = 0.07, p = 0.40), while the relationship was stronger for males (r = 0.28, p < 0.001). That is, the longer a male was followed, the larger the home range recorded, thus indicating some continual shifting of location by males during the study period. Clearly, the above considerations leave most of the variance in home range size unexplained and additional factors must be sought.

Another way to express the tendency of the crayfish to stay in a limited area is to calculate the average number of days that individuals
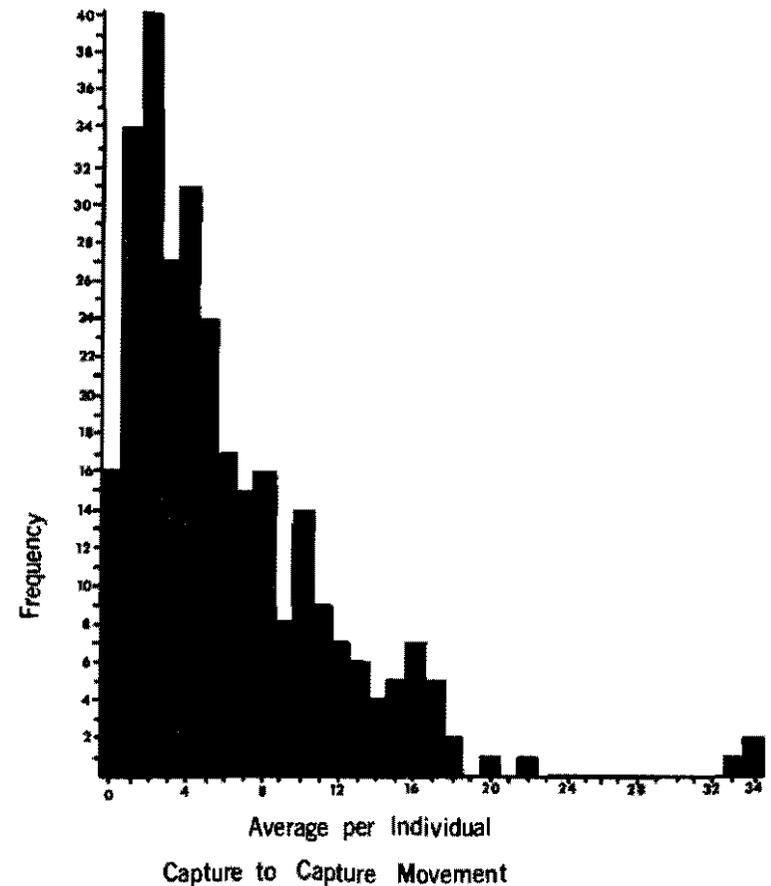

Average per Individual

Capture to Capture Movement

Fig. 6.—Frequency distribution of the averages for individual crayfish of capture-to-capture movement, in number of grid markers. Each grid area is 5.5 m long

were found in the same marker area ± one marker on either side. This averaged 17.7 days for males and 26.4 days for females (t = 2.42, p = 0.016; variance significantly higher in females, F = 9.65, p < 0.001) and ranged from zero to 68 days for males and zero to 262 days for females. There was no difference (t = 0.34, p = 0.73) in the number of times males (3.6 average) and females (3.5) were captured during a stay in the same area.

The types of habitats the individuals were caught in during these stays in one area are listed in Table 1. It would appear that females tended to be found in (stay in) burrows more consistently than males, although the most consistent individual was a male which was found in the same burrow 18 times over a period of 34 days. The large number

TABLE 1.—Distribution of habitats in which individuals were found, during the period they were found within the same grid area ± one marker

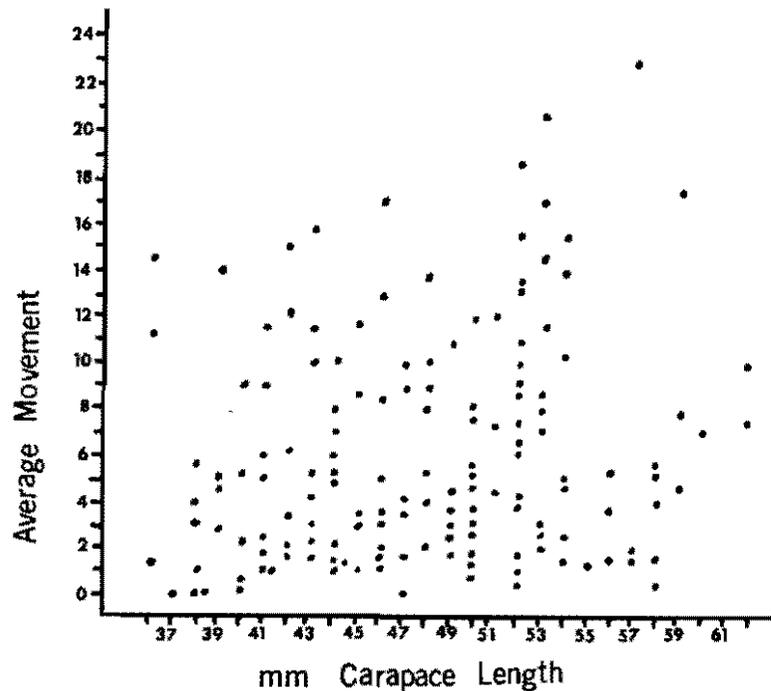|	Males	Females
Burrow	31 (21.6%)	56 (37.1%)
Open (night)	29 (23.1%)	31 (20.5%)
Variable	65 (48.5%)	49 (32.4%)
Under rock	5 (3.7%)	7 (4.6%)
Other	4 (3.1%)	8 (5.4%)

Fig. 7.—Relationship between size of female crayfish and individual average of capture-to-capture movement, in number of grid markers

of individuals occupying differing habitats means that animals could and did remain in one area of the stream even though they were not consistently remaining in one type of location. Comparing the micro-habitat distribution of the "good" individuals (Table 1) with that of the total study sample (Fig. 3), it appears that habitat occupation is similar for the two samples.

Frequently, when an animal moved it was over most of the distance recorded as its total home range. That is, most of the home range recorded for it was covered from one capture to the next. For 68.4%
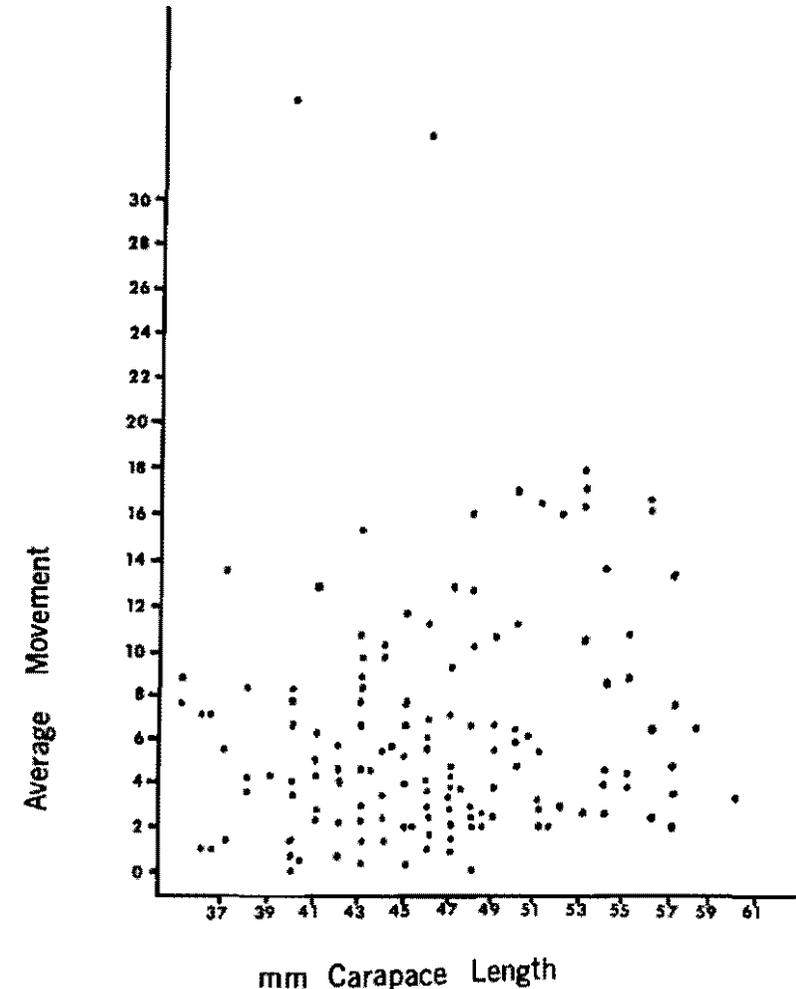

Fig. 8.—Relationship between size of male crayfish and individual average of capture-to-capture movements, in number of grid markers

of the females and 60.7% of the males, the total range, or within one marker of the total range, was covered in one capture-to-capture movement. Some movements were quite fast; one male moved 292 m upstream in just 2 days. The general direction of movements for individuals varied and was about equally distributed up- and downstream (Table 2).

A pattern we noticed a number of times was that an animal was found in the same area for some weeks, but after a molt, it was found some distance away. Not all animals could be followed this way (no molts recorded, never found again after a moult), but data on 86 males and 61 females were available (chi-square = 4.74, p < .05, comparing sexes as to proportion of animals which could be followed after a molt). Of these individuals, 72% of the males and 64% of the females moved over a considerable distance (50 m) within a week of molting *and* had been limited in their movements (same markers ± two markers) in the previous weeks. For example, a 49 mm c.l. female was marked and recaptured in October 1971 and recaptured in the same marker area in May 1972. It then molted to 52 mm and was found in June and July in an area 170 m downstream. A 44-mm male was found four times in one area in June; it molted (to 50 mm) and next was found three times in July and August in an area 66 m upstream.

Another aspect of the daily movements of these crayfish is the extent of movement from day to night. The total sample was examined for cases in which temporally contiguous day-night captures were available for individuals. A total of 457 such records (213 male and 244 female) were present in the data sample. The average day-night movement was 4.4 markers or 24.2 m, less than the average capture-to-capture movement when time of capture was not considered. There was no significant difference between the sexes in the average extent of day-night movement (3.6 markers for males, 5.0 markers for females, t = 1.94, p < 0.05). For both sexes, about one quarter of these day-night records involved capture in the same grid area. Where there was a difference between day and night location of capture, slightly more cases involved a night location downstream of the daytime location than the reverse. However, for neither sex was there a significant difference in the extent of movement downstream (at night) compared to upstream.

Of particular interest was the frequent case of night location (movement into) in one area of shallow water (#997) just down-

TABLE 2.—General direction of movements for individual crayfish. "None" indicates an average movement for a crayfish of two grid markers or less

	Males	Females
None	40 (28.7%)	56 (36.8%)
Downstream	30 (21.5%)	27 (17.7%)
Upstream	38 (27.3%)	29 (19.1%)
Down and upstream	31 (22.5%)	40 (26.4%)

stream from the culverts (Fig. 1). A large portion of the night captures were in this area, and 37 female and 19 male cases of movement into area 997 at night were present in the data sample (chi-square = 5.7, p < 0.025, for sexual difference being by chance).

Another aspect of the movements revealed by examination of day-night capture locations was the frequent occurrence of day-night-day or night-day-night captures in which the repeated time = capture = location was the same. Among 69 records of such sequences, in 44 cases the repeated time = capture = location was the same and in 25 cases the repeated time = capture = location was different. For example, a 54-mm c.l. female was captured twice in burrows in grid area 47 during the day and in the open in area 45 at night, 1 day before the second daytime capture. Similarly, a 42-mm c.l. female was captured twice in area 32, in the open at night, and in a burrow in area 35 during the day between night captures. The pattern of these sequences indicates that crayfish are moving up- or downstream, in the open at night, and returning to the same daytime area (and usually occupying a burrow). Conversely, some records show crayfish returning to the same night area, some meters from a daytime location. How these animals orient during these movements (sometimes over 25-m distance) is an open question.

Variation within the study area.—Although our study was confined to one portion of one stream, this area was not uniform in its physical features. When the data are examined by grid location, certain interesting differences are apparent. First, there are very significant differences in the average size of crayfish caught in different grid areas (one-way analysis of variance gives p < 0.0001). The mean size of animals was smaller at the E end of the study area, one section of thick vegetation and at the W end of the study area. Larger animals were found especially in four grid areas which were portions of the stream, with loamy soil or clay banks permeated by extensive burrow systems.

Consideration of the captures by sex in the various areas reveals three distinct regions. The downstream area (grid areas 1-27) contained a majority of females, 61.3% of the 1194 captures (chi-square = 30.5, p < 0.005, assuming a null hypothesis of equal numbers of males and females). The middle portion of the study area (grid areas 28-50) contained a majority of males, 61.6% of the 1428 captures (chi-square = 166.0, p < 0.005), while the upstream portion (areas 51-999) contained a majority of females, 58% of the 1612 captures (chi-square = 18.1, p < 0.005).

Looking at the percentage of intermolt animals, grid area 997 (44% intermolt) constitutes one main area of interest. Compared with the percentage of intermolt animals outside this area (62.3%), the lower proportion of intermolt captures is very significant (chi-square = 37.8, p < 0.005 comparing area 997 with other areas). Since the "resident" animals (*see below*) cannot account for the high frequency of premolt, postmolt and molting animals present, it is clear that animals move into area 997 just before or just after a molt.

The high percentage of intermolt animals in the culverts above area 997 (95% and 89% intermolt) shows that the movement associated with a molt is not just upstream, but apparently to this specific area.

Examination of the proportion of daytime captures by grid shows that certain areas, with higher proportions of daytime captures, had good burrow systems which were regularly productive. The areas with particularly low proportions of daytime captures had few burrows but either organic-rich mud or clean sand bottom.

The degree to which animals were found in the same area on successive captures varied greatly from area to area. The number of animals with repeated captures in the same grid area was divided by the number of captures of nonresident animals, and multiplied by 100 to give percentage residency. The areas of higher residency were almost all areas of extensive burrow systems. The exception is area 997, which had some burrows dug under the root systems of vegetation, but displayed a high residency value due, in large part, to repeated night captures.

DISCUSSION

The movements of any organism in its environment are bound to be complex. This is particularly true when the organism undergoes periodic cycles of growth, such as molting. Our data on this population of *Orconectes virilis* indicate that the movements can indeed be complex. Many individuals stayed in the same area, often the same burrow, for a number of weeks. Thus if one followed only a few individuals, one could conclude that crayfish are stationary. Data from a larger sample, however, show that some individuals are stationary for a while and then move some distance, while other crayfish are not stationary, at least during any part of the period they were followed.

The high level of marked animals found during the later portion of the study (over 90% of the crayfish found were previously marked) is noteworthy when compared to other mark-recapture studies of crustacea. George (1965), in a survey of such studies, mentions 23% recapture as the highest rate. However, most such studies deal with either quite mobile species and/or very large populations in an "unbounded" portion of an aquatic environment. While most of the crayfish were not found during each collection (presumably in burrows beyond our reach), the animals we found were clearly part of a resident population that for the most part stayed in the study area.

The average distance moved from capture-to-capture (33 m) seems to indicate rather large movements for a small animal. However, the average is not a good descriptor for a highly skewed distribution. By far the most common distances moved were small (less than 5.5 m); yet distances much greater than the average (over 66 m, for example) were also common (245 instances).

These data agree in general with those of Merkle (1969) on the movements of *Orconectes juvenalis*. With a limited data sample (n = 5), she found considerable variability in home range length (9.4 to 47.0 m) over a 25-day period. As in our own population, she noted a

tendency to stay in a very limited area for some days, as well as movement to a new area. Within the sample available, Merkle found no correlation between home range size and animal size or sex. Camougis and Hichar's (1959) study of *O. virilis* in a pond in Massachusetts indicated rather common movement of crayfish over the entire pond (45 x 180 m), which agrees, in general, with our data. Goellner (1943) also reported rather long movements (130 m) in some individuals of *O. immunis*.

Our data on direction of movement for *O. virilis* agree with Goellner's (1943) observations on *O. immunis*, where movements were rather equally distributed in direction. In his study of *O. nais* in an Oklahoma stream, Momot (1966) found primarily upstream movement. However, Momot's population experienced large variations in water level (flooding) and as we observed (unpubl. data), this greatly influences movement of crayfish. The spring downstream and autumn upstream movements reported by Henry (1951) for *Pacifastacus klamathensis* are not obvious for our population of *O. virilis*. In their study of movements of *O. virilis* in lakes, Fast and Momot (1973) suggest that aggression by large males forces females into deeper water. Such a pattern does not appear likely in the stream population we studied.

The differences in movement data of male and female *O. virilis* in our study were real but small. Thus, they would be best detected in a quantitative study of many animals, rather than by limited data. Clearly there were no differences in size of home range or in the average capture-to-capture movements of males and females. However, females did tend to be found in one area longer (and there was no difference in the total length of time individuals were followed). Thus, when females moved, they moved farther than males, yet they tended to remain in one area longer. The most interesting sexual difference was that there was no correlation between animal size and extent of movement for males, but there was a significant correlation for females. This means that other factors, as yet unmeasured, must account for more of the variance in movement in the case of males. The positive correlation for males between size of home range and length of time followed and the shorter length of time found in one area indicate more frequent movement from one area to another in the case of males, although the extent of movement was not different for the sexes.

The significant size and sex differences along the length of the study area are difficult to explain but at least indicate a mating system quite different from that reported for *Procambarus* (Payne, 1972), where male-female pairs occupying single burrows for extended periods is the norm. The variables most clearly affecting an understanding of home range are residency and intermolt frequency by grid. The areas of highest residency had loamy soil or clay banks which were extensively burrowed in, rather than sandy soil and/or very low sloping banks. Thus, the average home range size of crayfish should be smaller

in loamy soil or clay bank areas. In this way, home range size could be used as a measure of environmental adequacy for the species studied. The movement of crayfish into shallow, low-flow, sandy areas (such as 997) about the time of a molt and the subsequent frequent movement of recently molted crayfish into new areas indicate some of the more obvious complexity of daily movements in these arthropods. These complexities will result in the measurable home range size of individuals being larger than if such "special" movements did not occur. Whether the movement of molting animals to one part of the environment is related to the strictly physical features of such areas (higher temperatures by 3-4 C, lower flow rate, presence of fine sand that could replenish the grains in the statolith organ) or to correlated biological features (particular type or quantity of vegetation, social aggregation of postmolt animals) can only be elucidated by additional observations and experiments.

It is not clear why crayfish often move from one area to another after a molt. In 46 cases we could document, individuals did not move after a molt. These crayfish can easily enlarge a burrow to accommodate any increase in size which occurs at molting. Moreover, after the first few weeks of summer collections, all the burrows were as wide as our arms, thus no immediate tactile feedback from "an undersized burrow" would be available to a postmolt animal. The actual process of molting often took place in burrows, judging from the captures we made of very soft individuals and the location of recently shed exoskeletons. This is logical in view of the defenseless condition of recently molted crustacea. Also, ovigerous females tended to stay in burrows more regularly and, as their eggs matured, females tended to be found in the deepest parts of burrows. Similar tendencies have been noted for *O. immunis* (Tack, 1941) and *Procambarus hayi* (Payne, 1972).

The fact that these crayfish dug and occupied burrows at all is in contrast to the published accounts for *O. virilis*, although Lunt (pers. comm.) has observed burrowing in Illinois populations. Caldwell and Bovbjerg (1969) and Bovbjerg (1970) report that this species does not burrow extensively, and Aiken (1968b) reported no burrowing activity at all, after specifically looking for such behavior in the field. In our study, burrows in heavy clay were often shorter than burrows in loose soil, but activity in both soil types was frequent. Burrow construction and maintenance by young crayfish (under 10 mm c.l.) were frequently observed in sandy areas of the stream. The contrast in burrowing behavior in Aiken's (1968b) study and ours could be due to differences in the behavioral repertoires of the crayfish populations studied; however, it is more probably a result of habitat differences. The river in Aiken's study had a bottom made of rocks and mud, while the most heavily burrowed areas of our stream were clay or loam banks. Where the stream bottom was rocky-sandy or muddy, no large burrows occurred.

The variability in the movements of these crayfish makes any de-

scription of a typical individual tenuous. However, for many of these crayfish, the following may apply. During the day, individuals are rather quiet in burrows or under rocks; at night they may come out into the stream bed. They return to a burrow in the same area during the day, although, particularly after a molt, the crayfish may move 50-200 m during several nights of movement. The crayfish may remain in the new area of the stream for some weeks, again occupying a burrow by day and wandering in the open stream at night. Such a pattern of movement leaves open further study of social structure of this species in the field. Whether individuals show transient territoriality and/or some form of hierarchy, as reported for laboratory situations (Bovbjerg, 1953), can be elucidated only by additional field observations.

Why these crayfish are nocturnal (as also reported by Bovbjerg, 1970 and Roberts, 1944) is puzzling in view of the (1) nocturnal activity of some of their major predators (raccoons, snapping turtles) and (2) feeding habits of *O. virilis.* Direct field observations and gut analyses indicate this species is an omnivore which feeds predominantly on vegetation. Work in progress indicates that the (nocturnal) movement of the crayfish into the open in the stream may be associated with acquisition of special items, *i.e.,* not the main food in their diet.

Field experiments on the factors influencing daily movements in this population will be reported in another paper.

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