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ORIGINAL PAPER

Who's what? Prompt recognition of social status in crayfish

Laura Aquiloni · Vera Gonçalves · Alberto F. Inghilesi · Francesca Gherardi

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Abstract Crayfish are excellent model organisms to study the proximate mechanisms underlying the maintenance of dominance hierarchies in invertebrates. Our aim here was to investigate whether *Procambarus clarkii* males use social eavesdropping to discriminate dominant from subordinate crayfish. To this end, we conducted an experiment composed of a "passive" and an "active" phase. In the passive phase, "focal" individuals were allowed (treatment 1) or not (treatment 2) to see and smell two size-matched crayfish fighting while, in the subsequent active phase, they were allowed to freely interact with the fighting dyad. None of the recorded variables showed any significant difference between the two treatments, but, invariably, focal individuals were able to promptly discriminate dominant from subordinate crayfish. This study provides evidence that male crayfish recognize the social status of a conspecific without the need of direct or indirect experience with it and avoid dominants—and thus dangerous opponents—by means of a badge of status. A form of "winner and loser effects" could also contribute to the structuring of dominance/subordinate relationships. The implication of these results in understanding the maintenance of dominance hierarchies in invertebrates are discussed and compared with findings previously achieved in the context of mate choice by *P. clarkii* females, who do appear to use eavesdropping to identify dominants and subordinates.

Keywords Status recognition · Hierarchy · Individual recognition · Invertebrates · Crayfish

Introduction

In the majority of animal species, agonistic interactions between conspecifics lead to the formation of relatively stable dominance hierarchies in which individuals are ranked based on who wins against whom (Wilson 1975). Among invertebrates, crayfish are excellent model organisms to study the proximate mechanisms adopted to establish and maintain dominance hierarchies (Gherardi et al. 2010a). They exhibit easily identifiable behavioural patterns that escalate giving rise to fights of increased severity until dominance hierarchies are formed (Bovbjerg 1953; Bruski and Dunham 1987; Huber and Kravitz 1995; Zulandt-Schneider et al. 2001; Bergman et al. 2003; Gherardi and Pieraccini 2004). At that point, the number and intensity of fights decrease, and crayfish behave consistently with the social status achieved: the dominant displays a raised posture, is the initiator of most attacks and gains first access to resources, whereas the subordinate displays a submissive posture, escapes from the dominant's attacks and has limited access to resources (Herberholz et al. 2003; Song et al. 2006).

The low level of overt aggression required for the maintenance of hierarchies is adaptive (Goessmann et al. 2000), since both fighting costs and risks of injuries are reduced (Goessmann et al. 2000; Edwards and Herberholz 2005), but what determines stability in hierarchies is still under debate. This may result from (1) a change in the internal state of the

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L. Aquiloni · V. Gonçalves · A. F. Inghilesi · F. Gherardi
Dipartimento di Biologia Evoluzionistica "Leo Pardi",
Università di Firenze,
Via Romana 17,
50125 Firenze, Italy

L. Aquiloni (✉)
Dipartimento di Biologia Evoluzionistica, Università di Firenze,
Via Romana 17,
50125 Firenze, Italy
e-mail: laura.aquiloni@unifi.it

opponents due to repeated wins/losses (“confidence” hierarchies; Barnard and Burk 1979) or (2) the recognition of the opponent’s rank through a “badge” of status (a pheromone, a posture or a behaviour) (“assessment” hierarchies; Barnard and Burk 1979), which is under the control of one individual’s internal state (Copp 1986; Bruski and Dunham 1987; Zulandt-Schneider et al. 1999, 2001; Breithaupt and Eger 2002).

Crayfish (Van der Velden et al. 2008) and other crustacean decapods (the river crab *Potamon fluviatile*; Vannini and Gherardi 1981; the American lobster *Homarus americanus*; Karavanich and Atema 1998; Gherardi et al. 2010b) are also capable of “true individual recognition” (Tibbetts and Dale 2004): animals may learn the individually distinctive characteristics of a conspecific and associate these characteristics with experiences of wins or losses that they have gained from preceding encounters with that particular individual.

To test the above-listed hypotheses about the mechanisms that maintain stable dominance hierarchies, previous research has focused on pairwise interactions, in which each individual acquires information of the other in a direct way (but see Zulandt et al. 2008). Yet, in natural populations, interactions take place within a wider social context where multiple individuals are present and where indirect assessment is possible (Davis and Huber 2007; Martin and Moore 2008). In social networks, cues emitted by a sender and directed to a single receiver are often picked up by other receivers nearby: the latter can thus acquire accurate and low-cost information about the sender and can use such information in subsequent encounters with it (“social eavesdropping”; Peake 2005).

Since its first formulation, much work on social eavesdropping has focused on vertebrates, particularly on teleost fishes (e.g. Earley and Dugatkin 2002), birds (Mennill et al. 2002), dolphins (Götz et al. 2006) and primates (Crockford et al. 2007). Only recently was social eavesdropping described in two invertebrate species: the crayfish *Procambarus clarkii* (Aquiloni et al. 2008; Aquiloni and Gherardi 2010) and the fiddler crab *Uca mjoebergi* (Milner et al. 2010). Females of *P. clarkii* learn who the winner is at the individual level by watching a pair of size-matched males fighting and then use this information to choose the dominant as a mate. These results led us to hypothesise that social eavesdropping is also used by crayfish in the context of aggression because it is a means that allows them to cheaply assess the strength of potential enemies, which is particularly advantageous when combat is highly expensive in terms of the energy and time lost and of the risks entailed in fighting against strong opponents (Johnstone 2001).

Notwithstanding the obvious advantages offered by eavesdropping, its contribution to acquiring information about the social status of potential opponents is still unknown in crayfish. To fill this gap in knowledge, we investigate here whether *P. clarkii* males improve their ability to discriminate the social status of a pair of conspecifics by watching and smelling them fighting.

Material and methods

Collection of animals and holding conditions

About 200 adult males were collected using baited traps from Lake Trasimeno (Umbria, Italy) in May 2010, before the onset of reproduction. Once in the laboratory, for each individual, we measured the cephalothorax length (from the tip of the rostrum to the posterior edge of the carapace), and the length and the width of the major chela using a Vernier calliper to the nearest 0.1 mm. Prior to the start of the experiment, crayfish were maintained in a natural light/dark cycle at room temperature (28°C) and fed ad libitum with live *Calliphora* sp. larvae. Water was changed weekly.

Only hard-shelled, intact individuals with a cephalothorax length of 38.1–59.2 mm were used to form trios. Since dominance depends on body size (Bovbjerg 1953), for each trio, we selected crayfish of a similar size (±2 mm). They were individually marked on their carapace with a waterproof paint and kept in isolation in opaque plastic aquaria ($25\times15\times25$ cm) for at least 2 weeks, which is sufficient time to reset any previous social experience (Hemsworth et al. 2007). In no case did the crayfish meet each other prior to the experiment.

Experimental design and apparatus

The experiment was composed of two subsequent phases, the “passive” and the “active” phase. For each trial, we used two elliptical, plastic aquaria (length, 65 cm; width, 40 cm; water level, 10 cm) (modified after Aquiloni et al. 2008) and a trio of size-matched male crayfish. Both phases were preceded by an acclimation period (10 min) during which the crayfish were visually isolated from each other by a T-shaped opaque wall that divided aquaria in three equivalent compartments: one occupied by the focal individual and the remaining two by one of the other two crayfish (the “fighting dyad”) each. The trial started with the removal of the wall.

During the passive phase, the focal individual was kept in a plastic box (10×4 cm; height, 22 cm), the walls of which were either (1) transparent and finely drilled (hole diameter, 3 mm; hole density 4 cm^{-2}) in treatment 1 or (2) opaque and not drilled in treatment 2. So, only in treatment 1 could focal individuals see/smell the fighting dyad. Before the start of the active phase, focal individuals were removed from the box and were allowed to freely interact with the other two crayfish.

Between the two phases, the relative position of the two fighting individuals was randomly switched. All crayfish were used only once to avoid pseudo-replications. Between trials, the experimental apparatus was thoroughly washed with clean tap water. The experiment was conducted in June and July 2010 during 0800–1400 h reaching a total of 13 replicates per treatment.

Collection of data

Both phases, lasting 30 min each, were video-taped using a Samsung digital camera (VP-L800). Video-tapes were then blindly analysed by an unbiased researcher (VG). During the passive phase, we computed the number and duration of fights and the dominance percentage for each crayfish of the fighting dyad (the number of the fights won on the total number of fights in percentage). A fight started when one crayfish approached the other and ended when one crayfish (the loser) ran away, backed off or tail-flipped away from the other (the winner) at a distance longer than one body length for at least 10 s. The dominant was the individual winning more than 70% of fights. When the hierarchy in the fighting dyad was not clearly established, the trial was excluded from the analysis.

During the active phase we recorded:

1. The crayfish (either the dominant or the subordinate) of the fighting dyad to which the first approach of focal individuals was directed;
2. Latency, i.e. the time between wall removal and the first approach by focal individuals to one of the fighting crayfish;
3. The duration of the fights involving focal individuals;
4. Their intensity. To each fight, classified as avoidance, threat, weak and strong physical interaction and unrestrained fighting (modified from Bruski and Dunham 1987), a score was assigned from 1 (avoidance) to 5 (unrestrained fighting);
5. The total number of fights;
6. The percentage of dominance reached by focal individuals with respect to each crayfish in the fighting dyad.

Statistical analyses

Data were first tested for normality and homogeneity of variance using the Kolmogorov–Smirnov and Levene test, respectively, which allowed us to use parametric tests only when appropriate. Specifically, the latency was analysed using two-way ANOVAs with male's social status (dominant or subordinate) and treatment taken as fixed factors (statistic, *F*). The time spent by focal individuals fighting with dominant or subordinate opponents at each intensity was analysed using a general linear model for repeated measures (GLM; statistic, *F*), followed by Tukey's post hoc tests. In this analysis, treatment and intensity were taken as between-subject factors, whereas the social status of the opponent as a within-subject factor. The total time spent fighting was compared between treatments using *t* tests (statistic, *t*). When the data did not comply with normal distributions, non-parametric techniques were used. Frequency data were analysed using *G* tests after William's correction (H_0=uniform distribution of frequencies; statistic, *G*). The total number of interactions was tested with the Mann–Whitney *U* tests for independent data (statistic, *U*). Moses tests for the extreme reaction (Moses 1952, 1964; Sprent and Smeeton 2001) were used to compare differences in the intensity of fights.

The level of significance under which the null hypothesis was rejected is α=0.05. Text and figures give mean values ± SE.

Results

Passive phase

The mean percentage of fights won by dominant individuals on the total fights in the dyad was 75.9±4.2% independently of the assigned treatment (t_{24}=1.045, P=0.306). No difference was found in either the number (U=115, n=26, P=0.116) or the duration of fights (t_{24}=−0.574, P=0.571) per dyad between the two treatments.

Active phase

Focal individuals most often directed their first approach to subordinate rather than dominant crayfish (19 vs 7, G_1=5.645, P=0.014) with shorter latencies (ANOVA, $F_{1,25}$=19.302, P=0.0001), independently of the treatment (GLM, $F_{1,25}$=0.272, P=0.607) (Fig. 1). No difference in the intensity of the first fight was found between treatments: intensity was always higher in the fights with dominant crayfish (median score, 4 vs. 2) (Moses test=19, n=26, P=0.014).

Similarly, the duration of subsequent fights (Fig. 2) did not vary with either treatment (GLM, $F_{1,120}$=0.003, P=0.956) or the opponent's social status (GLM, $F_{1,120}$=1.797, P=0.183) but with fight intensity (GLM, $F_{4,120}$=12.937, P=0.0001), being longer at higher intensities (Tukey's post hoc, 1<2=4<3<5 scores). Fights generally reached intensity 3 independently of treatments (GLM, $F_{1,120}$=2.196, P=0.073) and the social status (GLM, $F_{1,120}$=0.722, P=0.397). In both treatments (GLM, $F_{1,24}$=1.295, P=0.266), the dominance of focal individuals was higher when they combated with subordinate crayfish (GLM, $F_{1,24}$=7.572, P=0.01).

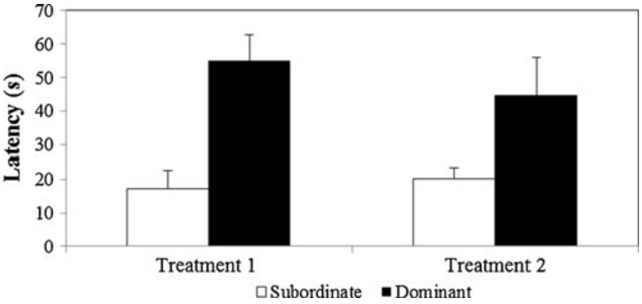

Fig. 1 Mean latency (±SE) between wall removal and the first approach by focal individuals to subordinate (*open bars*) and dominant crayfish (*filled bars*) of the fighting dyad in treatments 1 (n=13) and 2 (n=13)

Discussion

This study provides robust evidence that male crayfish can discriminate the social status of unknown conspecifics without the need of having previously eavesdropped on opponents' fights. Our results, in fact, show that, during the active phase, the behaviour of focal individuals is independent of whether or not they had been allowed to previously experience the fighting dyad through visual and chemical cues. Instead, their behaviour depends on the social status of the two other crayfish, which appears to be discriminated without the need for previous perceptual experience with them. Independently of the treatment, the first approach of focal individuals was mostly directed to subordinate crayfish, while dominants were avoided. Their fights with dominants also reach higher intensities than with subordinate crayfish.

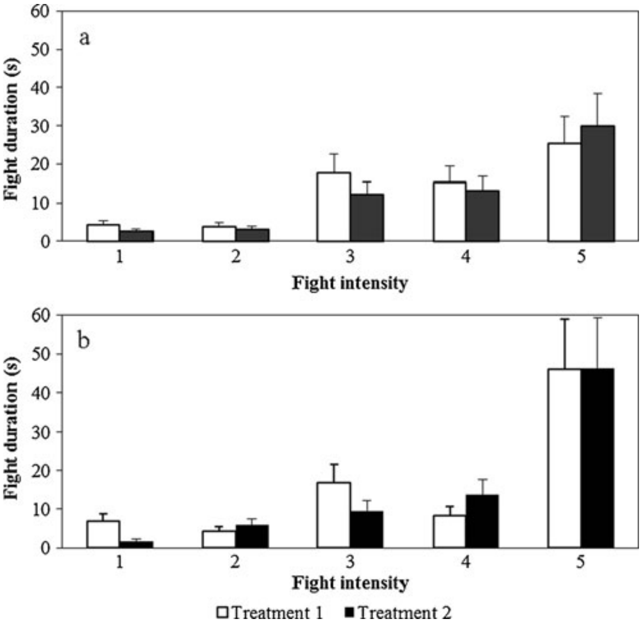

Fig. 2 Mean time (±SE) spent by focal individuals fighting at five levels of intensity with (**a**) dominant and (**b**) subordinate crayfish of the fighting dyad in treatments 1 (n=13, *open bars*) and 2 (n=13, *filled bars*)

This prompt discrimination between dominants and subordinates suggests that, at least in the context of aggression, *P. clarkii* behaviour results from either the recognition of the dominant badge of status or a quick comparison between the set of stimuli denoting agonistic level as emitted by the opponents, regardless of whether the focal male had any previous experience with them. Urine-borne chemicals, perhaps associated with tactile, hydrodynamic or visual stimuli, are known to play a role in communicating the status in stomatopods (Caldwell and Dingle 1979) and in many decapods (i.e. *H. americanus;* Karavanich and Atema 1998; *Nephrops norvegicus;* Katoh et al. 2008; *Orconectes rusticus;* Bergman and Moore 2005), *P. clarkii* included (Zulandt-Schneider and Moore 2000). However, a variety of other intrinsic and extrinsic factors, associated with the physical superiority of the dominant (Ranta and Lindstrom 1993; Rutherford et al. 1995), dietary effects (Vye et al. 1997), moult stage (Tamm and Cobb 1978) and the experience of previous agonistic encounters (Rubenstein and Hazlett 1974) might also contribute to recognising the agonistic level of unknown individuals.

Interestingly, in contradiction with our results here, the choice of dominant males by *P. clarkii* females is made only after having eavesdropped on two males fighting (Aquiloni et al. 2008; Aquiloni and Gherardi 2010). To interpret this apparent discrepancy, at least three explanations might be suggested. Firstly, social eavesdropping might be context-dependent being exclusively used to gather information during mate choice: through this ability, females compare the fighting ability of potential mates and then choose the highest-quality male available, whereas status recognition allows for a quick discrimination between the more and the less dangerous opponent at that moment. Secondly, the two sexes may rely on different neural pathways to acquire and process information. Male and female crustaceans often use cues from different media to perceive and discriminate the quality and the status of conspecifics (Herberholz 2007). For example, *P. clarkii* discriminates sex and mate quality using both sight and smell if females, but smell alone if males (Aquiloni and Gherardi 2008; Aquiloni et al. 2009). Finally, social eavesdropping might be useless in conditions such as hierarchies which are transient, relative and highly dependent on the social context (Graham and Herberholz 2009). Although size is a reliable predictor of fighting outcome (Bovbjerg 1953), a slight alteration of social contexts induces a quick switch of the order in a hierarchy, for example, when a group is repeatedly reconstituted (Dugatkin et al. 1994) or when the order followed to add the same individuals to the reconstituting group is reverted (Landau 1965; Bernstein and Gordon 1980). In natural crowded populations, fighting groups of *P. clarkii* quickly change in the number and identity of their members. In such a dynamic social environment, crayfish may benefit more by promptly assessing the current status of their rivals than by remembering their previous one.

A further interesting result of our current study is that focal individuals always acquire an intermediate position in the hierarchy between the dominant and the subordinate crayfish of the fighting dyads whereas, in *O. rusticus* (Zulandt et al. 2008), the crayfish that have observed conspecifics fighting was more often the loser when allowed to freely interact with other, unknown individuals. Our result is consistent with the winner and loser effects (Dugatkin 1997; Hemelrijk 1999; Hsu et al. 2006), a phenomenon occurring in a variety of taxa among vertebrates (Chase 1974; van de Poll et al. 1982) and invertebrates (Theraulaz et al. 1995), crayfish included (Copp 1986; Bergman et al. 2003). Indeed, focal individuals are introduced into an already structured hierarchy in which subordinate crayfish, with experiences of loss, are more prone to avoid conspecifics and to escape from them, whereas dominant crayfish are bolder, tending to approach conspecifics and to persist fighting.

In synthesis, we have shown that, in the context of aggression, *P. clarkii* males promptly recognise the social status of their opponents without the need to have experience with them either indirectly (by watching and smelling them fighting) or directly (by fighting with them). However, the role of the behavioural context and social environment, along with the nature of the putative badge of status, requires further studies to better understand how these factors interact in structuring dominance hierarchies.

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