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Hermit crab, *Pagurus middendorffii*, males avoid the escalation of contests with familiar winners

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Prior contest outcomes often affect subsequent contest behaviour (winner/loser effects). If contestants discriminate between familiar and unfamiliar opponents, individual recognition may alter the strength and/or manner of winner/loser effects. We examined whether hermit crabs, *Pagurus middendorffii*, changed their contest behaviour based on winner/loser effects, whether they distinguished a familiar opponent from an unfamiliar opponent, and how the familiarity with the opponent related to the winner/loser effects in male–male contests. Males of this species show precopulatory guarding behaviour, and male–male contests often occur between a guarding male and an intruder. In contests between unfamiliar males, intruders use self-assessment during the initial contact phase and mutual assessment during the physical combat phase to determine their behaviours. Precopulatory guarding males and females collected in the field were used in two consecutive trials of male–male contests. Losers in the first trial were used as focal intruders in the second trial with (1) a familiar opponent that had won the first trial, (2) an unfamiliar opponent that had won the first trial with another intruder, or (3) a naïve opponent with no trial experience. Focal intruders did not alter their aggressiveness against either unfamiliar or naïve opponents in the second trial. However, they rarely initiated physical combat against familiar opponents in the second trial. When they initiated combat, they gave up sooner against familiar opponents than against unfamiliar opponents. These results suggest that intruders are able to distinguish familiar opponents from others and decrease their aggressiveness only when they encounter familiar opponents. Our study therefore shows loser effects in *P. middendorffii* related to the familiarity with the opponent and suggests intruders can obtain information about their opponents during the initial encounter.

Many animals engage in contests over limited resources, and contestants with a higher fighting ability are more likely to acquire the resources (reviewed in Arnott & Elwood, 2008, 2009; Hardy & Briffa, 2013). Although physical attributes of contestants (e.g. body and/or weapon size) are well known to correlate with fighting ability (e.g. Lindström, 1992; Sneddon, Huntingford, & Taylor, 1997; reviewed in Andersson, 1994; Arnott & Elwood, 2009; Emlen, 2008), prior contest outcomes also have an important role in determining behaviour during the contest and/or the outcomes (reviewed in Hsu, Earley, & Wolf, 2006; Rutte, Taborsky, & Brinkhof, 2006). Since contestants would be able to use prior contest outcomes to estimate their own fighting ability (i.e. self-assessment; Fawcett & Mowles, 2013) in relation to average fighting ability of other individuals in the population, contestants with prior experience may alter the self-assessment of their respective fighting abilities and change motivation in the contest via self-assessment (Rutte et al., 2006; Whitehouse, 1997): prior winners are more likely to engage in and win subsequent contests (winner effect), whereas prior losers are more likely to be less aggressive and lose subsequent contests (loser effect). Such winner/loser effects have been reported in many taxa such as reptiles (Garcia et al., 2012; Zucker & Murray, 1996), fishes (Hsu & Wolf, 1999; Oliveira, Silva, & Canário, 2009), insects (Okada & Miyatake, 2010; Reaney, Drayton, & Jennions, 2011), spiders (Kasumovic, Elias, Punzalan, Mason, & Andrade, 2009; Kasumovic, Elias, Sivalinghem, Mason, & Andrade, 2010) and crustaceans (Fujimoto, Hirata, & Nagayama, 2011; Moore, 2007).

The winner/loser effects differ in strength and manner between species although loser effects may be more common and usually longer lasting than winner effects (Hsu et al., 2006). For example, males of the black field cricket, *Teleogryllus commodus*, show loser effects during nonphysical contests, whereas there are no loser effects if the contest escalates into aggressive behaviour (Reaney

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et al., 2011). Winner effects are not found in physical or nonphysical contests in this cricket (Reaney et al., 2011). Both winner and loser effects are of approximately the same magnitude in the jumping spider *Phidippus clarus*, although loser effects last longer than winner effects (Kasumovic et al., 2010). The parasitoid wasp *Eupelmus vuilleti* showed winner effects in fighting for hosts whereas a significant loser effect was not observed (Goubault & Decuignière, 2012). Thus, effects of prior contests appear to be species specific, and the process and/or outcome of a contest still require further investigation (Hsu et al., 2006; Mesterton-Gibbons, 1999).

When animals repeatedly encounter each other, they may memorize past outcomes of interactions with specific individuals and use the experience to modify subsequent interactions with the same individuals (see van Doorn, Hengeveld, & Weissing, 2003). For example, as a result of recognition, the levels of aggression for familiar neighbours are often lower than for strangers (i.e. 'dear enemy' effect; Temeles, 1994). Recent studies have demonstrated the ability of individual recognition in invertebrates (Caldwell, 1985; D'Ettorre & Heinze, 2005; Karavanich & Atema, 1998; Tricarico, Borrelli, Gherardi, & Fiorito, 2011; Yurkovic, Wang, Basu, & Kravitz, 2006) as well as vertebrates (Jennings, Gammell, Carlin, & Hayden, 2004; López & Martín, 2001). The ability to distinguish between familiar and unfamiliar individuals may affect the strength and/or manner of winner/loser effects. When a dyadic dominance relationship between two contestants has been determined by past contest(s), the contestants might behave as winner/loser in subsequent contests (Dugatkin & Earley, 2004). Once a dominance relationship has been established, dominants and subordinates typically decrease the number of intense combat interactions as shown for example in the lizard *Podarcis hispanica* (López & Martín, 2001) and *Drosophila melanogaster* (Yurkovic et al., 2006). Subordinates of the American lobster, *Homarus americanus*, also avoid a second fight with familiar dominants but not with unfamiliar ones. They aggressively fight and often win during contests with the latter (Karavanich & Atema, 1998).

There is also evidence that *Pagurus* hermit crabs recognize other individuals based on a previous encounter(s) and/or dominance relationship. Hazlett (1969) held four individuals of the hermit crab *Pagurus bernhardus* in a tank for a week and then introduced an unfamiliar individual into the tank. The four crabs initiated intense aggressive interactions with the unfamiliar crab much more often than with the familiar ones. Gherardi and Tiedemann (2004a) showed that subordinate crabs of *Pagurus longicarpus* were likely to initiate interactions with unfamiliar dominant crabs more often than familiar ones and escalated the fight only when the opponent was unfamiliar. Subordinate crabs in these species behaved as losers only when they faced familiar dominants. Strength and the manner of winner/loser effects may therefore differ depending on the familiarity with the opponent in male–male contests of hermit crabs.

Males of *Pagurus* hermit crabs show precopulatory guarding behaviour in which the male grasps, with the left cheliped, the aperture of the gastropod shell occupied by a sexually mature female over periods of several days, and compete for mates against solitary males during the precopulatory guarding (Hazlett, 1968; Suzuki, Yasuda, Takeshita, & Wada, 2012; Wada, Tanaka, & Goshima, 1999). Larger males have been shown to be more likely to win this contest in *Pagurus filholi* (Okamura & Goshima, 2010; Tanikawa, Yasuda, Suzuki, & Wada, 2012), *Pagurus nigrofascia* (Yasuda, Suzuki, & Wada, 2011) and *Pagurus middendorffii* (Wada et al., 1999). Yasuda, Takeshita, and Wada (2012) demonstrated that male–male contests of *P. middendorffii* are divided into two phases based on whether intruders initiate escalation of the contest with physical combat behaviour: initial contact phase (before escalation) and physical combat phase (after escalation). Intruders of this species use self-assessment during the initial contact phase and mutual assessment (i.e. individuals take into account their own fighting ability and that of the opponent; Fawcett & Mowles, 2013) during the physical combat phase to decide their behaviours (Yasuda et al., 2012), suggesting that they can use information from both their own and the opponent's fighting ability. They may thus show winner/loser effects in the subsequent male–male contest. Furthermore, if the males also distinguish a familiar opponent from an unfamiliar one, they may alter their contest behaviour depending on both the previous contest outcomes and the familiarity with the opponent. These possibilities related to prior contest experience have never been investigated in the context of male–male contests in *Pagurus* hermit crabs including *P. middendorffii*.

Here we examined (1) whether winning or losing a contest causes any changes in the decision to escalate a subsequent contest, (2) whether males distinguish familiar opponents from unfamiliar ones in male–male contests and (3) how winner and/or loser effects are related to the familiarity with the opponent in *P. middendorffii*. To do this, we conducted two sequential trials of male–male contests in *P. middendorffii*, using three groups of males; we manipulated the contest experience and/or familiarity and compared male behaviours between the trials and/or between the groups.

METHODS

We collected 178 precopulatory guarding pairs of *P. middendorffii* from a large area of the intertidal rocky shore (about 60×10^4 m^2; Nagata, 1983) during 13–30 November 2012 at Kattoshi, southern Hokkaido, Japan (41°44′N, 140°36′E). This species is common in the study site (Wada, Goshima, & Nakao, 1995) with a mean density of more than 200 individuals/m^2 (Wada, Arashiro, Takeshita, & Shibata, 2011). The mating season of this species is from late October to early December in the study site (Wada et al., 1995). Each pair was placed in a small vinyl pouch with sea water and transported to the laboratory within 30 min. In the laboratory, we checked that the males were intact and still guarding females, and the male and female of each pair were separately maintained in plastic cups (300 ml) without food to avoid copulation before the experiment. Also, to avoid any change in reproductive state in both sexes and motivational state in males, all experimental trials were conducted within 6 h of collection. No crabs were injured, lost any appendages or died throughout the experiment including during the contests.

Experimental Design

The experiments involved two sequential trials of male–male contests. Guarding pairs were divided into three experimental groups based on the type of second trial (see Table 1) and randomly assigned to the experimental sets in each group. Since intruders were focal males, we chose one male from a guarding pair in each set as intruder and males in the remaining pairs as owners (see below). Each intruder took part in two contests: after intruders lost in the first trial (trial 1), they encountered a given owner in each group in the second trial (trial 2). In group 1, losers encountered naïve owners with no experience in trial 1. In group 2, losers encountered unfamiliar owners that had won trial 1 (randomly chosen from the other set). In group 3, the losers again encountered the familiar (=same) owners from trial 1 (see Appendix 1 for details).

For each contest, we used three (group 1) or two (group 2 and 3) pairs as a set, which were randomly assigned from guarding pairs collected on the same sampling day as each other (group 1, $N = 24$