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Aggressive interactions, shelter competition, and mating interference as potential mechanisms relating to species displacement among crayfish of the genus *Orconectes*

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AGGRESSIVE INTERACTIONS, SHELTER COMPETITION, AND MATING
INTERFERENCE AS POTENTIAL MECHANISMS RELATING TO SPECIES
DISPLACEMENT AMONG CRAYFISH OF THE GENUS ORCONECTES

A Thesis

Presented to

The Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of
Master of Arts

by

Barbara Mansfield Munjal

1980

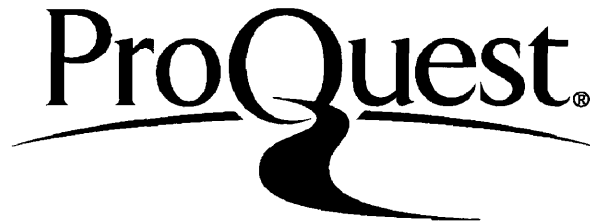
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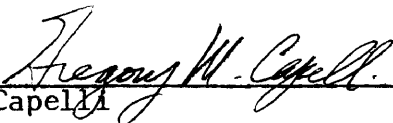
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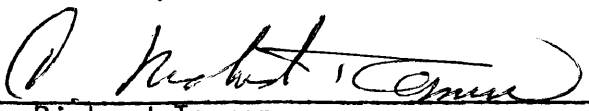
Approved, April 1980



Gregory M. Capella



Mitchell Byrd



C. Richard Terman

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ABSTRACT

Using laboratory experiments, I tested the hypothesis that aggressive interactions and competition for shelter and mates might be potential mechanisms accounting for the displacement of Orconectes virilis by O. propinquus, and of both these species by O. rusticus, in Wisconsin. In aggressive interactions in the absence of shelter and in competition for shelter, results were consistent with the hypothesis: O. rusticus was usually dominant, with O. virilis least successful and O. propinquus generally intermediate. However, when crayfish were allowed to compete in an experiment designed to duplicate natural shelter conditions more closely, no competitive exclusion occurred. In mating experiments, O. rusticus mated approximately as often with females of the other species as did males of the other species, but males of the other species mated proportionately much less frequently with O. rusticus females. This suggests that hybridization or other forms of mating interference differentially favoring O. rusticus may be important in the species displacements.

AGGRESSIVE INTERACTIONS, SHELTER COMPETITION, AND MATING
INTERFERENCE AS POTENTIAL MECHANISMS RELATING TO SPECIES
DISPLACEMENT AMONG CRAYFISH OF THE GENUS ORCONECTES

INTRODUCTION

Crayfish (Decapoda, Cambaridae) are a common component of lake and stream communities throughout most of the United States. In some lakes crayfish standing crop may be several times that of all other benthic fauna combined (Momot, 1967). Recent studies suggest that crayfish, because of their ability to utilize biomass from various trophic levels, have a significant potential for influencing both the structure of aquatic communities and energy flow pathways when their numbers are large (Flint and Goldman, 1975; Langlois, 1935; Abrahamsson, 1966; Dean, 1969; Taub, 1972; Capelli, 1975; Magnuson et al., 1975).

In the extensive lake district of northern Wisconsin (including all of Vilas county and portions of surrounding counties), seven species of crayfish occur, but three are by far the most abundant: Orconectes virilis (Hagen), O. propinquus (Girard), and O. rusticus (Girard) (Capelli, 1975; Fig. 1). Circumstantial evidence strongly suggests that O. virilis is native to the area, or, at least, was the first species to colonize the area sometime after the retreat of the last glaciers approximately 10,000 years ago (Creaser, 1932; Capelli, 1975). O. propinquus, however, was probably introduced about fifty years ago, and O. rusticus was almost certainly intro-

Fig. 1. Three species of crayfish of the genus Orconectes, used in this study.

a) O. rusticus (left) and O. virilis

b) O. propinquus

c) (top to bottom) O. propinquus, O. rusticus, O. virilis



a



b



c

duced, probably about thirty years ago (Capelli, 1975). Nothing is known for certain of the ways by which introductions have occurred but a likely mechanism for the two most recent invaders involves use of crayfish as bait by fishermen from more southerly regions (Capelli, 1975). Presumably such introductions are still occurring. In addition, however, both O. propinquus and O. rusticus appear to be extending their ranges within northern Wisconsin via displacement of O. virilis along natural waterways (Capelli, 1975).

In general, O. propinquus appears to be able to displace O. virilis and O. rusticus appears to be able to displace both O. virilis and O. propinquus (Capelli, 1975). The situation is complicated by apparent hybridization between O. rusticus and O. propinquus in some lakes (Capelli and Capelli, 1980).

The replacement of the other two species by O. rusticus may be particularly significant in regard to effects on community structure. Strong circumstantial evidence indicates that in many areas where O. rusticus has become abundant macrophytic vegetation has declined drastically (Capelli, 1975, plus unpublished data). No data exist, however, on the effects of such reduction on other community components, such as young fish, which utilize the macrophytic vegetation for shelter.

All three species are similar in general habitat preferences: clear, well-oxygenated water with a firm (usually rocky) substrate (Crocker and Barr, 1968; Capelli, 1975). Capelli (manuscript in

preparation) examined the relationship of numerous physical-chemical variables to crayfish abundance and species composition in 70 lakes. Although physical-chemical factors varied somewhat in their importance to the abundance of individual species, all three species exhibited considerable overlap in habitat preference and important controlling variables.

Species tend to be isolated on a lake to lake basis. In most lakes, only one species is present; in lakes with more than one species, one species is always at least several times more abundant than the others (Capelli, 1975, plus unpublished data). These observations are consistent with the competitive exclusion principle which predicts that ecologically similar species will not be able to coexist, assuming some kind of resource limitation. However, nothing is known of the actual mechanisms preventing coexistence or allowing displacement among these species.

Crayfish are aggressive animals and, at least under laboratory conditions, will establish definite dominance hierarchies (Bovbjerg, 1953). A number of factors affect agonistic behavior. Dominant crayfish tend to be larger and/or Form I males.¹ Form II males

¹In most crayfish species, the adult males alternate via molts between recognizable morphological forms, known as Form I and Form II. The most conspicuous differences between the two involve the anatomy of the copulatory stylet. Mating occurs only in Form I; such individuals are also generally considered to be more aggressive than those in Form II.

(nonbreeding form) and immature males are similar to females in exhibiting a generally reduced level of aggressive activity, and poorer competitive abilities in aggressive encounters. Females tend to respond to aggressive encounters with sexually mature males more passively than if the encounter had occurred between individuals of the same sex (Mason, 1970; Bovbjerg, 1956; Ameyaw-Akumfi, 1976; and Pippitt, 1977).

Extrinsic factors can also affect levels of aggression. Up to a point, the higher the population density, the more frequent the aggressive encounters become (Bovbjerg, 1956); this is probably due to increased visual and tactile contacts.

Competitive exclusion, involving a number of mechanisms, has been suggested as an explanation for several of the observed distribution patterns among other crayfish species (Aiken, 1965; Fitzpatrick, 1967; Capelli, 1975; Rhoades, 1944; Eberly, 1960; Penn and Fitzpatrick, 1963; Crocker and Barr, 1968; and Bovbjerg, 1970). In some cases (Penn and Fitzpatrick, 1963; Bovbjerg, 1970) direct aggressive interaction between species has been suggested as an important competitive mechanism maintaining existing distribution patterns or allowing species displacements. In these studies evidence for the importance of aggressive interactions has been based on laboratory experiments involving direct "fight" type encounters, or competition for resources such as substrate in highly simplified environments.

To determine the extent to which behavioral interactions might account for, or are consistent with, the observed species displace-

ment in northern Wisconsin, I studied aggressive interactions, competition for physical resources (shelter and substrate type), and competition for mates among O. propinquus, O. virilis, and O. rusticus under laboratory conditions. Based on the field data described above, my general working hypothesis was that O. propinquus should be able to outcompete O. virilis, and O. rusticus should be able to outcompete both O. propinquus and O. virilis (O.r. > O.p. > O.v.).

I. MATERIALS AND METHODS

Crayfish were collected in Vilas County, Wisconsin and shipped via air to Williamsburg, Virginia, where they were maintained in 150-400 liter aquaria containing filtered, aerated water. Temperature was maintained at 15^oC. Photoperiods were continually adjusted to approximate conditions in Wisconsin. Dim night lighting, just sufficient to allow an acclimated observer to see adequately, was left on continuously. Tetramin was provided as food.

Crayfish were kept separated by species and sex. Only Form I males and adult females were used in experiments. Most individuals were approximately 30 mm carapace length;² none were smaller than 25 mm. In all competition experiments, competing individuals differed in size by no more than 1 mm carapace length. When individual identification was necessary crayfish were marked using either Liquid Paper or nailpolish on the dorsal side of the carapace or on the chelae.

Experiment 1: Aggressive Interactions in the Absence of Shelter.

Round plastic pans (24 cm diameter) were filled with 2500 ml of water

²Carapace length, measured from the tip of the rostrum to the beginning of the abdomen on the dorsal side of the animal, is the most commonly used index to size for crayfish. In most species it is very close to 0.5 total length.

(depth = 9 cm) (Fig. 2). Two male crayfish of different species were placed in each pan. Food was not provided. Crayfish were allowed to acclimate for 24 hours. After 24 hours, each pair was observed until at least five interactions were recorded. Following Bovbjerg's methods (1952), interactions were classified as threat, strike, fight, or avoidance (collectively known as tension contacts). In each tension contact, one individual could be classified as dominant and the other as subordinate. The "winner" for each pair was based on the number of dominant versus subordinate contacts. Within a given experiment involving a particular species combination, no individuals were used in more than one trial.

Similar experiments were run using either three males or three females per pan, each of different species.

All data were taken during daylight hours.

Experiment 2: Competition for Shelter. Pans identical to those used in experiment 1 were provided with shelters. Shelters consisted of plastic drinking tumblers cut in half (length = 10 cm, height = 3 cm when placed on the bottom of the pan) (Fig. 3). Only one crayfish could occupy the shelter at a time without close physical contact. Food was not provided.

To determine preference for the shelter by the crayfish, single individuals were placed in each pan. After a fifteen hour acclimation period individuals were checked once an hour for ten hours and recorded as being either in or out of the shelter.

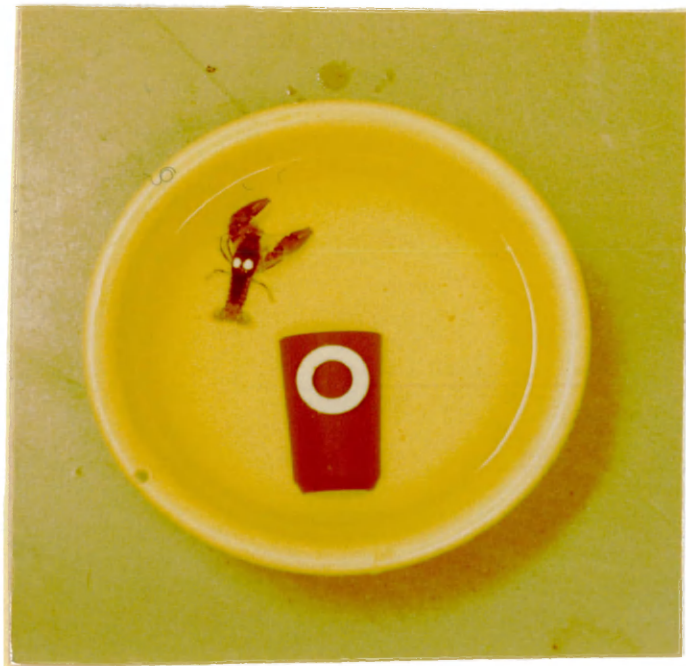
Fig. 2. Pans used in experiments on aggressive interactions among crayfish. Note contact between two crayfish in pan.



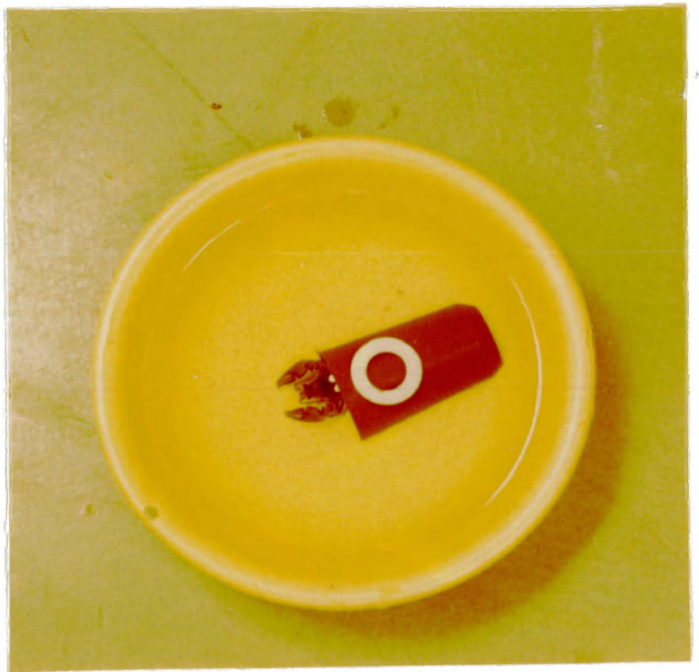
- Fig. 3. a) Closeup view of shelter made from drinking tumbler cut
in half.
- b) Overhead view of shelter in pan with crayfish.
- c) Overhead view of crayfish in shelter in pan.



a



b



c

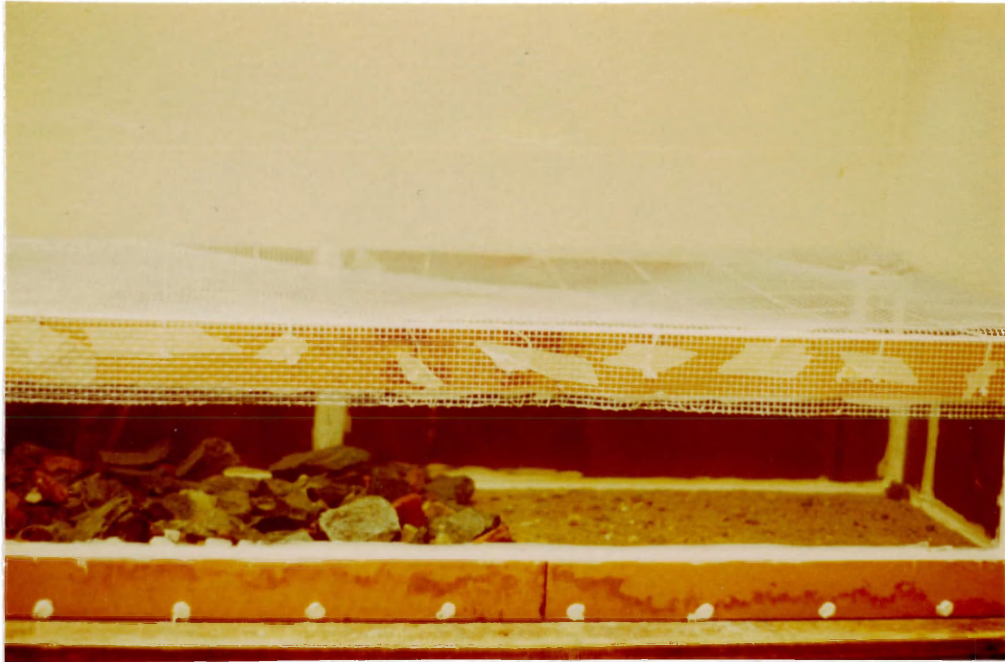
In competition experiments, two crayfish of different species were placed in each pan. After fifteen hours, data were taken once an hour for ten hours on which species occupied the shelter. Similar experiments were run using three individuals each of a different species. Within a given experiment involving a particular species combination, no individuals were used in more than one trial.

Experiment 3: Competition for Shelter with One Species Given a Time Advantage. Crayfish were paired and experiments were run as described in Experiment 2. However, in each case one individual was placed in the pan twelve hours before the other. Data on shelter occupancy were taken once an hour for ten hours beginning one hour after the second crayfish was introduced. Because of natural mortality among experimental crayfish, only combinations involving *O. rusticus* - *O. virilis* and *O. rusticus* - *O. propinquus* could be tested.³

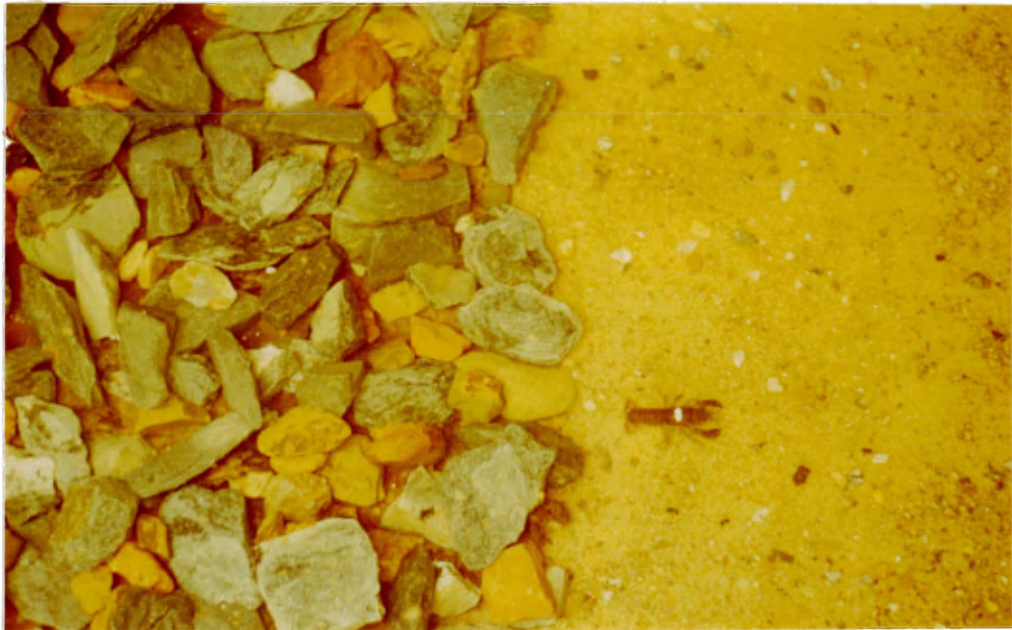
Experiment 4: Competition for Preferred Substrate. The substrate of a large tank (135 cm long x 60 cm wide x 20 cm high) was divided into two equal halves: one consisting of sand and the other of larger rocks and gravel (Fig. 4). Only the rock and gravel half provided any potential shelter. To determine substrate preference under monospecific conditions ten individuals of each species were dropped into the center of the tank and allowed 15 hours to acclimate. Data were then taken once an hour for ten hours on the substrate

³This experiment was actually conducted last among those described here.

Fig. 4. a) Side view of experimental tank used in substrate preference/displacement tests.
b) Overhead view of same.



a



b

type occupied by each individual. Similar experiments were then run in which two or three species were tested together. In the latter experiments, ten individuals of each species were used so the total number of crayfish in the tank was either twenty or thirty.

Experiment 5: Competition for Mates. A 162 liter tank (135 cm long x 60 cm wide x 20 cm high) was provided with a substrate of sand with scattered rocks and gravel. In each experiment, ten females of a given species, ten males of the same species as the females, and ten males of a different species were placed in the tank. Females used were generally a few millimeters carapace length smaller than males since males tend to mate most readily with slightly smaller females (Stein, 1975). All males had been separated from females for at least 4 days.

All crayfish were marked for individual recognition. At approximately one hour intervals for the next ten to fifteen hours, the tank was checked and matings in progress were recorded. Observation periods extended into early night hours. Experiments were continued the following day so that a total of twenty to thirty checks were made. Since crayfish matings typically last for long periods (0.5 to 5 hours), this observation method probably detected most mating that occurred during the twelve to fifteen hour observation period each day. Very brief matings and matings occurring in early morning hours were missed. However, I am assuming that such matings were not significantly different from those represented in my subsample.

II. RESULTS

Experiment 1: In almost every crayfish pair one individual was clearly dominant and the other subordinate after 24 hours, i.e., almost always, all five tension contacts used to determine a "winner" were won by the same individual. Results are generally consistent with the hypothesis that O. rusticus should do best and O. virilis should be at the greatest disadvantage (Table 1). In experiments involving paired males, both O. rusticus and O. propinquus won fourteen out of fifteen trials with O. virilis.

Results with O. propinquus/O. rusticus pairs are less clear-cut. When 30 mm males were used, neither species showed a significant advantage; when 25 mm males were used, O. rusticus won the majority of encounters but the results were still not quite significant at the .05 level.

In experiments involving three crayfish per pan, with both males and females, results were also consistent with my hypothesis (Table 2). O. rusticus was dominant most of the time with only a few instances of second place finishes, or even more rarely, third.

Table 1. Results of dominance tests among paired male crayfish¹, in the absence of shelter. Probabilities are based on the binomial distribution and refer to the likelihood of obtaining the given results if the null hypothesis (no difference in competitive ability between species, i.e., the probability of either species being dominant in a given pan is .5) is true.

¹In this and succeeding tables, species names are abbreviated as follows: Or = O. rusticus, Op = O. propinquus, Ov = O. virilis.

Pairing	Size (mm)	n	Dominance Results	p
Or - Ov	30	15	Or:Ov = 14:1	< .001
Or - Op	25	17	Or:Op = 12:5	.072
Or - Op	30	15	Or:Op = 8:7	.500
Op - Ov	30	15	Op:Ov = 14:1	< .001

Table 2. Results of dominance tests among groups of three crayfish. Probabilities are based on the binomial distribution and refer to the likelihood of obtaining the observed number of first place finishes for O. rusticus if the competitive abilities of all three species were the same (i.e., if the probability of an O. rusticus "win" were 0.33). n = number of groups of 3 crayfish.

		Dominance			
		Rank	Or	Op	Ov
♂ n = 15	First	12	2	1	(p < .001)
	Second	2	11	2	
	Third	1	2	12	
♀ n = 11	First	7	4	0	(p < .005)
	Second	3	4	4	
	Third	1	3	7	

O. propinquus usually finished second, especially among males, but occasionally ranked first or third. O. virilis was at the bottom of the hierarchy most of the time. Results were statistically highly significant.

Experiment 2: Both sexes of all species showed a strong preference for the shelters when tested individually (Table 3). Although data were not taken until fifteen hours after the crayfish had been introduced to the pans, I noted that most individuals entered the shelters within minutes after being placed in the pans.

Results for groups of two and three crayfish are summarized in Table 4. In most cases one crayfish was in the shelter and the other was outside the shelter when data were taken. Hence, the sum of the observed occurrences "alone in shelter" at the right hand side of Table 4 is usually close to the total number of observations made (= 100). In most cases when neither individual could be categorized as "alone in shelter", it was because both were outside the shelter. The only exception was among the 25 mm pairs of O. rusticus and O. propinquus. In this experiment the "alone in shelter" categorization was appropriate to only 60 of the 100 observations. During most of the other observations both crayfish occupied the shelter.

Overall, these results are consistent with my hypothesis. Among paired individuals O. propinquus dominated O. virilis in shelter occupancy and O. rusticus dominated both O. propinquus and O. virilis.

Data from groups of three crayfish are also consistent with the hypothesis. In all cases, the number of shelter occupancies by the

Table 3. Shelter occupancy of crayfish tested singly for various species, sex, and size groups (10 crayfish x 10 observations/crayfish = 100 observations for each group).

	Species	Size (mm)	# obs. in shelter/100 obs.
♂	Or	25	100
	Or	30	100
	Op	25	100
	Op	30	95
	Ov	30	100
♀	Or	30	99
	Op	30	98
	Ov	30	100

Table 4. Results of shelter occupancy tests among various groups of crayfish. In all cases the number of occupancies of the dominant species were significantly greater ($p < .01$) than that expected if the competitive abilities of each species were equal.

	Pair/Group	Size (mm)	n	Alone In Shelter
♂	Or - Ov	30	10	Or:Ov = 87:10
	Or - Op	25	10	Or:Op = 45:25
	Or - Op	30	10	Or:Op = 95:3
	Op - Ov	30	10	Op:Ov = 73:22
	All Three	30	10	Or:Ov:Op = 95:2:1
♀	Or - Ov	30	10	Or:Ov = 82:14
	Or - Op	30	10	Or:Op = 86:14
	Op - Ov	30	10	Op:Ov = 74:20
	All Three	30	10	Or:Op:Ov = 60:30:4

dominant species was statistically significantly higher than that of the subordinate species.

Experiment 3: When O. rusticus was given a twelve hour advantage, it continued to dominate in shelter occupancy, as expected (Table 5). When either of the other two species was given a time advantage, O. rusticus still occupied the shelter to a significantly greater extent.

Experiment 4: Table 6 summarizes results of substrate preferences for various sex, species and size groupings, both alone and in combination with other groupings. When single groupings of crayfish were alone in the tank, individuals spent most of their time in the cobble area which provided shelter, although 30 mm O. propinquus males were found on the sand close to half the time. My hypothesis would predict that when certain groupings were placed together in the tank, some displacement, i.e., an increase in the number of observations on sand, might occur in one or both of the groups. For example, O. rusticus might be expected to cause an increase in the number of observations on sand for either of the other two species. However, significant increases did not occur except for O. propinquus females in the presence of O. virilis females and in the presence of both O. virilis and O. rusticus females. Even when twenty or thirty crayfish were present in the tank (Corresponding to a density of 25/m² and 37/m², respectively --- much higher than typical maximum natural densities of about 15/m²), crayfish apparently found adequate shelter on the cobble substrate.

Table 5. Results of shelter occupancy tests among male crayfish, when one species was given a 12-hour advantage. The first species indicated in each pairing is the one given the time advantage. In all cases, results are significantly different ($p < .01$) from those expected if competitive abilities were equal.

Pairing	Size (mm)	n	Alone In Shelter
Or - Ov	30	10	Or:Ov = 96:4
Ov - Or	30	10	Or:Ov = 87:13
Or - Op	25	10	Or:Op = 73:17
Op - Or	25	10	Or:Op = 58:28

Table 6. Substrate occupancy among groups of crayfish, when given a choice of sand vs. cobble, for various species, sex, size groups alone and in the presence of other species. * indicates a significant increase in number of observations on sand in comparison with the number of observations on sand when the given species was alone ($p < .05$, chisquare test for 2 x 2 contingency table).

		<u># obs. on sand/100 obs.</u>					
	Species	Size (mm)	Alone	With Or	With Op	With Ov	With both
♂	Or	25	5	--	5	--	--
	Or	30	14	--	14	6	18
	Op	25	23	34	--	--	--
	Op	30	42	46	--	26	28
	Ov	30	14	5	8	--	7
♀	Or	30	6	--	7	6	5
	Op	30	9	12	--	30*	19*
	Ov	30	1	2	0	--	2

Experiment 5: Table 7 summarizes mating results among the various male and female combinations of crayfish. When O. propinquus females were present, O. propinquus males mated with them, but O. rusticus males also mated with them just as often (Table 7 a). However, when O. rusticus females were present with the same combination of males, O. rusticus males mated much more often with O. rusticus females than did O. propinquus males (Table 7 b). A similar pattern occurred in the O. rusticus - O. virilis combinations. O. rusticus males mated with their own females, but they also mated with O. virilis females just as often as O. virilis males mated with the latter. O. virilis males, however, mated only with O. virilis females (Table 7 c,d). Sample sizes are small in the O. propinquus - O. virilis combinations but these data follow a similar pattern: O. virilis males did not mate with females of the other species (in this case, O. propinquus) but males of the other species mated with female O. virilis as well as females of their own species.

Table 7. Interspecific vs. intraspecific matings among combinations of crayfish.

♂	♀	<u>Matings</u>	
Op	Op	Op X Op:	12
Or		Or X Op:	16
Or	Or	Or X Or:	22
Op		Op X Or:	3
<hr/>			
Op	Ov	Ov X Ov:	8
Or		Or X Ov:	7
Or	Or	Or X Or:	8
Ov		Ov X Or:	0
<hr/>			
Op	Ov	Ov X Ov:	8
Ov		Op X Ov:	6
Op	Op	Op X Op:	3
Ov		Ov X Op:	0
<hr/>			

DISCUSSION

In almost all experiments, O. rusticus was generally superior to the other two species in competitive abilities; and O. virilis clearly demonstrated the least competitive ability. The relationship of the competitive ability of O. propinquus to that of the other species, particularly O. rusticus, was less clear-cut, but the data generally indicate an intermediate position. Thus, the results of this study are consistent with the hypothesis that direct aggressive interaction may be, in part, a mechanism responsible for the displacement of O. virilis by both O. rusticus and O. propinquus, and of O. propinquus by O. rusticus.

Numerous potential mechanisms might allow such an advantage to become significant in a real-world situation in which resources were limiting, but it is at present impossible to determine exact mechanisms that would operate in the field. For example, shelter may be an important resource for crayfish in regard to predator avoidance, but it is likely that it is of greatest importance to crayfish much smaller than those tested here (Stein and Magnuson, 1976). It may also be especially important for females which, when encumbered with eggs and young for several weeks, remain secluded most of the time. Individuals about to molt also typically seek shelter. In both the

latter cases, avoidance of cannibalism (Capelli, 1975) may be the prime reason for seeking shelter. In any case, the fact that the adults tested in my study utilized and competed for shelter so readily suggests that, for whatever reasons, it is in fact an important resource.

The direct relevance of my experiments on aggression in the absence of shelter is less clear. Aside from shelter space, the most likely resource to be competed for routinely would probably be food. In an environment in which preferred food was patchily distributed, it is conceivable that O. rusticus might simply exclude other species from preferred areas.

My substrate preference/competition experiments show the importance of knowing the extent to which resources are actually limiting in a field situation before firm conclusions can be drawn regarding displacement mechanisms. When crayfish were given a fairly typical substrate, with much shelter potential, no displacement occurred. At present, no data are available on the extent to which either food or shelter are limiting in the lakes of northern Wisconsin. In many lakes, however, casual observations (Capelli, per. com.) suggest that neither is likely to be limiting.

Other factors also complicate the analysis. O. propinquus does not grow as large as either O. rusticus or O. virilis (maximum carapace length of about 40 mm for O. propinquus, vs. 55-60 mm for the other species). Size is probably an important factor in determining success in aggressive encounters (Bovbjerg, 1956; Lowe, 1956). Although not

described among my experiments above, I found that the advantage of O. propinquus over O. virilis in aggressive interactions in the absence of shelter, and with shelter, could be reversed in favor of O. virilis if 30 mm individuals of the latter were tested against 25 mm O. propinquus. Little is known, however, of specific comparative growth rates of the three species under natural conditions, or how this factor may relate to potential competition.

Perhaps the most significant and interesting results are those from the mating experiments. In all three species described here, mating occurs in the field over an extended period from August until early May (Capelli, 1975). Following mating, females retain a waxy sperm plug in a small external cavity (seminal receptacle, or annulus ventralis). Fertilization occurs externally at the time eggs are laid in May (Capelli, 1975).

Although sample sizes are small, my data clearly suggest that O. rusticus males tend to mate interspecifically much more often than do males of the other species. Or, expressed another way, one might predict from the data (Table 7) that in a mixed population of O. rusticus and O. propinquus, proportionately more O. propinquus females would be carrying an "incorrect" sperm plug (i.e., one from the other species) than would O. rusticus females. Capelli and Capelli (1980) have documented the existence of apparent O. rusticus x O. propinquus hybrids in one northern Wisconsin lake. However, they report that there are no known lakes where hybrids are abundant or numerically dominant and conclude that the offspring of such interspecific matings,

even if occasionally viable, are probably not as fit as non-hybrids. This fact, in combination with my data, suggests that O. rusticus may gain an advantage by interfering with the successful reproduction of O. propinquus to a greater extent than that to which O. propinquus interferes with O. rusticus reproduction.

Although Capelli and Capelli (1980) found no evidence of O. rusticus x O. virilis hybrids, my data (Table 7) suggest that a similar interference mechanism may occur: one would predict that in a mixed population of these species, more O. virilis females would have "incorrect" sperm plugs than would O. rusticus females.

Although sample sizes are even smaller in the O. propinquus x O. virilis mating tests, results are consistent with a mechanism similar to those described above which would give O. propinquus an advantage over O. virilis.

It is also noteworthy that in these mating experiments the resultant hierarchy based on interference potential would be once again O. rusticus > O. propinquus > O. virilis. Very little is known about the details of crayfish reproduction. For example, no information is available about any of the following for any crayfish species, although all points are highly relevant to determining the extent to which mechanisms suggested above may be operative:

- a) Females may mate many times prior to egg production and fertilization. Which male actually fertilizes the eggs, i.e., first, last, or does the female retain sperm from more than one?

- b) What percentage of matings actually result in sperm plug formation? Do species differ in this regard?
- c) Does this percentage change if mating is inter-specific vs. intraspecific?

In conclusion, the results of my work support the general hypothesis that behavioral differences, particularly as related to aggressive interactions and competitive abilities, may in part account for the described species displacements. However, my work must be viewed as general and preliminary; much more detailed analysis of all aspects of it, particularly in regard to what actually happens in the field, will be required before firm conclusions about displacement mechanisms can be drawn.

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