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Behavioural determinants of agonistic success in invasive crayfish

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ABSTRACT

Ecosystems today increasingly suffer invasions by multiple invasive species, some of which may share similar advantageous life history traits and ecological niche. In such cases, direct competition can influence invasion success of both species, and provide insights into competition without co-evolution in species equally novel to the environment. We used two widespread crayfish invaders of freshwater ecosystems of Europe, signal crayfish (*Pacifastacus leniusculus*) and spiny cheek crayfish (*Orconectes limosus*), to investigate how behavioural decisions in agonistic encounters contribute to competitive advantages in the absence of adaptation to either opponents or an environment. In direct competition against novel but comparable opponents, the key factor for establishing clear dominance of *P. leniusculus* in interspecific bouts was its greater tendency towards continued engagement in high-intensity fights. With *O. limosus* individuals consistently retreating from staged bouts as fights became more intense, *P. leniusculus* individuals did not need to adapt their strategy to be successful, suggesting that their agonistic behaviour intrinsically predisposed them to win. While both species are detrimental to invaded ecosystems, our results indicate that aggressive behaviour of *P. leniusculus* against unfamiliar opponents could allow it to more easily outcompete other comparable species and consequently present a potentially greater threat for native ecosystems.

1. Introduction

Sharing an ecological niche often leads to direct competition for resources (Shea and Chesson, 2002). Eventually, competition will either cause co-evolution and niche divergence, or drive the weaker competitor to extinction (Shea and Chesson, 2002). Biological invasions offer an insight into the early stages of these processes. While many factors ultimately contribute to the success of an invader (Kolar and Lodge, 2001; Van Kleunen et al., 2010), dominance in direct competitive interactions is an important predictor of the ability to access key resources in a novel environment through competitive displacement (Gherardi and Cioni, 2004; Pintor et al., 2008). Presence of an invasive species often leads to rapid evolutionary changes in both invaders and native species (Shine, 2012), but early success of an invasion will predominantly stem from pre-existing traits that that turn out to be advantageous in a novel situation. While the focus is usually on competition between native and invasive species, a scenario when different invaders compete between each other allows us to compare which components of an agonistic repertoire prime some invasive species to outcompete both native species and other successful invaders in invaded ecosystems. Since the co-occurring invaders in a direct competition over an ecological niche have not yet had the evolutionary time to adapt to opponents or the environment, competition between such species provides us with a rare opportunity to study comparable agonistic behavioural strategies of different species in an ecologically relevant context.

Agonistic behaviour can result in competitive advantages even against evidently successful species in a novel environment. The success in competitive interactions is contingent on timing of a series of decisions made by each contestant, including whether and when to initiate, escalate, retaliate, or withdraw (Maynard Smith, 1982; Huber and Kravitz, 1995). These behavioural decisions give rise to strategies used for conflict resolution in competitive interactions, and are inextricably linked to the balance between benefits and costs of fighting, often in the shape of clearly defined sequential assessment of ritualized fighting (Enquist and Leimar, 1983), which in turn reduces the costs of repeated escalated tests of fighting prowess or resource-holding potential (Parker, 1974). We investigated how such decisions can lead to differential success in two species of increasingly co-occurring crayfish invaders.

Invasive crayfish affect many of the world's waterways and already outnumber native crayfish in some regions of Europe (Holdich et al., 2009). The species in our trials, the signal crayfish (*Pacifastacus leniusculus*) and the spiny cheek crayfish (*Orconectes*

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limosus), both have a history of adverse effects in European waterways (Holdich et al., 2009), where they exhibit an increasing range overlap. In their invasive range in Europe, *P. leniusculus* and *O. limosus* already co-occur (e.g. in Poland: Krzywosz et al., 2006) or are present in the same catchment and are destined to encounter each other in the near future (e.g. in Croatia: Hudina et al., 2009; the Netherlands: Roessink et al., 2009; UK: Holdich and Black, 2007). Both invaders share favourable life history traits which have contributed to their invasion success, such as high fecundity, early maturation and fast growth (Souty-Grosset et al., 2006).

Agonistic behaviour is an important aspect of crayfish ecology, with several studies demonstrating high levels of fighting in natural populations (Davis and Huber, 2007; Fero and Moore, 2008). Crayfish exhibit stereotyped agonistic behaviour with many commonalities across species, and individuals from different species readily engage in fights (Bovbjerg, 1956). This spurred a history of successful cross-species comparisons (e.g. Blank and Figler, 1996; Söderbäck, 1991; Tierney et al., 2001; Gherardi and Cioni, 2004; Hudina et al., 2011), and made it possible to set up staged fights between two different species to determine which components of agonistic strategies contribute to success in fights against unfamiliar, interspecific individuals.

Previous intraspecific comparative studies demonstrated higher aggressiveness of *P. leniusculus* over three congeneric Orconectes species (excluding *O. limosus*; Tierney et al., 2001), while interspecific studies involving both species used in our trials recorded a clear advantage of *P. leniusculus* in interspecies bouts with *O. limosus* (Hudina et al., 2011). However, the reasons for this latter lopsided outcome in competition over resources are not readily apparent, especially with respect to the apparent similarities in the ways these species compete for resources. While other factors such as transmission of crayfish plague substantially contribute to the overwhelming success of crayfish invaders over native species (Holdich et al., 2009), outcome of direct competition between invaders that share both a niche and a mode to fight the competitors for it offers useful insights into their potential future invasion success, distribution, and impact. Given that world's ecosystems are becoming increasingly homogenized in terms of biodiversity (Dudgeon et al., 2006; Olden and Rooney, 2006; Baiser and Lockwood, 2011) with an increasing number of ecosystems suffering multiple invaders (Johnson et al., 2009), studies that are able to predict the outcome of ecological interactions between otherwise successful invaders are becoming increasingly relevant for conservation and management efforts (cf. Ruscoe et al., 2011).

By investigating behavioural decisions in agonistic encounters of two species lacking co-evolutionary adaptation to either an opponent or an environment, we aim to highlight the differences in agonistic strategies that contribute to the observed discrepancy in interaction outcomes. Key differences in behavioural decisions that make up agonistic strategies can therefore be considered (pre-)adaptive in terms of future interspecific competition and invasive potential. This kind of competition is therefore analogous to a game-theoretic scenario involving two comparable species. The results of our study provide insights into the early evolutionary stages of ecological competition over niches, and offer a glimpse into the processes that may shape our future ecosystems.

2. Methods

2.1. Study animals

While *P. leniusculus* and *O. limosus* have been increasingly co-occurring in European waterways (cf. Hudina et al., 2011 and references therein), in order to avoid any familiarity with opponents from other species, individuals of both species were collected from allopatric populations in the Netherlands. Individuals were collected by hand nets and fykes (Hudina et al., 2011). Out of all captured crayfish (332 *P. leniusculus* and 428 *O. limosus* individuals), only intact and intermolt adult males (mean carapace length: $\mathrm{CL}_{P.\ leniusculus} = 35.4 \pm 5.1$ mm; $\mathrm{CL}_{O.\ limosus} = 34.2 \pm 2.8$ mm) were selected for trials.

Crayfish are not included in the Dutch national legislation (Experiments on Animals Act, 1996), or in the EU legislation (Council Directive 86/609EEC and 210/63/EU) that regulates the protection of animals used for experimental and scientific purposes. While no licence was required for the study, animals were kept with care, and housed in communal tanks where they were separated in order to avoid both injuries and overcrowding. All animals were provided with shelter, fed regularly, and kept under favourable controlled conditions. No injuries were observed during the staged trials. Since the release of invasive species back into the watercourse is forbidden by the Dutch regulatory system (Flora and Fauna Act), upon the end of all trials, animals were sacrificed by hypothermia, in concordance with procedures used in other relevant studies (e.g. Aquiloni and Gherardi, 2010).

2.2. Experimental set-up

The general components of an experimental protocol followed the one described in detail in Hudina et al. (2011). Prior to trials, individuals were weighed and measured and each crayfish was marked using waterproof paint. Marked animals of different species were housed separately in tanks in the laboratory at Alterra, Wageningen UR, The Netherlands, for three weeks under controlled conditions (light regime 12:12 L:D, water temperature 19–21 °C, pH 7.8–8.1) and were fed three times a week with fish pellets and peas. Ten animals were housed per aquarium, each visually separated from the other using dividers that allowed water circulation, but prohibited physical contact. This period of social isolation is commonly used to prevent the outcome of observed fights being affected by recent agonistic experiences (e.g. Huber and Kravitz, 1995; Stocker and Huber, 2001; Bergman et al., 2003). Agonistic interactions were staged between pairs of adult intermolt size-matched individuals, with differences between contestants kept within 10% for weight, carapace length, and claw length, in concordance with established criteria for size-matching in crayfish interactions (e.g. Söderbäck, 1991; Schroeder and Huber, 2001; Fero et al., 2007). All trials were performed under artificial light that was also used in general housing conditions.

Pair members were kept in complete isolation for 24 h (cf. Hudina et al., 2011) prior to being placed inside two compartments separated by an opaque removable divider in the trial arena. Trial arena was a glass aquarium (50 × 30 cm) with a substrate mixture of sand and gravel, and filled with 15 cm of water. Water was provided from the same source that supplied the communal tanks (average values of water characteristics: $T = 20.5$ °C, pH 7.8). In the trial arena, individuals were allowed an acclimation period of 5 min in two separate compartments divided by an opaque removable divider. After this acclimation period, the divider was lifted and the interaction was videotaped for 15 min. The tank was thoroughly washed between trials. Agonistic interaction began when two individuals were within one body length of each other and overtly reacted to the presence of an opponent. The interaction ended when the contestants were separated by a distance longer than one body length for at least 5 s. We recorded the total number of agonistic interactions per pair, as well as total duration of agonistic interactions per pair, maximum intensity (five-level scale adapted from Huber and Kravitz, 1995 and Stocker and Huber, 2001), and initiation and retreat intensity (three-level scale adapted from Huber and Kravitz, 1995 and Stocker and Huber, 2001) for each pair. We then calculated the duration and number of high intensity (HI) bouts per pair