1988

Evaluation of Possible Reproductively Mediated Character Displacement in the Crayfishes, Orconectes rusticus and O. sanbornii

Mark J. Butler IV
Old Dominion University, mbutler@odu.edu

Original Publication Citation

Butler IV, M.J. (1988). Evaluation of possible reproductively mediated character displacement in the crayfishes, *Orconectes rusticus* and *O. sanbornii*. *Ohio Journal of Science, 88*(3), 87-91.

Evaluation of Possible Reproductively Mediated Character Displacement in the Crayfishes, *Orconectes rusticus* and *O. sanbornii*[1]

MARK J. BUTLER IV, Department of Biological Sciences, The Florida State University, Tallahassee, FL 32306-3050

ABSTRACT. *Orconectes rusticus* is replacing several species of crayfishes in north-central and northeastern North America, including *O. sanbornii* in Ohio. Recent evidence suggests that the species replacements may be driven by asymmetrical reproductive success favoring *O. rusticus*. Nonetheless, some sympatric associations appear locally persistent. Because crayfish demonstrate size-assortative mating and there is a disparity in the sizes of the species, further divergence in the sizes of the species in sympatry could enhance reproductive isolation, ultimately providing a mechanism for character displacement. To test this hypothesis the size differentials between crayfish collected from allopatric and sympatric populations in east-central Ohio were compared with expected differences. The possibility of clinal variation in size was addressed by comparing crayfish sizes along a continuous allopatric-sympatric-allopatric species gradient within one stream. The initial character displacement hypothesis was not substantiated by comparisons of allopatric and sympatric populations within or among streams for male or female *O. rusticus* or male *O. sanbornii*. However, female *O. sanbornii* size distributions were consistent with unilateral character displacement.

OHIO J. SCI. 88 (3): 87-91, 1988

INTRODUCTION

The classic definition of character displacement (Brown and Wilson 1956) involves two closely related species with overlapping geographical distributions that are less similar in sympatry than allopatry. The original explanation for character displacement centered on two mechanisms: interspecific competition or interspecific mating coupled with inviable hybrid offspring. Either process could favor the divergence of various key traits. Grant (1972) later described character displacement in more detail. Although he acknowledged the potential for reproductively based species divergence, he concentrated on competitive hypotheses. This perspective has pervaded the study of character displacement since then (Slatkin 1980, Strong et al. 1984, Taper and Case 1985). Much of the recent criticism that research on character displacement has received centers on the paucity of autecological data available to substantiate claims of competition and on the inability of many studies to reject the alternative hypotheses of clinal variation or allopatric character release (Grant 1972, Hespenheide 1973, Strong et al. 1979, 1984, Grant and Abbott 1980, Strong and Simberloff 1981). These objections are untenable in the system described in this paper because 1) interspecific interactions driving species replacement and possibly character displacement are documented and apparently do not involve competition *per se;* 2) allopatric-sympatric population gradients are localized and are thus not subject to geographical clines; and 3) sympatric associations are more recent than the allopatric condition, negating the possibility of character release.

In a previous study I investigated the replacement of a native Ohio crayfish, *Orconectes sanbornii,* by an introduced crayfish, *Orconectes rusticus,* and evaluated several mechanisms that might drive species replacements (Butler and Stein 1985). During that study we noted that the size ratios (i.e., carapace lengths and chelae lengths) of the species were more disparate in sympatry (1.29:1; *O. rusticus* vs. *O. sanbornii*) than in allopatry (1.13:1), and that these deviations were consistent with character displacement. *Orconectes rusticus* was introduced into the Licking River drainage (Knox and Licking counties, Ohio) sometime after Turner's (1926) initial crayfish survey, but before 1967 (R. Jezerinac, unpubl. data). Thus the species have been interacting for at least 10 generations, a short but demonstrably sufficient time for the evolution of a variety of traits in many animal groups (Doyle and Hunte 1981, Reznick 1982, Rice 1985, Endler 1986). Although *O. sanbornii* had been extirpated from some stream sites by *O. rusticus* since the last census of the area (east-central Ohio; R. Jezerinac, unpubl. data), many sympatric populations persisted. Similar situations have been reported in southern Ohio (Flynn and Hobbs 1984), northern Wisconsin (Capelli 1982, Capelli and Magnuson 1983, Lodge et. al. 1986), and Ontario (Berrill 1978, Tierney and Dunham 1984).

Rapid evolution of divergent traits requires strong selection. Phenotypic correlations between species, particularly from only a few sites, cannot be accepted as evidence for character displacement (Endler 1985). Thus the existence of a sufficiently powerful selective agent must also be demonstrated. Several independent studies on crayfish mating and reproduction suggest that such a mechanism may exist (Capelli and Capelli 1980, Capelli 1982, Tierney and Dunham 1982, 1984, Berrill 1985, Butler and Stein 1985, Butler 1985, Lodge et al. 1985, 1986). *Orconectes rusticus* males rarely engage in heterospecific copulations, whereas male *O. sanbornii* and *O. propinquus* (a species closely related to *O. sanbornii* and native to Wisconsin and Canada) frequently mate heterospecifically with small *O. rusticus* females (Tierney and Dunham 1984, Butler and Stein 1985, Berrill 1985, but see Capelli and Capelli 1980, Capelli 1982). Females that mate heterospecifically experience reductions in reproductive success of 50 to 90% (Berrill 1985, Butler and Stein 1985). Although the selection of small *O. rusticus* females by *O. sanbornii* (or *O. propinquus*) males lowers recruitment for all species, the relative recruitment of *O. rusticus* is potentially greater. This probably occurs because only large males (i.e., *O. rusticus*) can copulate with large *O. rusticus* females (Tierney and Dunham 1984,

[1]Manuscript received 4 March 1987 and in revised form 31 August 1987 (#87-13).

Berrill and Arsenault 1982, 1984), and large females are generally more fecund than small females (Fielder 1972, Lorman 1980, Hazlett 1983, Salmon 1983). A mating system of this type should precipitate a decline in the population size of the native species (*O. sanbornii* or *O. propinquus*) unless the populations are subject to substantial immigration or the conflicting species become more reproductively isolated.

Sympatric divergence in the relative size of the two species is one possible isolating mechanism. Most heterospecific matings should occur between small *O. rusticus* females and *O. sanbornii* males because orconectid crayfish mate with individuals of similar size (Berrill and Arsenault 1982, 1984), *O. rusticus* is generally larger than *O. sanbornii* (Turner 1926, Butler and Stein 1985), and *O. rusticus* males demonstrate greater species-specific mate selectivity (Tierney and Dunham 1984, Butler and Stein 1985). Individuals that mate heterospecifically will experience lowered reproductive success relative to other individuals in sympatric populations because their fecundity is reduced and hybrids are apparently nonviable (Capelli and Capelli 1980, Smith 1981, Berrill 1985, Butler and Stein 1985). Thus, relatively larger *O. rusticus* and smaller *O. sanbornii* might be selectively favored in sympatry, leading to character displacement in body size and other highly correlated characters like chelae length (Stein 1975, Stein et al. 1977). I tested this hypothesis by examining the allopatric and sympatric size distributions of two crayfish species within and among several Ohio streams.

METHODS

I visited a total of 32 stream sites in northern Licking and Knox counties in 1984 and located only two *O. rusticus-O. sanbornii* sympatric populations and four allopatric *O. rusticus* populations. The remaining sites yielded only *O. sanbornii* populations. Therefore, crayfish were collected from the two sympatric, the four allopatric *O. rusticus*, and five nearby allopatric *O. sanbornii* locales in five east-central Ohio streams in July, 1984. All five streams sampled are low gradient, third-order streams that drain agricultural watersheds. *Orconectes rusticus* was collected at four allopatric sites in the Otter Fork, Muddy Fork, and North Fork of the Licking River and in Raccoon Creek. *Orconectes sanbornii* was collected at five allopatric sites in the North Fork and South Forks of the Licking River; both species were taken at two sympatric locations in the North Fork of the Licking River.

I examined interspecific size relationships on a smaller geographic scale by comparing the sizes of crayfishes from 11 locations along a 3-km transect of the North Fork of the Licking River. The transect sampled spanned an upstream allopatric *O. sanbornii* region, a downstream allopatric *O. rusticus* region, and an area of sympatry in between. Comparisons made between allopatric and sympatric sites within a short section of stream alleviate the potential problem of differentiating character displacement from geographic clines in body size.

Most adult *O. rusticus* and *O. sanbornii* reside in stream pools and runs (Butler and Stein 1985), so crayfish were collected only from these habitats to reduce possible bias owing to size-specific habitat use. I used a handnet to collect crayfish and captured all crayfish sighted in the open or under rocks. At some sites, crayfish densities were quite low and repeated sampling yielded only small sample sizes. The sex, carapace length, and chela length of each crayfish were recorded in the field, and the animals were then released. Carapace length (CL; anterior tip of rostrum to posterior mid-dorsal edge of the cephalothorax) served as the dependent variable in the analyses because it is a standard measure of crayfish size and is an accurate indicator of aggressive dominance and mating success (Heckenlively 1970, Rubenstein and Hazlett 1974, Berrill and Arsenault 1984, Butler and Stein 1985). Carapace length is also significantly positively correlated with chela length (Stein 1975). Statistical analyses run on chelae lengths yielded results identical to those for carapace lengths, so only data for carapace lengths are reported. Only adult crayfishes greater than 20 mm CL (i.e., those capable of reproduction; Lorman 1980, Fielder 1972, Berrill and Arsenault 1984) were used in the analyses.

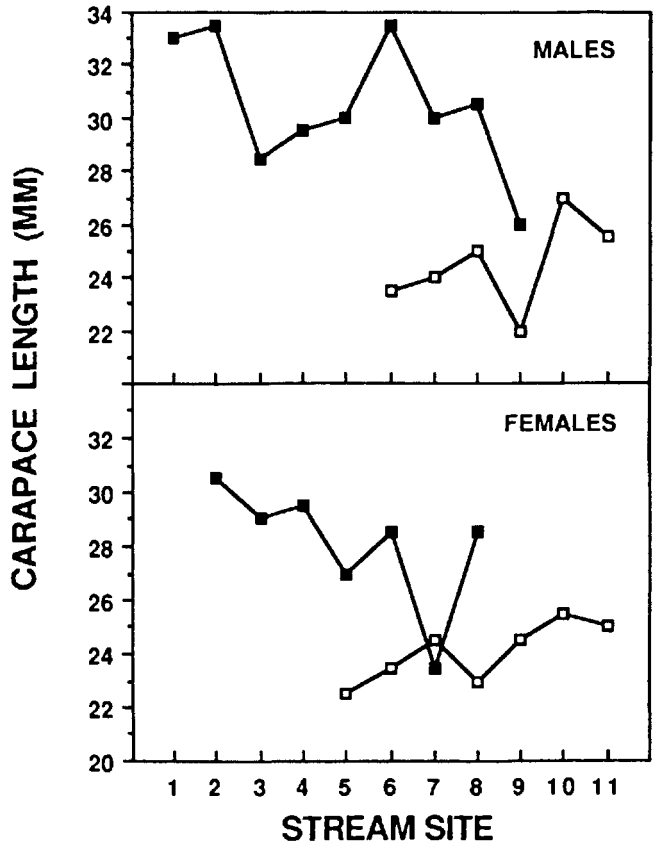

FIGURE 1. Mean carapace lengths for male and female *Orconectes rusticus* (solid squares) and *Orconectes sanbornii* (open squares) at 11 sites along a 3-km transect of the North Fork Licking River, Licking and Knox counties, Ohio. Note that the transect spanned two allopatric zones and a zone of sympatry in between. Twenty-five to 35 crayfish were collected at each site.

Size-frequency data were first analyzed in one-factor, fixed-effects analyses of variance (ANOVA; factor = collection site) to determine if sizes differed among sites. Bonferroni *a priori* multiple comparison tests (Kirk 1982) were then used to test whether crayfish size differed between allopatric and sympatric sites. I also used Wilcoxon Rank-Sum tests (Hollander and Wolfe 1973) to determine if ranks of the mean sizes (CL) of both species and sexes at each site corresponded with the predicted size relationship (i.e., *O. rusticus* should be larger in sympatry than in allopatry, whereas the reverse should be true for *O sanbornii*). In another test, relative size differences between the two species in allopatry vs. sympatry were compared in two-sample *t*-tests.

Relative differences at each site, rather than absolute differences among sites, may be the most relevant parameter to measure with respect to natural selection. The dependent variable values for this analysis were generated by computing the difference in the mean sizes (CL) of the two species in each possible pairwise comparison among sites within allopatry and sympatry. If character displacement had occurred, I expected a larger relative difference in size between species in sympatry as compared to allopatry. Separate tests were performed on males and females in all analyses. Identical analyses were performed on the data from different streams, as well as on the within-stream data.

RESULTS

There were significant (ANOVA; $P < 0.05$) differences in the sizes (CL) of both *O. rusticus* and *O. sanbornii* males and females among stream locations. Crayfishes were generally smaller in sympatry than allopatry (Bonferroni test; $P < 0.05$; Table 1). *Orconectes sanbornii* males and females were always smaller in sympatry (Wilcoxon Rank-Sum test; $P < 0.05$), whereas the smallest

TABLE 1

Descriptive statistics for crayfishes collected in July, 1984 at 11 stream sites in Licking and Knox counties, Ohio. Carapace lengths are in mm. The specific location of each site is given in Appendix Table 1. N = sample size.

Species	Site	Carapace Length ($\bar{x}$ ± 1 SD) Males	Carapace Length ($\bar{x}$ ± 1 SD) Females	N Males	N Females
Allopatry-					
O. sanbornii	1	26.5 (2.8)	27.3 (4.9)	12	9
	2	25.4 (4.6)	24.7 (4.8)	9	4
	3	29.6 (5.4)	27.2 (3.6)	11	19
	4	26.4 (3.4)	25.7 (2.6)	37	62
	5	26.9 (4.0)	26.9 (2.9)	19	16
O. rusticus	6	27.0 (3.6)	27.2 (4.6)	25	10
	7	33.1 (5.1)	28.6 (4.3)	30	21
	8	26.8 (6.7)	24.3 (6.3)	7	4
	9	35.6 (5.4)	35.3 (5.7)	5	3
Sympatry-					
O. sanbornii	10	24.4 (3.4)	23.8 (2.5)	27	26
	11	25.4 (2.9)	24.1 (2.9)	14	15
O. rusticus	10	30.2 (5.3)	27.2 (4.0)	52	26
	11	26.2 (6.1)	26.9 (4.8)	12	16

O. rusticus size ranks were evenly distributed among allopatric and sympatric locales ($P = 0.27$ and $P = 0.40$ for males and females, respectively). Relative differences in the mean ($\bar{x}$) sizes of the species were similar in allopatry and sympatry (*t*-test; $P > 0.05$), but *O. rusticus* males were generally larger than *O. sanbornii* males in allopatry ($\bar{x}$ = 3.7 mm difference) and sympatry ($\bar{x}$ = 3.3 mm). Similarly, female *O. rusticus* were generally, though not significantly, larger than *O. sanbornii* females in allopatry ($\bar{x}$ = 2.5 mm difference) and sympatry ($\bar{x}$ = 3.1 mm difference).

Both species and sexes differed in size among sites along the North Fork Licking River transect (ANOVA; $P < 0.05$; Fig. 1). Changes in the size of *O. rusticus* males did not correspond with interspecific association, but *O. rusticus* females and *O. sanbornii* males and females were significantly (Bonferroni test; $P < 0.05$) smaller in sympatry. However, if sites were ranked by crayfish size for both species and sexes, only *O. sanbornii* females were consistently smaller in sympatry than allopatry (Wilcoxon Rank-Sum test: $P < 0.005$). The relative size differences between the two species in allopatry and sympatry, by sex, were not significant (*t*-test; $P > 0.05$). On average, males differed by 4.8 mm CL in allopatry and 6.2 mm CL in sympatry; females differed by 3.7 mm CL and 3.2 mm CL in allopatry and sympatry, respectively.

DISCUSSION

The results of this field survey provide no compelling evidence for bilateral (i.e., both species) displacement of carapace length, either among or within streams, in sympatric orconectid crayfish populations. When data from individual collection sites within or among streams were pooled in an overall test for size disparities in allopatry vs. sympatry, both species and sexes were smaller in sympatry. However, the *O. rusticus* data were strongly influenced by large deviations at just a few sites. When the sites were considered individually, only *O. sanbornii* was consistently smaller in sympatry (i.e., unilateral size divergence).

Are these results compatible with other possible predictions of character displacement? Although both species experience lowered reproductive success in sympatry, the effect on the native species is more acute (Butler and Stein 1985, Berrill 1985). Because selection operates on relative fitnesses (see Endler 1986 for review), a unilateral reduction in size by a native species, *O. sanbornii* in this case, could act as a prezygotic isolating mechanism promoting local sympatric persistence, a mechanism not previously considered. If this occurred, small *O. sanbornii* females would be assured of only intraspecific copulations, because the size-assortative mating system and the larger size of *O. rusticus* would thwart heterospecific mating attempts by the nondiscriminantly mating *O. sanbornii* males. Confirmation of this hypothesis requires explicit comparisons of size-specific mating behavior and reproductive success in allopatric and persistent sympatric crayfish populations. Those kinds of data are not currently available.

Comparisons of the relative sizes of the species at specific allopatric and sympatric sites may be the most valuable means of detecting character displacement, because it is the relative size of individuals that drive species interactions. Thus, the customary approach of comparing absolute sizes among sites has little relevance to selection and character displacement. In this study, *O. sanbornii* was smaller than *O. rusticus* in both sympatric streams and at four of five sympatric locations along the North Fork Licking River transect. Despite the smaller size of *O. sanbornii* in sympatry, there was no statistical evidence for larger interspecific size ratios in sympatry than in allopatry. Whether the size differential between the species at sympatric locations is sufficient to preclude replacement of *O. sanbornii* is unknown and warrants further investigation.

The persistence of sympatric crayfish populations may also be enhanced by a number of mechanisms besides character displacement. For example, high rates of immigration, particularly movement from allopatry to sympatry, might swamp the effects of selection and extend local persistence. In fact, site-to-site variation in immigration due to differences in physical barriers or population density is an appealing explanation for the variable rates of replacement observed in seemingly similar lakes and streams (Rhoades 1962, Berrill 1978, Capelli 1982, Butler and Stein 1985, Flynn and Hobbs 1984, Lodge et al. 1986). Segregation of species by habitat or differential susceptibility to predation are also plausible mechanisms that might sustain sympatric associations. There is circumstantial evidence supporting these hypotheses (Penn and Fitzpatrick 1963, Schwartz et. al. 1963, Bovbjerg 1970, Rorer and Capelli 1978, Medvick 1979, Collins et al. 1983, Butler and Stein 1985). Behavioral reproductive isolation via chemosensory-controlled mate selection may explain why some sympatric Canadian crayfish assemblages appear stable (Ameyaw-Akumfi and Hazlett 1975, Itagaki and Thorp 1981, Tierney and Dunham 1982, 1984), although this hypothesis has not been addressed explicitly.

Finally, it might be argued that the size differences observed in sympatry may be due to differences in the two species' growth rates in sympatry, not character displacement. For example, *O. rusticus* might monopolize food resources and inhibit the growth of *O. sanbornii*.

This alternative seems rather weak, given that there is no evidence that these species differ in aggressive tendencies or compete for food (Butler and Stein 1985). There is limited laboratory and field data available on growth rates for the two species, but interspecific comparisons are confounded by differences in laboratory conditions and field sites (Fielder 1972, Lorman 1980, Butler 1983). Although there seems to be little support for this alternative, it should be noted that if this hypothesis were true the effects on species persistence would be the same as character displacement, namely greater divergence in the relative sizes of the species in sympatry, reduced interspecific copulations, and enhanced reproductive isolation.

In summary, the results of this study are consistent with the hypothesis that *O. sanbornii* may avoid replacement by *O. rusticus* via a unilateral reduction in size in sympatry. Selection for the most fertile *O. sanbornii* individuals, presumably the smaller size classes that are relatively immune to the mating and reproductive anomalies experienced by larger individuals, may drive the evolution of smaller individuals. Several alternative hypotheses are tenable as well, but data that might discriminate among these competing ideas are either circumstantial or nonexistent. Further research on this topic should focus on size-specific mate selection and reproductive success, comparisons of allopatric and sympatric growth rates, interdemic rates of immigration, and chemosensory-mediated mate choice as possible mechanisms facilitating species coexistence in orconectid crayfish.

ACKNOWLEDGMENTS. I thank K. Butler for his assistance in the field and P. Greenwood, H. H. Hobbs III, D. Lodge, D. Wilber, and two anonymous reviewers for critiquing earlier drafts of this manuscript. This research was conducted with the aid of a Sigma Xi Grant-in-Aid of Research and a Florida State University College of Arts and Sciences Fellowship.

APPENDIX TABLE 1

Crayfish collection site locations in Licking and Knox counties, Ohio. SR = state route; TR = township route.

Site	Location description
1	Licking County, Burlington Township. North Fork Licking River, 0.5 km east of the intersection of SR 661 and TR 19.
2	Licking County, Harrison-Lima Township. South Fork Licking River at TR 34.
3	Licking County, Lima Township. South Fork Licking River at TR 155.
4	Knox County, Hilliar Township. North Fork Licking River, 0.5 km west of TR 112.
5	Licking County, Bennington Township. North Fork Licking River at SR 657.
6	Licking County, Bennington Township. Otter Fork Licking River at TR 56.
7	Licking County, Bennington Township. North Fork Licking River, 0.5 km east of TR 56 at TR 19.
8	Licking County, Newark Township, City of Newark. Licking River, 0.25 km south of the intersection of SR 16 and SR 79.
9	Licking County, Lima Township. Muddy Fork Licking River at TR 38.
10	Knox County, Hilliar Township. North Fork Licking River at TR 19.
11	Licking County, Bennington Township. North Fork Licking River, 0.25 km southeast of the intersection of TR 114 and TR 19.

LITERATURE CITED

Ameyaw-Akumfi, C. and B. A. Hazlett 1975 Sex recognition in the crayfish *Procambarus clarkii*. Science 190: 1225-1226.

Berrill, M. 1978 Distribution and ecology of crayfish in the Kawartha Lakes region of southern Ontario. Can. J. Zool. 56: 166-177.

——— and M. Arsenault 1982 Spring breeding of a northern temperate crayfish, *Orconectes rusticus*. Can. J. Zool. 60: 2641-2645.

——— and ——— 1984 The breeding behavior of a northern temperate Orconectid crayfish, *Orconectes rusticus*. Anim. Behav. 32: 333-339.

——— 1985 Laboratory induced hybridization of two crayfish species, *Orconectes rusticus* and *O. propinquus*. J. Crust. Biol. 5: 347-349.

Bovbjerg, R. V. 1970 Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). Ecology 51: 225-236.

Brown, W. L. and E. O. Wilson 1956 Character displacement. Syst. Zool. 5: 49-64.

Butler, M. J. IV 1983 An analysis of replacement mechanisms governing range expansion in crayfish. Columbus: The Ohio State Univ. Thesis.

——— and R. A. Stein 1985 An analysis of the mechanisms governing species replacements in crayfish. Oecologia 66: 169-177.

——— 1985 Crayfish: tyrant or prude? Nat. Hist. 95: 4.

Capelli, G. M. and J. F. Capelli 1980 Hybridization between crayfish of the genus *Orconectes:* morphological evidence (Decapoda: Cambaridae). Crustaceana 39: 121-132.

——— 1982 Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). Limnol. Oceanogr. 27: 741-745.

——— and J. J. Magnuson 1983 Morphoedaphic and biogeographic analysis of crayfish distribution in northern Wisconsin. J. Crust. Biol. 3: 548-564.

——— and B. L. Munjal 1983 Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*. J. Crust. Biol. 2: 486-492.

Collins, N. C., H. H. Harvey, A. J. Tierney, and D. W. Dunham 1983 Influence of predatory fish density on trapability of crayfish in Ontario lakes. Can. J. Fish. Aquat. Sci. 40: 1820-1828.

Doyle, R. W. and W. Hunte 1981 Demography of an estuarine amphipod (*Gammarus lawrencianus*) experimentally selected for high "r": a model of the genetic effects of environmental change. Can. J. Fish. Aquat. Sci. 38: 1120-1127.

Endler, J. A. 1986 Natural selection in the wild. Princeton, NJ: Princeton Univ. Press.

Fielder, D. D. 1972 Some aspects of the life histories of three closely related crayfish species *Orconectes obscurus, O. sanbornii,* and *O. propinquus*. Ohio J. Sci. 72: 129-145.

Flynn, M. F. and H. H. Hobbs III 1984 Parapatric crayfishes in southern Ohio: evidence of competitive exclusion? J. Crust. Biol. 4: 382-389.

Grant, P. R. 1972 Convergent and divergent character displacement. Biol. J. Linn. Soc. 4: 36-69.

——— and I. Abbott 1980 Interspecific competition, island biogeography, and null hypotheses. Evolution 34: 332-341.

Hazlett, B. A. 1983 Parental behavior in decapod crustacea. *In:* S. Rebach and D. W. Dunham (eds.), Studies in adaptation: the behavior of higher crustacea. New York: J. Wiley and Sons; pp. 171-193.

Heckinlively, D. B. 1970 Intensity of aggression in the crayfish *Orconectes virilis* (Hagen). Nature 225: 180-181.

Hespenheide, H. A. 1973 Ecological inferences from morphological data. Ann. Rev. Ecol. Syst. 4: 213-229.

Hollander, M. and D. A. Wolfe 1973 Nonparametric statistical methods. New York: J. Wiley and Sons.

Itagaki, H. and J. H. Thorp 1981 Laboratory experiments to determine if crayfish can communicate chemically in a flow-through system. J. Chem. Ecol. 7: 115-126.

Kirk, R. E. 1982 Experimental design: procedures for the behavioral sciences. 2nd ed. Monterey, CA: Brooks/Cole Pub. Co.

Lodge, D. M., A. L. Beckel, and J. J. Magnuson 1985 Lake bottom tyrant. Nat. Hist. 94: 32-37.

———, T. K. Kratz, and G. M. Capelli 1986 Long-term dynamics of three crayfish species in Trout Lake, Wisconsin. Can. J. Fish. Aquat. Sci. 43: 993-998.

Lorman, G. 1980 Ecology of the crayfish *Orconectes rusticus* in northern Wisconsin. Madison: Univ. of Wisconsin. Dissertation.
Medvick, P. 1979 Aggressive interactions and predation avoidance in young-of-the-year of three species of crayfish (*Orconectes*). Madison: Univ. of Wisconsin. Dissertation.
Penn, G. H. and J. F. Fitzpatrick, Jr. 1963 Interspecific competition between two sympatric species of dwarf crayfishes. Ecology 44: 793-797.
Reznick, D. 1982 The impact of predation on life history evolution in Trinidadian guppies: genetic basis of observed life history patterns. Evolution 36: 1236-1250.
Rice, W. 1985 Disruptive selection on habitat preference and evolution of reproductive isolation: an exploratory experiment. Evolution 39: 645-656.
Rhoades, R. 1962 Further studies on Ohio crayfishes. Cases of sympatry of stream species in southern Ohio. Ohio J. Sci. 62: 27-33.
Rorer, W. E. and G. M. Capelli 1978 Competitive interaction between two Mountain Lake crayfish species, with life history notes. Vir. J. Sci. 29: 245-248.
Rubenstein, D. I. and B. A. Hazlett 1974 Analysis of the aggressive behavior of the crayfish *Orconectes virilis* by character analysis. Behavior 50: 193-216.
Salmon, M. 1983 Courtship, mating systems, and sexual selection in Decapods. *In:* S. Reback and D. W. Dunham (eds.), Studies in adaptation: the behavior of higher Crustacea. New York: J. Wiley and Sons; pp. 143-171.
Schwartz, F. J., R. Rnbelmann, and J. Allison 1963 Ecological population expansion of the introduced crayfish, *Orconectes virilis*. Ohio J. Sci. 63: 266-273.
Slatkin, M. 1980 Ecological character displacement. Ecology 61: 163-177.
Smith, D. G. 1981 Evidence for hybridization between two crayfish species (Decapoda: Cambaridae: Orconectes) with a comment on the phenomenon in Cambarid crayfish. Amer. Midl. Nat. 120: 405-407.
Stein, R. A. 1975 Sexual dimorphism in crayfish chelae: functional significance limited to reprodnctive activities. Can. J. Zool. 54: 220-227.
———, M. J. Murphy, and J. J. Magnuson 1977 External morphological changes associated with sexual maturity in the crayfish (*Orconectes propinquus*). Amer. Mid. Nat. 97: 496-502.
Strong, D. R., L. A. Szyska, and D. Simberloff 1979 Tests of community-wide character displacement against null hypotheses. Evolution 33: 897-913.
——— and D. S. Simberloff 1981 Straining at gnats and swallowing ratios: character displacement. Evolution 35: 810-812.
———, ———, L. G. Abele, and A. B. Thistle 1984 Ecological communities: conceptual issues and the evidence. Princeton, NJ: Princeton Univ. Press.
Taper, M. L. and T. J. Case 1985 Quantitative genetic models for the coevolution of character displacement. Ecology 66: 355-371.
Tierney, A. J. and D. W. Dunham 1982 Chemical communication in the reproductive isolation of the crayfishes *Orconectes propinquus* and *Orconectes virilis* (Decapoda, Cambaridae). J. Crust. Biol. 2: 544-548.
——— and ——— 1984 Behavioral mechanisms of reproductive isolation in crayfishes of the genus *Orconectes*. Amer. Midl. Nat. 111: 304-310.
Turner, C. 1926 The crayfishes of Ohio. Ohio Biol. Surv. Bull. 30: 145-195.