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ORIGINAL PAPER

Past ownership makes crayfish more aggressive

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Abstract There is plenty of evidence that resource value is one of the most important non-strategic variables in animal fighting behavior. Here, we tested whether the past ownership of a shelter might modify the agonistic behavior of the crayfish *Austropotamobius pallipes*, eventually increasing its probability to win when it reencounters a previously met conspecific away from that resource. The agonistic behavior of familiar pairs composed of size-matched males was observed for an hour; after that, the two contestants had been kept in isolation for 2 days, either in the presence or in the absence of a shelter. Specifically, in the isolation phase, a shelter was offered to (1) both crayfish, (2) no crayfish, (3) the dominant crayfish only, and (4) the subordinate crayfish only. The following combat was conducted in the absence of any refuge. The crayfish that previously owned a shelter showed a higher aggressive motivation to fight than the individuals kept without a shelter. Particularly, in the pairs (4), subordinate crayfish were even more aggressive than dominants but were never able to invert hierarchies. Taken together, our results confirm the role played by shelters as determinants of agonism and also show, for the first time, how the behavior of crayfish and their internal state may be affected by their past ownership of a resource.

Keywords Past ownership · Shelter · Fighting behavior · Crayfish · *Austropotamobius pallipes*

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Introduction

Most animals engage fights for the access of crucial but limited resources, such as mate, food, or shelter (Hack et al. 1997; Bridge et al. 2000; Lindström and Pampoulie 2005). A multiplicity of factors governs the intensity and duration of such fights (Enquist and Jakobsson 1986), but the value of the resource at stake (RV) is likely to be the most important non-strategic variable in fighting behavior (Enquist and Leimar 1987; Parker 1974; Riechert 1998). RV results from the combination between the inherent quality of the resource (the absolute resource value) and the value that an animal assigns to it as the effect of its internal state (the subjective or relative resource value; McNamara and Houston 1989). Absolute and relative RVs together affect an animal's motivation to fight. So, this is generally higher in hungry rather than in satiated individuals (Griffiths 1992; Hazlett et al. 1975; Lawton 1987; Stocker and Huber 2001; Wilcox and Ruckdeschel 1982) or in reproductive males in the presence of a female when the probability to find another mate is low (Keeley and Grant 1993).

Several empirical studies have investigated the effects of RV on the outcome of fights, most often confirming the hypothesis that a contestant that expects a greater benefit from winning is generally more likely to do so (e.g., Austad 1983; Bridge et al. 2000; Cant et al. 2006; Smith et al. 1994; Tibbetts 2008). The influence that the perceived ownership of a resource (through the phenomena of “prior exposure” or “prior residence”) has on the behavior of a contestant has been shown in several invertebrates and vertebrates (Austad 1983; Beaugrand and Zayan 1985; Bentley et al. 2009; Chellappa et al. 1999; Enquist and Leimar 1987; Fayed et al. 2008; Figler et al. 1976; Hack et al. 1997; Humphries et al. 2006; Peeke et al. 1995; Riechert

1984). However, in all the above-listed studies (except Hack 1997), the resource was “physically” present during the contests and in close proximity to the contestants. On the contrary, our interest here is to understand whether the past ownership of a shelter has still an influence on the agonistic behavior of its owner even in its absence.

Since Bovbjerg (1953, 1956), crayfish have been often used as model organisms to understand several relevant aspects of the agonistic behavior in invertebrates. Many species form, at least in confined environments, stable dominance hierarchies that secure prior access to a given resource (in *Orconectes virilis*: Bovbjerg 1953; *Cambarellus shufeldtii*: Lowe 1956; *Procambarus clarkii*: Copp 1986; *Procambarus acutus acutus*: Gherardi and Daniels 2003; *Austropotamobius pallipes*: Tricarico et al. 2005). Among the different resources, shelters are usually limited in the habitat and serve multiple functions (Bovbjerg 1970; Capelli and Magnuson 1983; Lodge and Hill 1994). They minimize the risks of predation (DiDonato and Lodge 1993; Englund 1999; Englund and Krupa 2000; Garvey et al. 1994; Hill and Lodge 1999; Lodge and Hill 1994; Olsen et al. 1991), allow for the successful completion of reproduction (Figler et al. 2001, 2005), and, in some species, even attract mates (Bergman and Moore 2003). The important role that a shelter plays in the lifecycle of crayfish explains its strong effect on agonism; in its presence, the intensity of fights increases (Bergman and Moore 2003; Edsman and Jonsson 1996), and shelter occupancy makes the owner more likely to win (Martin and Moore 2008).

A large number of studies has focused on the association between dominance and the use of a shelter (e.g., Capelli and Hamilton 1984; Fero et al. 2007; Herberholz et al. 2003; Martin and Moore 2008) and on the intra- and interspecific competition for its access (e.g., Gherardi and Cioni 2004; Gherardi and Daniels 2004; Figler et al. 2005; Peeke et al. 1995), but none have ever analyzed whether its past ownership influences the agonistic behavior of an individual when it is absent during the contest.

The white-clawed crayfish, *A. pallipes*, offers an ideal opportunity to investigate this issue. This species forms stable dominance hierarchies in the laboratory (Tricarico et al. 2005). The completion of its life cycle also depends on the available hiding places. It is not considered an active burrower such as other species (e.g., *Pacifastacus leniusculus*, *P. clarkii*, many *Orconectes* species; Hobbs 1988; but see Holdich 2003) but uses crevices in the river banks, stones, roots, and decaying wood as refuges (Bernardo et al. 1997; Garcìa-Arberas and Ralo 2000; Grandjean et al. 1996; Renai et al. 2006). The importance of shelters for *A. pallipes* has been confirmed by Gherardi and Cioni (2004), who showed their more extensive use by this species with respect to other freshwater decapods (the crayfish *P. clarkii* and the river crab *Potamon fluviatile*).

Based on the above premises, our hypothesis was that the past ownership of a shelter makes *A. pallipes* males more prone to combat and more able to win even in its absence.

Material and methods

Subjects, collection, and housing

To eliminate any factor that could induce an obvious bias to our experiments, only sexually mature, hard-shelled *A. pallipes* males in good conditions (no mutilations or visible parasites) were collected by hand from the streams Gattaia and Corsalone (northern Tuscany, Italy) in July 2008. In the laboratory, we measured their cephalothorax length (from 2.5 to 4.5 cm) and the width and length of both chelae. Crayfish were maintained in PVC aquaria (50×75 cm) containing constantly aerated water at the temperature of 18°C (±1°C), under a natural 14:10 h light/dark cycle regime and were fed every second day with a 0.1 g larva of *Sarcophaga calliphora*. The maintenance phase lasted for a maximum of 2 weeks. After the experiment, crayfish were returned to their collection site.

Experimental design

Experiments were conducted between 10:00 and 18:00 h. The experiments were composed of four phases, as follows.

Phase 1: isolation (1 week). One week was sufficient to remove any effect of previous social experience (Guiasu and Dunham 1997; Zulandt Schneider et al. 2001). Each individual was numbered on the cephalothorax using a white typing correction fluid for its recognition by the observer. Crayfish were kept isolated in opaque PVC aquaria (30×16 cm) with constantly aerated water and with a shelter; a shelter consisted of a brick (20×10×5 cm) that preliminary observations had shown to be used by crayfish and preferred over other types of refuge. Crayfish were fed every second day as in the maintenance phase.

Phase 2: familiarization (25 h). We formed a total of 41 size-matched pairs (maximum difference in the cephalothorax length and in the length of both chelae, 5%; in the width of both chelae, 2%). The two opponents were kept in an experimental tank (a circular opaque PVC container, diameter, 30 cm) without a shelter. Previous studies on this and other crayfish species (Gherardi and Daniels 2003; Tricarico et al. 2005; Tricarico and Gherardi 2007b) have shown that a 1-h contest, also in the absence of a shelter, does not cause injury to the experimental subjects. Additionally, when encounters appeared to escalate, yielding to the potential damage of at least one combatant, individuals were thus separated and the observation was considered over. In our study, one encounter only was interrupted and thus was discarded from the analysis. The tank was initially divided into two equal compartments separated by an opaque PVC divider for a 10-min acclimatization. Experiments started with the removal of the divider.

Crayfish behavior was video-recorded for 1 h using a Sony DCR-TRV33E for the analysis. Simultaneously, an experienced observer (E.T.) recorded the number of interactions and the winner of each interaction; winners were deemed the crayfish that did not retreat or that retreated after the opponent showed a motionless posture, typical of subordinates (Bruski and Dunham 1987). Dominants or alphas (and subordinates or betas) were defined as the crayfish winning more (and less) than 50% of the total interactions. No ties were ever recorded. Dominance averaged 78%. At the end of the observations, the pairs were left in the experimental aquaria for 24 h with an aerator.

Phase 3: maintenance with/without a shelter. Each crayfish from the 40 familiarized pairs were placed back into the same individual aquarium as used in isolation and were randomly assigned to one of the four categories of pairs that differed for the presence/absence of the shelter: (1) $\alpha^+\beta^+$ pairs (n=10): both crayfish had the shelter; (2) $\alpha^-\beta^-$ pairs (n=10): no crayfish had the shelter; (3) $\alpha^+\beta^-$ pairs (n=10): only alphas had the shelter; and (4) $\alpha^-\beta^+$ pairs (n=10): only betas had the shelter.

The crayfish were left undisturbed for 2 days in their respective aquaria and fed as in the maintenance phase. Previous observations (Tricarico and Gherardi, in prep.) had shown that, after 2 days of isolation, *A. pallipes* has not been stressed by the absence of a shelter and still recognizes the status of the former opponent.

Phase 4: reconstitution of the original pairs. For each pair, the original opponents were inserted into a novel experimental tank, following the same procedures as phase 2. After a 10-min acclimatization, their behavior was video-recorded for 1 h. No shelter was offered during the trials. A number code was given to each videotape for the subsequent reading by an observer, extraneous to the experimental design and to the authors' expectations but experienced in the description of crayfish behavior.

Data recorded

Along with dominance (the number of interactions won by a crayfish over the total interactions in percentage; see phase 2), during phase 4 we also recorded the parameters as follows:

1. Latency (in seconds), the time elapsed between the divider removal and the first interaction between the two opponents. One interaction begins when one crayfish approaches the rival and ends when one of them retreats to a distance of 10 cm for at least 10 s (Gherardi and Daniels 2003).
2. Percentage, and
3. Total duration (in seconds) of strong fights. Strong fights are here defined as the interactions in which at least one strong contact (see below) is executed.
4. Percentage of the approaches and of the strong contacts (i.e., chelae strikes and interlocked; Bruski and Dunham 1987), both indices of a high motivation to fight, performed by each of the two contestants.

We compared latency, percentage and duration of strong fights, dominance, and percentage of the strong contacts (these latter were considered as the sum of contacts performed by alphas and betas) among the different pairs; the percentage of the approaches and of the strong contacts were also analyzed per individual.

Statistical analyses

The analyses were conducted on the parameters recorded in phase 4. Data were tested for normality using the Kolmogorov–Smirnov test and for homogeneity of variance using the Levene test. Percentages were first normalized using the arcsine square root transformation. A one-way multivariate analysis of variance (MANOVA: statistic: F) was then used to compare all the recorded parameters among the different pairs; a two-way MANOVA was performed to compare the percentages of the approaches and of the strong contacts among the pairs and between alphas and betas. When we obtained significant F-ratios, we applied the Student–Newman–Keuls (SNK) multiple comparisons tests or the paired samples Student's t test (statistic: t) for the comparison between alphas and betas.

Figures give means (and SE). The level of significance at which the null hypothesis was rejected is α=0.05.

Results

The pairs differed significantly with respect to the dependent variables (F=17.34, df=5,34, p<0.0001). In $\alpha^-\beta^-$ pairs, latency was longer than the other pairs (F=10.44, df=3,40,

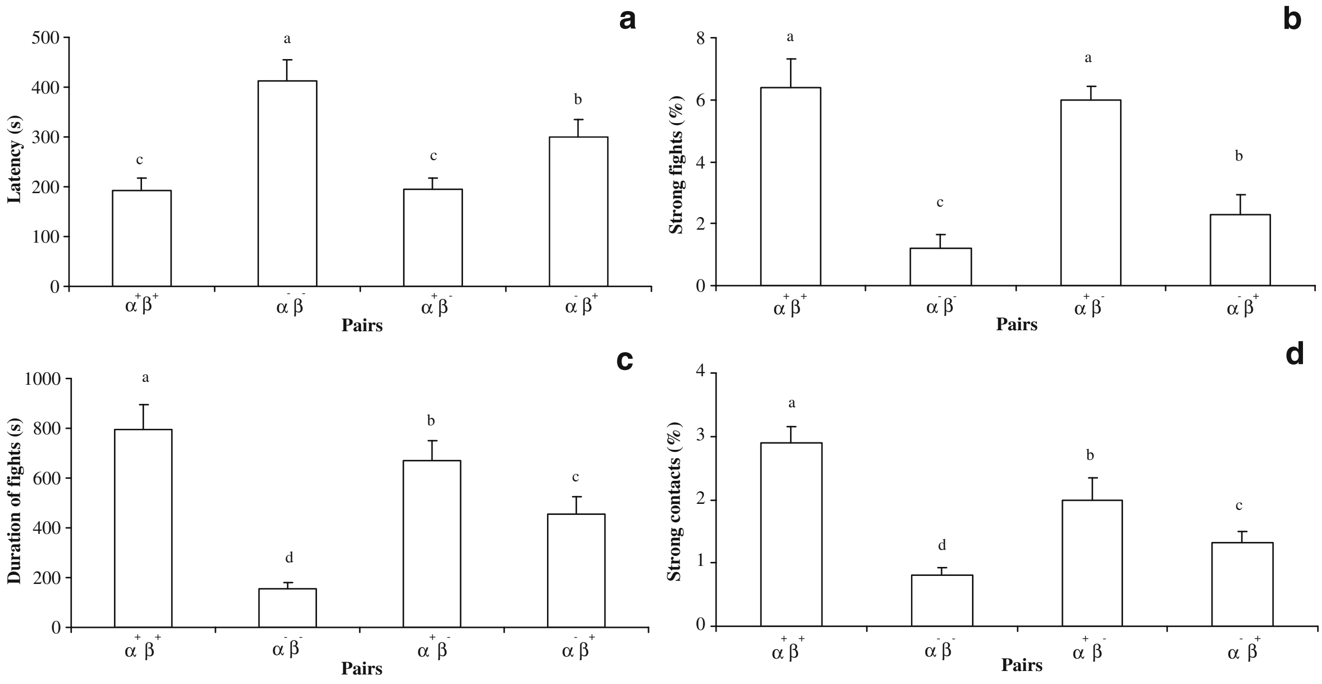

Fig. 1 Comparisons among the four categories of pairs ($\alpha^+\beta^+$=both crayfish with shelter; $\alpha^-\beta^-$=no crayfish with shelter; $\alpha^+\beta^-$=only alphas had the shelter; $\alpha^-\beta^+$=only betas had the shelter; n=10 for each pair) for (**a**) latency, (**b**) percentage of strong fights, (**c**) duration of strong fights, and (**d**) percentage of strong contacts. *Letters over bars* denote the hierarchy among pairs after Student Newman Keuls Multiple comparisons. *Bars* are means (+SE)

$p<0.0001$; $\alpha^-\beta^->\alpha^-\beta^+>\alpha^+\beta^-=\alpha^+\beta^+$), and strong fights were less numerous, shorter, and characterized by few strong contacts (number, $F=4.11$, $df=3.40$, $p=0.01$; $\alpha^+\beta^+=\alpha^+\beta^->\alpha^-\beta^+=\alpha^-\beta^-$; duration, $F=14.44$, $df=3,40$, $p<0.0001$; $\alpha^+\beta^+>\alpha^-\beta^+>\alpha^+\beta^-=\alpha^-\beta^-$; strong contacts, $F=14.32$, $df=3,40$, $p<0.0001$; $\alpha^+\beta^+>\alpha^+\beta^->\alpha^-\beta^+>\alpha^-\beta^-$; Fig. 1). Dominance was similar among pairs ($F=0.30$, $df=3,40$, $p=0.83$), and no inversion of hierarchies was observed. The two-way MANOVA showed significant differences among pairs and between hierarchical status ($F=17.41$, $df=3,75$, $p<0.0001$) with respect to the dependent variables. A significant interaction was also found between pairs and hierarchical status (Table 1). In all pairs, except $\alpha^-\beta^-$, the percentage of approaches and strong contacts significantly differed between alphas and betas, with these latter performing more approaches and strong contacts in $\alpha^-\beta^+$ pairs (t between 4.27 and 8.54, $df=9$, p between 0.0001 and 0.002; for $\alpha^-\beta^-$: t between 1.29 and 1.50, $df=9$, p between 0.17 and 0.23; Fig. 2).

Discussion

Our study clearly shows that the agonistic behavior of *A. pallipes* is affected by the past ownership of a shelter. In fact, previous owners showed a higher motivation to fight

Table 1 Comparisons among the four categories of pairs and between alphas and betas for percentage of approaches and strong contacts after two-way MANOVA (statistic: *F*), followed by Student Newman Keuls Multiple Comparisons

	Pairs				Hierarchical status				Pairs×hierarchical status		
	F value	*df*	*p* value	Hierarchy	*F* value	*df*	*p* value	Hierarchy	*F* value	*df*	*p*value
Approaches (%)	10.10	3	<0.001[a]	$\alpha^+\beta^->\alpha^+\beta^+=\alpha^-\beta^+>\alpha^-\beta^-$	51.28	1	<0.001[a]	alphas>betas	4.32	3	0.007[a]
Strong contacts (%)	23.64	3	<0.001[a]	$\alpha^+\beta^+>\alpha^+\beta^->\alpha^-\beta^+>\alpha^-\beta^-$	90.68	1	<0.001[a]	alphas>betas	17	3	<0.001[a]

Category pairs: $\alpha^+\beta^+$ =both crayfish with shelter; $\alpha^-\beta^-$ =no crayfish with shelter; $\alpha^+\beta^-$ =only alphas had the shelter; $\alpha^-\beta^+$ =only betas had the shelter; n=10 for each pair

[a] Significant differences

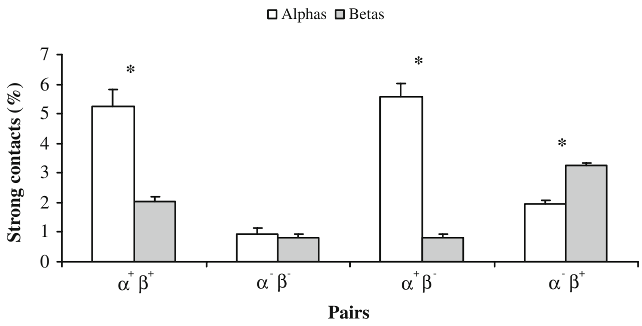

Fig. 2 Means (+SE) of the frequency of strong contacts in percentage distinguished between alphas and betas ($\alpha^+\beta^+$=both crayfish with shelter; $\alpha^-\beta^-$=no crayfish with shelter; $\alpha^+\beta^-$=only alphas had the shelter; $\alpha^-\beta^+$=only betas had the shelter; n=10 for each pair). *Asterisk* denotes a significant difference between alphas and betas after the paired samples Student's *t* test

than the individuals that had been maintained in its absence, as indicated by the more numerous approaches and strong contacts they executed.

Previous studies had shown that prior access to a resource and its ownership can affect behavior in different ways and in a multitude of taxa. In the hermit crab *Pagurus longicarpus*, individuals that had been subject to a worsening in the quality of their shell are more willing to initiate and escalate fights (Gherardi 2006; Tricarico and Gherardi 2007a). Insects may increase their foraging efficiency according to their past experience at particular sites (Ohashi and Thomson 2005). Prior experience, in concert with appropriate physiological conditions, also influences an insect's reproductive behavior. For example, male seaweed flies are more likely to mount females if they have had prior exposure to seaweed (Dunn et al. 2002); in the walnut fly, *Rhagoletis juglandis*, experience with a limiting resource such as a host plant or territory influences its mating behavior (Carsten and Papaj 2005); and the preference of the black field cricket females for given male traits depends on their prior exposure to a high- or a low-protein diet (Hunt et al. 2005). Males of the sparrow *Melospiza melodia* that previously held territories on a site, regardless of whether they were holding the same territory as the previous year, show higher levels of territory defense than males that are new to that site (Hyman et al. 2004). In the swordtail fish *Xiphophorus birchmanni*, food-deprived females are more motivated to explore the environment, displaying a stronger preference for chemical cues associated with a male nutritional state (Fisher and Rosenthal 2006), while in meadow voles *Microtus pennsylvanicus* an interruption in food availability of only 6 h inhibits the female interactions with males (Pierce et al. 2005).

In our study, both alphas and betas maintained in isolation without a shelter were less prone to attack and showed less numerous and lasting fights with few strong contacts. On the contrary, they were more aggressive when they have had previous access to a shelter: in $\alpha^-\beta^+$ pairs betas even displayed more strong contacts than alphas. However, as a confirmation that hierarchies may also depend on asymmetries in the intrinsic characteristics and social experience of the opponents (Tricarico and Gherardi 2007b), betas did not succeed in changing its rank. Similarly, the cichlid *Cichlasoma nigrofasciatum* subordinates, after having had access to a mate, tended to bite first in the subsequent contest, even though they did not always win (Keeley and Grant 1993).

Prior residence (or exposure) to a resource is known to overcome the inferior fighting ability of some species: it increases an animal's resource holding power (Fayed et al. 2008; Tricarico et al. 2008), thus affecting the agonistic behavior and the probable wins of the resident but always in the presence of that resource or of visual/chemical stimuli produced by it. On the contrary, in our study, the effects that a resource has on the agonistic behavior of the owner are evident also in its absence. Before our study, a similar phenomenon was observed only in the cricket *Acheta domesticus*: males that owned a burrow continued to win more encounters also when combated in an open arena, away from the burrow (Hack 1997). In both this and our case, the “mechanical” advantage of possessing a resource (Fayed et al. 2008) cannot be an explanation of the phenomenon, being the contestants away from it. It thus seems that the former condition of “resource owner” not only alters the internal state of the contestant, increasing the subjective value it assigns to that resource (and so its motivation to fight), but it is possibly memorized by an animal and alters its subsequent behavior without the need of being again exposed to the shelter. Indeed, crayfish have well-demonstrated memory capabilities: they recognize an opponent after 2 weeks of isolation (Hemsworth et al. 2007), establish associations between odors and predation risks (Hazlett et al. 2002), and remember the spatial configuration of a previously explored area (Barbaresi and Gherardi 2006).

In conclusion, our study pinpoints the relevant role of shelter as determinants of agonism in crayfish, and shows, for the first time, how the past ownership of these critical resources alters the behavior and the internal state of crayfish, even in their absence. In essence, our results here raise new and stimulating questions about the cognitive abilities of this taxon.

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