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Agonism and shelter competition between invasive and indigenous crayfish species

Francesca Gherardi and William H. Daniels

Abstract: Several crayfish species behave as biological invaders. Their establishment in an area has frequently been accompanied by the reduction or elimination of indigenous species. A laboratory study was designed to investigate whether the invasive crayfish *Procambarus clarkii* (Girard, 1852) is dominant over the indigenous (to Delaware) crayfish *Procambarus acutus acutus* (Girard, 1852) in either the absence or the presence of a shelter as a limited resource. As expected, we found that *P. clarkii* is more aggressive than the similarly sized *P. a. acutus*, thus confirming previous studies that demonstrated an inherent dominance of the invasive over the indigenous crayfish. We then hypothesized that species showing a lower preference for an offered shelter (*P. clarkii*) should be less motivated to defend it. To the contrary, in a competitive context *P. clarkii* excluded *P. a. acutus* from the shelter but did not use the resource. Caution must be used in extrapolating these laboratory studies to the field, and future studies should analyze multiple factors, including the autoecology of the two species and their reproductive potential and recruitment patterns. However, our results might help in highlighting the risks for freshwater biodiversity created by the uncontrolled translocations of *P. clarkii* and other similar invasive species.

Résumé : Plusieurs espèces d'écrevisses se comportent comme des envahisseurs biologiques. Leur établissement dans une région s'accompagne souvent de la réduction ou de l'élimination des espèces indigènes. Nous avons mis au point une étude de laboratoire pour voir si l'écrevisse envahissante *Procambarus clarkii* (Girard, 1852) est dominante par rapport à l'écrevisse indigène (au Delaware) *Procambarus acutus acutus* (Girard, 1852) en présence ou en absence d'abris comme ressource limitée. Comme prévu, *P. clarkii* est plus agressif que *P. a. acutus*, un animal de même taille, ce qui confirme les études antérieures qui ont démontré l'existence d'une dominance inhérente de l'écrevisse envahissante par rapport à l'indigène. Nous avons alors posé l'hypothèse selon laquelle l'espèce qui montre le moins de préférence pour l'abri offert (*P. clarkii*) devrait être moins motivée pour le défendre. Au contraire, dans une situation de compétition, *P. clarkii* élimine *P. a. acutus* de l'abri, sans pour autant s'en servir lui-même. Il faut être prudent en extrapolant ces résultats de laboratoire aux situations de terrain; les études futures devront analyser plusieurs facteurs, dont l'autécologie des deux espèces, leur potentiel reproductif et leurs patterns de recrutement. Néanmoins, nos résultats peuvent servir à souligner les risques pour la biodiversité créés par les transferts incontrôlés de *P. clarkii* et d'autres espèces envahissantes semblables.

[Traduit par la Rédaction]

Introduction

Recently, much scientific attention has been directed toward the ecological effects induced worldwide by species introduced by man outside their natural range. Although in some cases nonindigenous species have proved beneficial to man, they have often produced negative effects on indigenous communities (Holdich 1988) by causing a substantial loss of biodiversity (Diamond and Case 1986; Vitousek et al. 1996; Sala et al. 2000) and an increased "biotic homogenization" (Lodge 1993). Due to the strong affinity of humans for water as the result of commerce, transportation, or recreation, and the relative ease of aquatic species dispersal, freshwater biota are particularly vulnerable to the colonization by nonindigenous species (Lodge et al. 1998; Beisel 2001).

Together with zebra mussel (*Dreissena polymorpha*

(Pallas, 1771)) and coypu (*Myocastor coypus* (Molina, 1782)), several crayfish species are paradigmatic examples of freshwater invaders, their distribution often being the result of deliberate and accidental introductions by man into new river drainages, states, or continents (Hobbs et al. 1989; Gherardi and Holdich 1999; Lodge et al. 2000). The establishment of a nonindigenous species in an area has frequently been accompanied by the reduction or elimination of indigenous crayfish (e.g., Lodge et al. 1986, 2000; Holdich 1988; Hobbs et al. 1989; Olsen et al. 1991; Light et al. 1995; Söderbäck 1995). Other well-known threats to indigenous species are ongoing global changes affecting the freshwater environment, such as organic pollution, habitat destruction due to dams and water diversion, increased rice cultivation, poor land management, and higher salinity resulting from withdrawal of water for irrigation (Allan and Flecker 1993). These

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changes might enhance conditions for the successful establishment of introduced species (Hobbs et al. 1989; Holdich et al. 1997; Lindqvist and Huner 1999), further accelerating the decline of indigenous species.

Among the introduced species that pose serious threats to biodiversity, *Orconectes rusticus* (Girard, 1852) (a crayfish endemic to Illinois, Indiana, and western Ohio) has been especially successful in extirpating indigenous crayfish in Wisconsin (Capelli 1982; Capelli and Magnuson 1983), New England (Smith 1981), Canada (Berrill 1978), and Ohio (Butler and Stein 1985). Similarly, the spread throughout Europe of *Pacifastacus leniusculus* (Dana, 1852) and *Procambarus clarkii* (Girard, 1852) is negatively affecting several populations of the indigenous Astacidae (Gherardi and Holdich 1999).

The mechanisms behind such species replacements are often difficult to study and are poorly understood (Mather and Stein 1993; Lodge and Hill 1994; Söderbäck 1995; Westman et al. 2002). Competitive exclusion has often been invoked to explain the observed replacements (Penn and Fitzpatrick 1963; Bovbjerg 1970; Capelli 1982; Capelli and Magnuson 1983; Flynn and Hobbs 1984). However, multiple factors, such as differential susceptibility to predation, reproductive interference, and transmission of diseases and parasites, may interact in a complex fashion and may operate in synergy (Capelli and Capelli 1980; Butler and Stein 1985; Lodge et al. 1986; DiDonato and Lodge 1993; Mather and Stein 1993; Garvey et al. 1994).

The eastern white river crayfish, *Procambarus acutus acutus* (Girard, 1852), is native to Delaware and is distributed along the Atlantic slope of North America. Its taxonomic status is still debated and, in the absence of additional studies, a certain confusion persists in the literature, at least between the Louisiana white river crayfish and *Procambarus zonangulus* Hobbs and Hobbs, 1990, originally described from southwestern Texas (Hobbs and Hobbs 1990). The red swamp crayfish, *Procambarus clarkii*, is a potential invader (see, for example, Gherardi et al. 1999). From its natural range (northeastern Mexico and the south-central United States westward to Texas, eastward to Alabama, and northward to Tennessee and Illinois; Hobbs 1989), it was introduced for different reasons (e.g., aquaculture, commerce of live crustaceans, baits, pets) to as many as 15 states in the USA, Delaware included, and 25 other countries (Huner 1977; Huner and Avault 1979; Hobbs et al. 1989). Individuals of *P. clarkii* have often escaped from farm ponds and given rise to naturalized populations. The negative influence that *P. clarkii* exerts on indigenous communities and crayfish species is widely documented (Gherardi and Holdich 1999).

To assess the impact of adults of the introduced species on *P. a. acutus*, we conducted a laboratory study in which we first addressed the question of whether *P. clarkii* is dominant over the indigenous crayfish in agonistic interactions. An inherent dominance of the invasive over the indigenous species has been previously proved in other dyads of crayfish, i.e., in *Pacifastacus leniusculus* and *Astacus astacus* (L., 1758) (Söderbäck 1991), *P. leniusculus* and *Cambaroides japonicus* (de Haan, 1842) (Usio et al. 2001; Nakata and Goshima 2003), and *P. clarkii* and *Austropotamobius italicus* Faxon, 1914 (Gherardi and Cioni 2004), but not in *P. leniusculus*

and *Austropotamobius torrentium* (Schrank, 1803) (Vorburger and Ribi 1999).

Second, we investigated whether one species could exclude the other from access to a shelter and tested the assumption that agonistic dominance translates into an advantage in competition for resources. In fact, an energetically costly and time-consuming behavior such as fighting is adaptive only when it is rewarded in terms of prior access to resources (Case and Gilpin 1974), and an elevated social status gives advantage only when it assures the acquisition and maintenance of those resources (Wilson 1975).

Shelters are important resources for crayfish (Bovbjerg 1970), their availability being the "principal resource bottleneck" in crayfish populations (Hobbs 1991). They serve to minimize predation risks from mammals, fish, or other crayfish (Garvey et al. 1994; Lodge and Hill 1994; Englund 1999; Hill and Lodge 1999; Englund and Krupa 2000) and, in some species, to attract mates (Bergman and Moore 2003). The use of shelters also allows several crayfish species, such as *P. clarkii*, to withstand environmental extremes (e.g., high temperatures and dehydration) (Huner and Barr 1991). When coarse sediments in the soil and the absence of free water impede burrow excavation (Ilhéu et al. 2003), shelters may be limited (Bovbjerg 1970; Capelli and Magnuson 1983; Lodge and Hill 1994) also for those crayfish species known to be good burrowers, such as *P. clarkii* (Barbaresi et al. 2004). An inferior ability to compete for shelters may lead to a higher susceptibility to fish predation (e.g., Olsen et al. 1991; DiDonato and Lodge 1993; Garvey et al. 1994). Based on these premises, we hypothesized that the presence of a shelter as a limited resource should influence fighting behavior and that dominance order should translate into a differential capability to compete for its occupancy (Capelli and Hamilton 1984).

Methods

Maintenance in the laboratory

The study was conducted in January–February 2002 in Dover (Delaware, USA), using the facilities of the Department of Agriculture and Natural Resources at Delaware State University. Individuals of *P. a. acutus* (hereafter, *Pa*) and *P. clarkii* (hereafter, *Pc*) were made available from culture research ponds located in Delaware and Louisiana (USA), respectively. For a minimum of 3 weeks before the subsequent isolation (see below), crayfish, separated by species, were housed in four 2.4 m × 1.1 m × 0.5 m trays with a water flow-through system, maintained at a constant water temperature of 20 °C and at a lighting regime of 10 h light : 14 h dark, and fed a diet of commercial crayfish pellets every second day. The animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Isolation phase

To eliminate any factor that could induce an obvious bias to our experiments, only male, hard-shelled, sexually mature (form I) specimens with all appendages intact were included in our sampling. In fact, previous studies have shown that hierarchy in decapods is related to gender (e.g., Sinclair 1977),

molt stage (e.g., Tamm and Cobb 1978), reproductive condition (e.g., Debusse et al. 1999), morphotype (Guiasu and Dunham 1998), and mutilations (Gherardi et al. 2000). The selected animals were measured using a vernier caliper to determine the length of the cephalothorax (i.e., anterior tip of the rostrum to the posterior edge of the carapace) and the length of their major chela (i.e., propodus length), and weighed on an electronic balance. They were marked with waterproof paint in the center of their carapace and housed singly in opaque, 18.9-L PVC buckets (25 cm diameter) containing 5 L of aged tap water (aerated for several days to remove chlorine) and a 10 cm long piece of rigid, gray, straight PVC pipe (4 cm internal diameter) as a shelter (see experiment 2). The animals were kept under the same environmental and dietary regime as in the maintenance phase for 1 week before the experiments commenced. Previous studies with other crayfish species have shown that 1 week of isolation is enough to remove any prior social effects (Rubenstein and Hazlett 1974; Guiasu and Dunham 1999; Zulantz Schneider et al. 2001).

Experimental design

We conducted two sets of experiments on heterospecific pairs. In the first experiment ("agonistic dominance"), we examined whether one species was agonistically superior over the other by observing interactions between individuals in the absence of any potential resource. In the second experiment ("competition for a shelter"), we explored whether one species could exclude the other from a shelter. In a third experiment ("shelter use"), we analyzed the two species in individual aquaria to test whether shelter occupancy in a noncompetitive context was different than in the presence of a rival.

General procedure

To minimize potential asymmetries in their Resource Holding Potential (RHP) sensu Maynard Smith and Parker (1976), heterospecific pairs were formed by choosing individuals that differed in size by less than 3 mm for the cephalothorax length, less than 4 mm for the major chela length, and less than 6 g for their mass (Table 1). In fact, body and cheliped sizes are generally thought to be the most important indicators of RHP in crustaceans (Dingle 1983; Rutherford et al. 1995; Gherardi 2001). A morphometric analysis conducted on a larger sample of *Pa* and *Pc* showed that chela length increases in an allometric fashion with respect to the cephalothorax length in both species (after a log-log transformation, *Pa*: $y = 1.303x - 1.242$, $r = 0.7783$, $n = 149$, $P < 0.01$; *Pc*: $y = 1.464x - 1.820$, $r = 0.9411$, $n = 46$, $P < 0.01$). The *y*-intercepts (coefficient *a*) of the regression lines differed significantly between species ($t = 2.021$, $df = 192$, $P < 0.02$), being higher for *Pa* than for *Pc*, but the slope (coefficient *b*) did not differ between species ($t = 0.959$, $df = 191$, ns). In other words, at the same body size, *Pa* has a significantly longer chela than *Pc* and this difference remains constant with the growth of the individual.

Following the procedures of Penn and Fitzpatrick (1963), Capelli and Munjal (1982), Söderbäck (1991), Guiasu and Dunham (1999), and Gherardi and Daniels (2003), all experiments were staged in circular PVC containers (25 cm diam-

Table 1. Body size (cephalothorax length, mm), major chela size (propodus length, mm), and body mass (g) of pairs composed of *Procambarus acutus acutus* (*Pa*) and *Procambarus clarkii* (*Pc*) used in experiments 1 and 2.

Pair	Cephalothorax length		Propodus length		Body mass	
	<i>Pa</i>	<i>Pc</i>	<i>Pa</i>	<i>Pc</i>	<i>Pa</i>	<i>Pc</i>
Experiment 1: agonistic dominance						
1	50.5	48.2	50.2	46.3	35.1	29.3
2	45.3	46.6	46.4	46.3	29.5	30.8
3	44.3	45.6	43.4	39.3	28.5	25.5
4	44.7	45.4	45.0	47.9	26.7	27.5
5	46.5	49.4	48.0	50.4	30.3	33.7
6	45.4	47.9	44.2	45.0	30.4	31.0
7	45.2	48.0	41.4	44.3	28.2	29.2
Experiment 2: competition for a shelter						
1	44.6	41.7	42.3	39.3	26.4	20.5
2	44.7	44.7	42.2	42.4	26.4	24.3
3	43.4	41.5	38.3	39.7	23.8	19.4
4	39.2	42.0	36.0	38.6	19.1	19.9
5	43.2	43.5	33.2	43.0	22.3	22.4
6	40.7	39.6	40.2	36.7	22.4	17.3
7	40.7	40.5	40.8	37.4	22.0	19.6
8	45.0	45.2	40.7	40.0	27.1	25.0
9	35.0	37.0	31.6	32.4	14.7	15.7
10	40.7	41.0	36.0	39.6	16.6	19.1
11	48.4	49.0	50.7	48.0	33.9	35.5
12	43.4	46.2	43.0	43.0	25.1	30.7

eter) with 5 L of aged tap water. Certainly, agonism between crayfish kept in small aquaria is likely to be more intense than agonism in the field, as found by Bergman and Moore (2003) for *O. rusticus* and *Orconectes virilis* (Hagen, 1870). In fact, the space in small aquaria is too narrow for crayfish escapes and the "critical reaction" effect (Hediger 1950) increases. However, this limitation does not invalidate our purpose, to understand the dominance-subordination relationship between the two species.

All observations lasted 1 h and were performed between 0800 and 1600 at room temperature (around 20 °C). In no cases were crayfish shown to be disturbed by the observer. To annul the influence of starvation on agonism (Stocker and Huber 2001), each individual was regularly fed (and water was changed 1 h later) at the end of any bout of observation. Crayfish were used only once. With the exception of one case in experiment 1, no crayfish showed injuries at the end of experiments.

Experiment 1: agonistic dominance

We observed the agonistic behavior of seven heterospecific pairs during 5 consecutive days. One additional pair was discarded from our analysis because of the overnight death of one *Pa* at the fourth day of the experiment. Immediately before their first encounter, the members of each pair were introduced on opposite sides of a removable, opaque plastic divider placed in the experimental container. After 10 min of acclimation, the divider was lifted and our observations started. Between each 1-h observation period, the

two combatants were removed from the experimental container and returned to their individual containers for 10 min; the divider was then reinserted into the experimental container and the procedure described above was repeated.

The events occurring during any 1-h observation period were described on a tape recorder and from these data we obtained the following measures:

- (1) Total number of fights. A fight began when one opponent approached the other and ended when one of the two individuals ran away, backed off, or tail-flipped away from the other to a distance longer than one body length for at least 10 s. Tail-flipping away is a backward swimming response involving the sudden forward contraction of the abdomen.
- (2) Duration of fights (s).
- (3) The attacker in each fight, i.e., the individual that clearly approached the rival.
- (4) The winner of each fight, i.e., the individual that did not retreat or that retreated after the opponent had assumed a "Body Down" posture or remained motionless (see Bruski and Dunham 1987 for the description of these behavioral patterns). In the very few cases when both individuals retreated simultaneously, each was scored as losing to the other. If the observation period ended before an opponent retreated, the fight was not used to determine rank orders.
- (5) Observed behavioral patterns. Thirteen behavioral patterns, following Bruski and Dunham (1987), Gherardi and Daniels (2003), and Gherardi and Pieraccini (2003), were classified in the following six behavioral categories (behavioral patterns in parentheses): approach (Approaching, Following), retreat (Backwards, Run Away, Tail-flip), visual displays (Meral Spread, Lunge), weak contacts (Push, Antenna Tap), strong contacts (Interlocked, Chela Strike), and status signals (Body Up, Body Down). For the subsequent analysis, we computed the total number of behavioral patterns and the number of patterns per behavioral category.

Experiment 2: competition for a shelter

We analyzed the competition of 12 heterospecific pairs for a shelter. Shelters were similar to those used during the isolation phase (i.e., 10 cm long pieces of rigid, gray, straight PVC pipe). These artificial shelters had the length and internal diameter suitable for the size range of the individuals under study (Nakata and Goshima 2003). Because of their dimensions, shelters could be occupied by only one animal at a time. Pilot tests showed that the two species did not show consistently different occupancy of differently colored PVC pipes (in contrast, black shelters were preferred by the populations of *P. zonangulus* and *P. clarkii* studied by Blank and Figler 1996). During the isolation phase, shelter occupancy was recorded for 1 h/day. After 2 days, more than 50% of specimens of *Pa* and *Pc* were found to use the shelter, suggesting that 2 days is the minimum time required to accustom crayfish of both species to the artificial burrow.

At the beginning of the experiments, the two individuals were placed simultaneously into the opposite halves of the experimental container to avoid the effect of prior residence (Peeke et al. 1995) and their behavior was observed for 1 h during 2 consecutive days. In addition to the measures de-

scribed above for experiment 1, we also recorded the time spent by an individual inside the shelter. An animal was designated as being in the shelter if at least three fourths of its carapace was inside it.

Experiments 3: shelter use

Twelve individuals per species were kept isolated in the experimental container in the presence of a shelter as above. The duration of shelter occupancy during each 1-h period of observation was measured for each individual. Experimental animals were of the same size class (cephalothorax length: *Pa*, 37.7–43.6 mm; *Pc*, 45.5–50.4 mm) as the individuals tested in the other two experiments and were subjected during the isolation phase to the same procedure as in experiment 2.

Statistical analysis

We followed the techniques described by Sokal and Rohlf (1969) and Siegel and Castellan (1988). The assumptions of normality of data and homogeneity of variance were not met and some measures represented ordinal data. Therefore, we applied nonparametric tests. Mann–Whitney tests (statistic: *U*) were used to examine differences between independent samples, while related samples were analyzed by Wilcoxon's matched-pairs signed-ranks tests (statistic: *T*) and Friedman two-way analyses of variance by ranks (statistic: *F_r*). Multiple comparisons tests allowed us to determine which pairs of samples differed significantly when the null hypothesis was rejected by Friedman tests, α levels being adjusted by Bonferroni corrections. *G* tests (statistic: *G*) were used for frequency data. Following Siegel's (1956) recommendation, text and figures provide medians and interquartile ranges (first–third quartiles), which are the statistics most appropriate for describing the central tendency of scores in the ordinal scales analyzed by nonparametric tests. Except for cases with Bonferroni corrections, *P* values <0.05 were considered statistically significant.

Results

Experiment 1: agonistic dominance

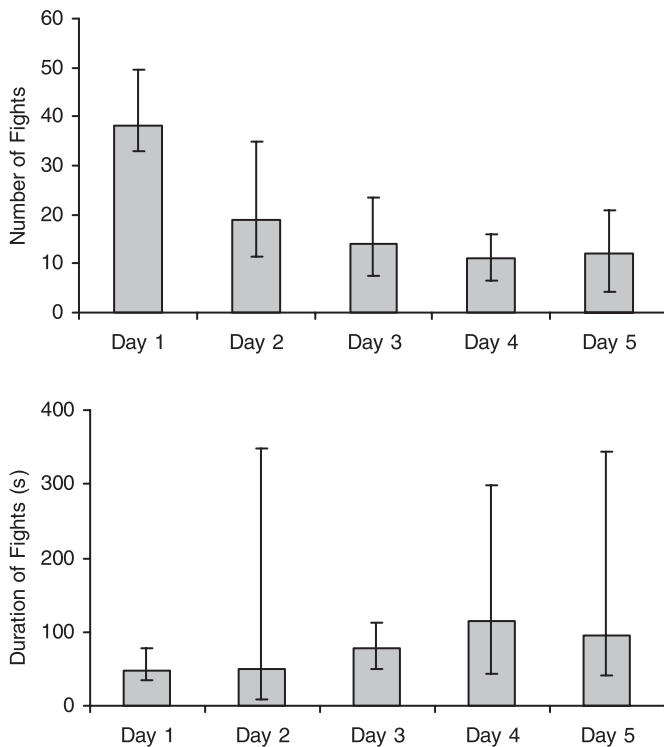
Number and duration of fights

The number of fights significantly decreased from day 1 to day 5 ($F_r = 15.884$, $n = 5$, $P < 0.01$), being higher in day 1 than in the subsequent days of combat (after a multiple comparisons test and Bonferroni correction, $P < 0.01$) (Fig. 1). Overall, the median time spent fighting was 1320 s per hour of observation ($n = 35$; range 1183–1669 s). Fights lasted, on average, 77.5 s ($n = 35$; range 44.6–316.5 s), their duration remaining constant ($F_r = 5.486$, $n = 5$, ns) over time (Fig. 1).

Attacks and wins

For the whole period of combat, *Pc* was the attacker more often than *Pa* ($U = 9-10.5$, $P < 0.05$). The number of attacks by *Pa* decreased ($F_r = 9.708$, $n = 5$, $P < 0.05$) from day 1 to day 5 (after a multiple comparisons test and Bonferroni correction, $P < 0.01$), but remained constantly high for *Pc* ($F_r = 9.374$, $n = 5$, ns) (Fig. 2). *Pc* was most often the winner ($U = 0.5-10.5$, $P < 0.05$) and the relative frequency of its wins never varied with time ($F_r = 1.594$, $n = 5$, ns; similarly, for

Fig. 1. Experiment 1: median values (and interquartile ranges) of number (top) and duration (bottom) of fights on each of the 5 days of combat (seven pairs of *Procambarus acutus acutus* and *Procambarus clarkii*).

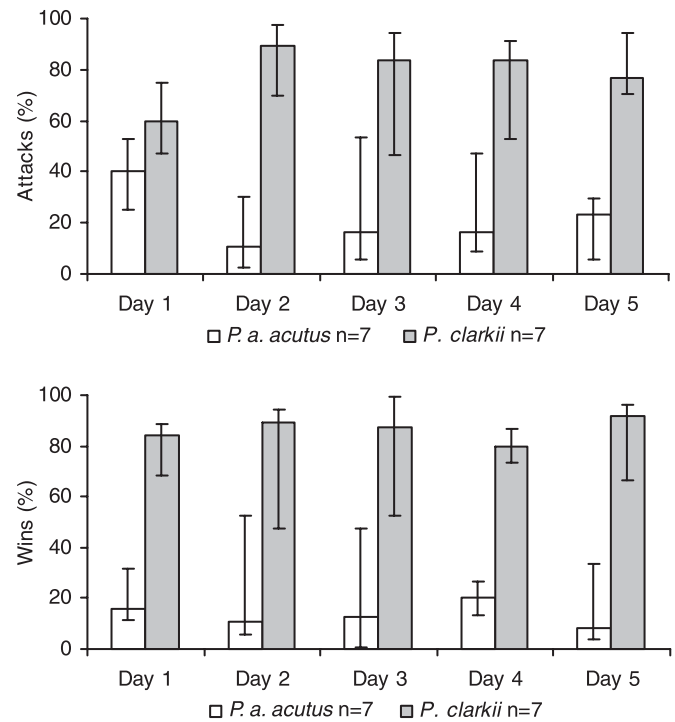


Pa, $F_r = 1.594$, $n = 5$, ns) (Fig. 2). Of the attacks by *Pc*, 72.7%–92.9% were followed by wins; in contrast, only 20%–37.5% of attacks by *Pa* were followed by wins.

Behavioral patterns

The relative frequencies of weak ($F_r = 11.588$, $n = 5$, $P < 0.05$) and strong ($F_r = 14.512$, $n = 5$, $P < 0.01$) contacts and of status signals ($F_r = 26.479$, $n = 5$, $P < 0.01$) significantly decreased with time for *Pa*. The execution of visual displays decreased with time for *Pc*, which, in contrast with *Pa*, increased its signaling of status ($F_r = 27.488$, $n = 5$, $P < 0.01$). For the other behavioral categories, F_r was < 9 (ns). After having pooled the data from the 5 days of study, we found that the dominant *Pc* approached the rival ($U = 0$, $n_1 = 7$, $n_2 = 7$, $P = 0.000$) and performed weak ($U = 3$, $n_1 = 7$, $n_2 = 7$, $P = 0.002$) and strong contacts ($U = 4$, $n_1 = 7$, $n_2 = 7$, $P = 0.003$) more often than *Pa*, while the subordinate *Pa* retreated more often than *Pc* ($U = 1$, $n_1 = 7$, $n_2 = 7$, $P = 0.001$) (Fig. 3). In contrast, no difference between species was found for visual displays ($U = 20.5$, $n_1 = 7$, $n_2 = 7$, ns) and status signals ($U = 13$, $n_1 = 7$, $n_2 = 7$, ns). Tail-flips were executed predominately by *Pa* (0–41/h) and were practically absent from *Pc*'s behavioral repertoire. The number of behavioral patterns performed during each fight did not vary with time for either species (*Pa*, 2.16–5.60/fight, $F_r = 5.371$, $n = 5$, ns; *Pc*, 4.20–6.08/fight, $F_r = 0.571$, $n = 5$, ns) and did not differ between *Pa* and *Pc* (average for the 5 days of study, $U = 17$, $n_1 = 7$, $n_2 = 7$, ns).

Fig. 2. Experiment 1: median values (and interquartile ranges) of relative frequency of attacks (top) and wins (bottom) performed by *P. a. acutus* and *P. clarkii* (seven pairs), compared among the 5 days of combat. In all days of combat we found a significant difference between species ($P < 0.01$ after Bonferroni correction).



Experiments 2 and 3: competition for a shelter and shelter use

Number and duration of fights

The number of fights (medians: 16 vs. 11; $T = 20.5$, $n = 12$, ns) and their duration (medians: 86 s vs. 60 s; $T = 17$, $n = 12$, ns) did not vary between days 1 and 2. A comparison of these measures between experiment 1 and experiment 2 in the first day of combat showed that fights were less numerous in the presence of a shelter than in the absence of a shelter ($U = 7$, $n_1 = 7$, $n_2 = 12$, $P < 0.002$) but fights in both experiments had the same duration ($U = 23$, $n_1 = 7$, $n_2 = 12$, ns).

Attacks and wins

Pc attacked the rival more often than *Pa* ($U = 26$, $n_1 = 12$, $n_2 = 12$, $P < 0.02$) and won the majority of fights ($U = 0$, $n_1 = 12$, $n_2 = 12$, $P < 0.001$). The relative frequency of either attacks or wins (Fig. 4) did not differ between days 1 and 2 for either species (*Pa*: attacks, $T = 38$, $n = 12$, ns; wins, $T = 26$, $n = 12$, ns; *Pc*: attacks, $T = 38$, $n = 12$, ns; wins, $T = 26$, $n = 12$, ns). Neither did the percentages of attacks ($U = 36$, $n_1 = 12$, $n_2 = 7$, ns) and wins ($U = 34$, $n_1 = 12$, $n_2 = 7$, ns) by *Pc* vary in the first day of combat between experiment 1 (absence of a shelter) and experiment 2 (presence of a shelter).

Behavioral patterns

Between days 1 and 2 we found in *Pa* an increase in the relative frequency of retreats ($T = 7$, $n = 12$, $P = 0.01$) and a decrease in the relative frequency of both weak ($T = 7$, $n = 12$, $P = 0.01$) and strong ($T = 12$, $n = 12$, $P < 0.05$) contacts.

Fig. 3. Experiment 1: frequency (median values and interquartile ranges) of each of the six behavioral categories analyzed (approaches, retreats, visual displays, weak contacts, strong contacts, and status signals), compared between species. Data from the 5 days of combat were pooled. **, $P < 0.01$.

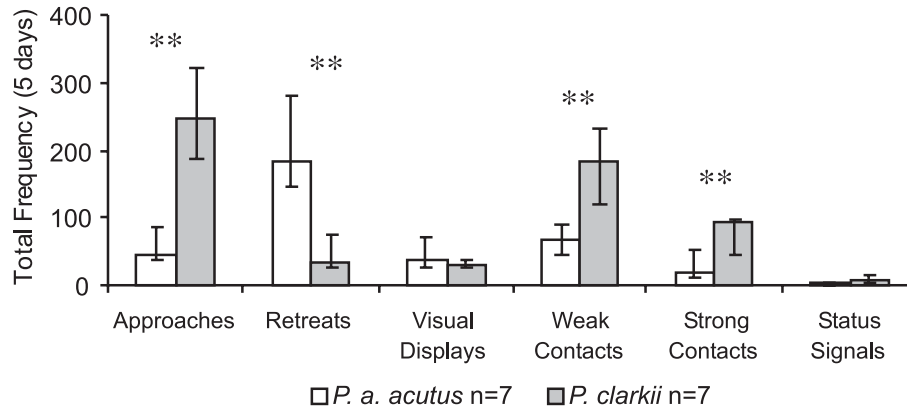
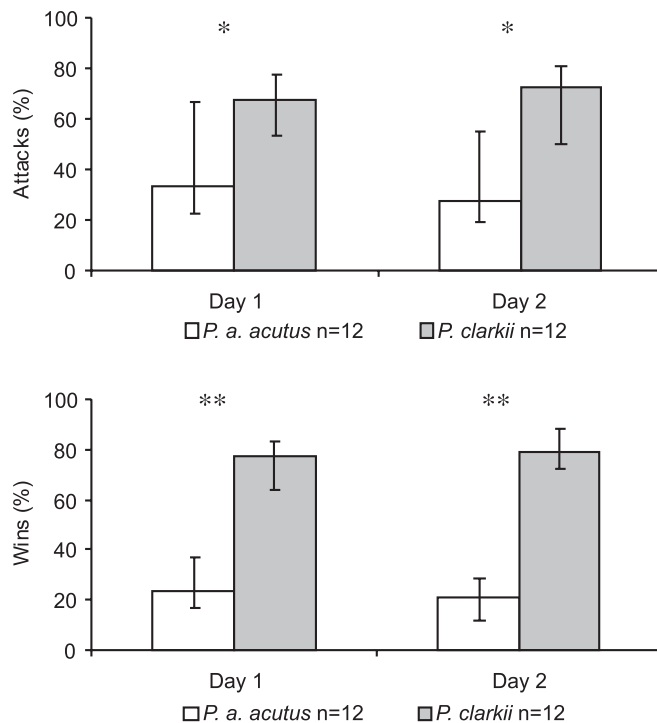


Fig. 4. Experiment 2: relative frequency (median values and interquartile ranges) of attacks (top) and wins (bottom) performed by *P. a. acutus* and *P. clarkii* (12 pairs), compared between 2 days of combat. *, $P < 0.05$; **, $P < 0.01$.



For the other behavioral categories in this species and for all the behavioral categories in *Pc*, T was >31 ($n = 12$, ns). After having pooled the recorded data from the 2 days of study, we revealed the same pattern as that shown in experiment 1, i.e., the dominant *Pc* approached the rival ($U = 17.5$, $n_1 = 12$, $n_2 = 12$, $P < 0.002$) and displayed weak ($U = 27$, $n_1 = 12$, $n_2 = 12$, $P < 0.02$) and strong contacts ($U = 25.5$, $n_1 = 12$, $n_2 = 12$, $P < 0.02$) more often than *Pa*, while the subordinate *Pa* retreated more often than *Pc* ($U = 2.5$, $n_1 = 12$, $n_2 = 12$, $P < 0.001$) (Fig. 5). In contrast, no difference was found between species for visual displays ($U = 71.5$, $n_1 = 12$, $n_2 = 12$, ns) and status signals ($U = 45$, $n_1 = 12$, $n_2 = 12$, ns). The comparison between experiment 1 and experiment 2 of the behavioral categories executed in the first day

of combat revealed no significant differences for either species ($U = 24-42$, $n_1 = 7$, $n_2 = 12$, ns).

Shelter occupancy

Shelter use was the same between the 2 days of combat ($T = 19$, $n = 12$, ns). Differences between species, analyzed separately for each day, were not significant (day 1: *Pa* vs. *Pc*, 747 s vs. 582 s, $T = 32$, $n = 12$, ns; day 2: *Pa* vs. *Pc*, 147 s vs. 437 s, $T = 19$, $n = 11$, ns), and the time spent in the shelter did not increase from the first to the second day of combat for either species (*Pa*, $T = 17$, $n = 11$, ns; *Pc*, $T = 10$, $n = 9$, ns). Exits from the shelter occurred spontaneously for *Pc*, whereas *Pa* was most often forcibly pulled from the shelter by *Pc* and chased away from it ($G = 32.381$, $df = 1$, $P < 0.001$) (Fig. 6). Results from experiment 3 showed that in a noncompetitive context *Pa* spent a longer time in the shelter than *Pc* ($U = 20$, $n_1 = 12$, $n_2 = 12$, $P < 0.002$) (Fig. 7). As a consequence, shelter occupancy by *Pa* was, in absolute terms, shorter in the presence than in the absence of a competitor ($U = 37$, $n_1 = 12$, $n_2 = 12$, $P < 0.05$). Contrary to our expectations, *Pc* did not make exclusive use of the shelter in the presence of a competitor but mostly remained in the open, exhibiting behavior similar to that in the non-competitive context ($U = 54$, $n_1 = 12$, $n_2 = 12$, ns).

Discussion

Consistent with the view of hierarchies as means to mitigate agonism (Wilson 1975), we found that the formation of a dominance relationship in the dyad *P. a. acutus* and *P. clarkii* was accompanied by a significant reduction over time in the number of fights (but the duration of fights remained constant) and the development in the loser of typical subordinate behavior (Copp 1986; Guiasu and Dunham 1997a, 1997b, 1999; Issa et al. 1999; Gherardi and Daniels 2003).

Our study validated the hypothesis that adult *P. clarkii* dominates over similarly sized *P. a. acutus*, despite having significantly shorter chelae (and therefore less efficient RHP; Maynard Smith and Parker 1976). In crayfish and in many other crustacean decapods, the size of the weapon is considered to be a major determinant of the dominance order (Bovbjerg 1953, 1956; Rabeni 1985; Pavey and Fielder 1996). Moreover, *P. clarkii* is more likely to prey upon *P. a. acutus* when the size difference is large (F. Gherardi, personal

Fig. 5. Experiment 2: frequency (median values and interquartile ranges) of each of the six behavioral categories analyzed (approaches, retreats, visual displays, weak contacts, strong contacts, and status signals), compared between species. Data from 2 days of combat were pooled. **, $P < 0.01$.

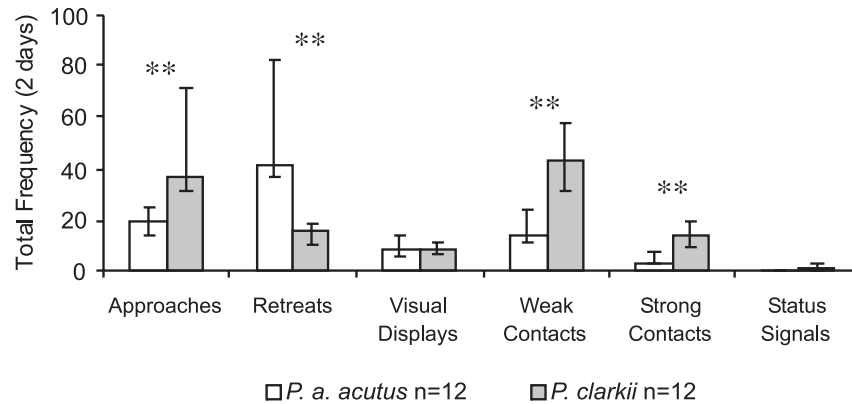
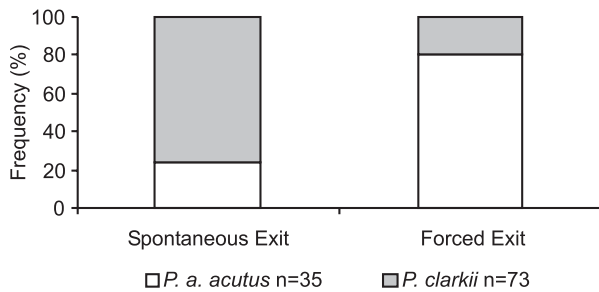


Fig. 6. Experiment 2: relative frequency of spontaneous and forced exits from the shelter compared between *P. a. acutus* and *P. clarkii*. Forced exits are instances in which a crayfish was evicted and chased away from the shelter by the rival.

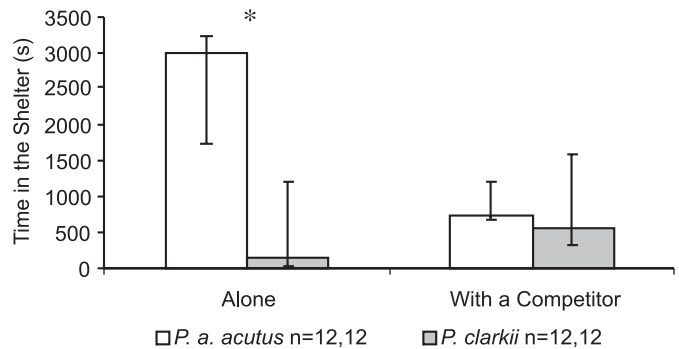


observations). In fact, as pointed out by Holdich and Domaniewski (1995), adult crayfish may prey on other crayfish species more extensively than previously thought. Interestingly, these asymmetries in agonistic potential of the two species might be reverted in young stages: data collected by Mazlum and Eversole (2005) from South Carolina showed that young-of-the-year and juvenile *P. a. acutus* grew faster and survived better than *P. clarkii* in different competitive settings when the two species were held together.

A further asymmetry between the two species was found in the two species' behavioral repertoires: *P. a. acutus* performed many more tail-flip escape behaviors than *P. clarkii*. By tail-flipping, the subordinate crayfish swims above the substrate, higher in the water column, where it is more vulnerable to fish predation (Garvey and Stein 1993; Guiasu and Dunham 1999). This can even lower the likelihood of survival for *P. a. acutus* as a direct consequence of the attacks performed by *P. clarkii*.

The establishment of a hierarchy has been shown to play a fundamental role in the acquisition and defense of shelters in many marine (e.g., fiddler crabs (Hyatt and Salmon 1978); lobsters (O'Neill and Cobb 1979; Cowan and Atema 1990)) and freshwater decapods (e.g., crayfish (Penn and Fitzpatrick 1963; Bovbjerg 1970; Capelli and Munjal 1982; Garvey et al. 1994; Blank and Figler 1996)). The crayfish literature reports several examples of dominant species competitively excluding subordinate crayfish from sheltered areas (Capelli and Munjal 1982; Söderbäck 1991; Blank and

Fig. 7. Experiments 2 and 3: median values (and interquartile ranges) of time spent in the shelter by the two species compared between noncompetitive (alone, experiment 3, 12 pairs) and competitive contexts (with a competitor, first day of experiment 2, 12 pairs). *, $P < 0.05$.



Figler 1996), whereas the availability of shelter-providing substrates constitutes one of the most important variables related to crayfish abundance (Capelli and Magnuson 1983). Similar results were obtained in laboratory studies in which dyads of invasive and indigenous crayfish species were compared for their agonistic potential (*P. leniusculus* and *A. astacus* (Söderbäck 1991); *P. leniusculus* and *A. torrentium* (Vorburger and Ribi 1999); and *P. leniusculus* and *C. japonicus* (Usio et al. 2001; Nakata and Goshima 2003)).

We found that fights between *P. a. acutus* and *P. clarkii* were less numerous and had the same duration when individuals competed for a shelter than when they battled in its absence. Somewhat surprising are the results obtained from the study of shelter occupancy. Because *P. clarkii*, in a non-competitive context, seemed to have a lower preference for the offered type of shelter than *P. a. acutus*, we expected that the former species would gain less from occupying the shelter than *P. a. acutus* and therefore would defend it less vigorously. It has been repeatedly demonstrated that differences in pay-off strongly influence the outcome of animal conflicts (Parker 1974; Maynard Smith and Parker 1976; Parker and Rubenstein 1981). Unexpectedly, *P. a. acutus* spent a shorter amount of time in the shelter in a competitive context than in the absence of a rival, mostly because *P. clarkii* evicted it from the shelter and chased it away. However, the exclusion

of *P. a. acutus* from the resource was not followed by *P. clarkii* making exclusive use of the shelter. To the contrary, the winner most often remained in the open, as in the noncompetitive context. To our knowledge, this type of behavior, which, following Hamilton's (1970) terminology, may be defined as "spiteful", has never been described in crayfish or in other crustaceans.

Obviously, caution must be used in extrapolating these laboratory results to the field, since at the moment we have scarce knowledge of agonism between the two species in the natural setting and we do not have any first-hand record of the actual disposability of resources in the natural habitat or their use by crayfish. However, laboratory experiments are invaluable in elucidating the behavioral mechanisms and the environmental components that affect aggression (Bergman and Moore 2003). By controlling different aspects of agonistic interactions, such as size, sex, and shelter accessibility, a researcher can test facets of agonistic behavior that are not easily controlled in a natural setting. And, with a few exceptions (Rorer and Capelli 1978), the results of several previous laboratory studies of the aggressive interactions between possibly competing crayfish species were also consistent with observed distributional patterns (Guiasu and Dunham 1999). Crayfish species expanding their range by competitively excluding other crayfish species are also the dominant species in interspecific contests staged in laboratory studies (Penn and Fitzpatrick 1963; Bovbjerg 1970; Capelli and Munjal 1982; Söderbäck 1991; Garvey and Stein 1993).

A shortcoming of our study is that we have limited our analysis to agonistic behavior. There are several mechanisms other than direct competition that may have an effect on species replacements. For instance, differential predation by fish seemed to have contributed to the replacement of the indigenous *O. virilis* and of the exotic *Orconectes propinquus* (Girard, 1852) by the exotic *O. rusticus* in northern Wisconsin lakes (DiDonato and Lodge 1993) and of *Orconectes sanborni* (Faxon, 1884) by *O. rusticus* in Ohio streams (Mather and Stein 1993). And the rapid displacement of *A. astacus* by *P. leniusculus* was possibly caused by the synergistic effects of interspecific competition, differential predation on juveniles of the two species, and reproductive interference between the two species (Söderbäck 1995).

To provide a more complete picture of the potential replacement of the indigenous crayfish by the invasive *P. clarkii*, future studies on *P. a. acutus* versus *P. clarkii* should analyze multiple factors, including the autoecology of the two species. Also, comparative studies of reproductive potential and recruitment patterns should be undertaken to determine the actual dominance–subordinance relationships between species. For instance, the more fecund and more frequently spawning *P. clarkii* (Huner 1994) was found to generate more recruits in Louisiana culture ponds than the faster growing and more aggressive *P. zonangulus* (Mazlum and Eversole 2005). In contrast, *P. a. acutus* produce fewer but larger eggs than *P. clarkii*, yielding significantly larger hatchlings (Mazlum and Eversole 2005). The body size advantage of the young, coupled with their faster growth, may induce the substitution of *P. clarkii* by *P. a. acutus*, as observed in culture ponds of South Carolina (Eversole et al. 1999; Mazlum and Eversole 2005).

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