

# Competitive interactions between co-occurring invaders: identifying asymmetries between two invasive crayfish species

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**Abstract** Ecosystems today increasingly suffer invasions by multiple invasive species. Complex interactions between invasive species can have different fitness implications for each invader, which can in turn determine the future progression of their invasions and result in differential impacts on native species and ecosystems. To this end, through pairwise and group scale experiments, we examined possible interaction outcomes, competition effects and their potential fitness implications for two widespread invasive species of crayfish that increasingly co-occur in freshwater ecosystems of Europe (*Pacifastacus leniusculus* and *Orconectes limosus*). In all trials, *P. leniusculus* demonstrated the potential to outcompete *O. limosus* in both staged encounters and

direct resource competition, being more likely to win heterospecific agonistic encounters and to acquire shelters at a higher rate. Observed dyadic dominance was translated to a broader social context of group-scale experiments, in which dominance of *P. leniusculus* was further strengthened by size differential between species. *O. limosus* was not able to compensate for competitive pressure by the dominant *P. leniusculus* and suffered wet weight loss and more frequent injuries in the presence of *P. leniusculus*. While both species are detrimental to native ecosystems, the ability of *P. leniusculus* to withstand competition pressure from another successful invasive species underscores its potential to establish dominant populations. Our results highlight the importance of understanding interspecies competition in prioritizing potential management activities or control efforts in contact zones.

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## Introduction

As the frequency of non-indigenous species introductions increases and their range expands, more and more ecosystems suffer multiple invasive species which are coming into contact (Ricciardi 2001).

Individual and cumulative effects of interactions between invaders in an ecosystem add another level of complexity to our attempts to understand the dynamics of biological invasions and to manage them. The presence of multiple invaders in an ecosystem may change interaction outcomes which would occur between one invader and native species (Preisser and Elkinton 2008). Several studies so far have demonstrated different interaction outcomes that might arise from the presence of multiple invaders, which range from negative (e.g. slower establishment or spread of invaders, invasive species replacements: Perry et al. 2000; Riel et al. 2009; La Pierre et al. 2010) to positive (i.e. facilitative interactions: Ricciardi 2001; Adams et al. 2003; Jordan et al. 2008) or neutral (e.g. Cope and Winterbourn 2004). However, such outcomes are complex to predict since they depend on interaction between biological and ecological characteristics of each of the invaders (e.g. Maezo et al. 2010) and characteristics of invaded system (e.g. Branch et al. 2010; Platvoet et al. 2009; Rius and McQuaid 2009). Moreover, interacting invaders may have to trade-off certain components of fitness in order to survive in a contact zone (e.g. Lewis 2001). Such fitness trade-offs might be asymmetrical between participants and could in turn affect their potential for further invasion and modify their individual effects on native species.

In attempts to understand and predict interaction outcomes and ecosystem effects of multiple invaders presence, both research into general patterns of invasion dynamics and species-specific studies are needed. To investigate the consequences of competitive interactions between potentially co-occurring invasive species, we used two highly successful invaders of European freshwater ecosystems, the signal crayfish (*Pacifastacus leniusculus*) and the spiny cheek crayfish (*Orconectes limosus*). Invasive crayfish can dramatically alter aquatic community composition and ecosystem functioning and lead to regime shifts through combined effects of consumption, bioturbation, mechanical destruction and excretion (Usio et al. 2009; Matsuzaki et al. 2009; Angeler et al. 2001). While in their native range in US the natural distribution of these species does not overlap (Lewis 2002; Hamr 2002), 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 species share some of the common life history traits such as fast growth rate, high fecundity, and early maturation (Souty-Grosset et al. 2006), which contribute to their invasive success. Moreover, their ability to successfully outcompete native crayfish species due to their aggressiveness (e.g. Söderbäck 1991; Usio et al. 2001; Pintor et al. 2008), favorable biological and ecological traits (e.g. Schulz and Smietana 2001) or transmission of diseases such as crayfish plague (e.g. Diéguez-Urbeondo 2006) can enhance their potential to drastically affect native crayfish populations. The efforts to contain their spread have so far elicited only limited success (e.g. Peay et al. 2006; Freeman et al. 2009) on a small-scale.

Despite their prevalence throughout Europe, the effects that these invaders could exert on each other and the effects of such interaction outcomes on their further invasion are poorly understood. Since agonistic behaviors in decapods are highly stereotyped (e.g. Davis and Huber 2007) and largely conserved throughout the taxa, spurring a history of successful cross-species comparisons (e.g. Bovbjerg 1970; Blank and Figler 1996; Söderbäck 1991; Guiasu and Dunham 1999; Tierney et al. 2001; Gherardi and Cioni 2004; Gherardi and Daniels 2004), invasive crayfish species present an ideal opportunity to study the consequences of contacts between highly similar invaders.

Competition for limited key resources between species which occupy similar ecological niches and use similar resources can have direct fitness consequences (e.g. Gherardi and Cioni 2004; Vorburger and Ribí 1999). While multiple ecological factors can influence the fitness benefits of dominance between such species (cf. Fero et al. 2007), dominance in direct competitive interactions is an important predictor of access to key resources (Wilson 1975), such as shelter, the ownership of which directly lowers the risk of predation and cannibalism in crayfish (e.g. Garvey et al. 1994; Figler et al. 2005). Our aim was therefore not only to investigate the asymmetries between focal species in their potential to establish dominance, but also to investigate asymmetries in effects of direct competition, and its potential fitness consequences, by comparing injury risk and growth in intraspecific interactions with those in interspecific interactions.

Several previous studies used growth parameter to measure competition (and predation) effects and its fitness implications in crayfish (e.g. Hill and Lodge 1999), and compared injury intensity and frequency to indirectly infer competition intensity (e.g. Söderbäck 1995). Furthermore, there is a link between selected parameters: agonistic encounters can compromise individual fitness since they imply injury risks which in turn deplete reserves that would be otherwise allocated to growth or reproduction (Sneddon et al. 1999; Rovero 2000). Retarded somatic growth has been recorded in injured animals as a result of appendage regeneration (Söderbäck 1995).

In order to examine implications of contact between co-occurring crayfish invaders we explored (i) whether one species possesses the ability to outcompete the other both outright in staged encounters and in direct competition for resources; (ii) whether this was due to the differences in the frequency and duration of agonistic interactions, comparing intraspecific values with those from interspecific trials to look for potential advantages, (iii) whether potential fitness consequences of competition are equal for both species in terms of resource acquisition, risk of injury and growth implications; and (iv) whether dominance observed in interspecies dyads will translate into dominance in interspecies groups which account for size differential between examined species. We discuss our results in relation to the influence of interspecific competition on the prevalence of a given invader in the zone of contact, but also in relation to their future spread and impact on native populations of crayfish species.

## Methods

### Study animals

Two crayfish species were collected by hand nets and fykes in September 2009 from allopatric populations. *P. leniusculus* (332 animals) were hand collected from a small stream in southern part of Netherlands (de Oude Leij near Tilburg), while *O. limosus* individuals (428 animals) were acquired from a watershed in the western part of the Netherlands (near Hardinxveld-Giessendam). Crayfish were brought to the Sinderhoeve experimental station, Renkum, The Netherlands where individuals of both species were kept in stocks (separated by species) in large pools for

a week for initial acclimatization to food regime. Previous studies have shown that outcomes of agonistic interactions are dependent upon the relative size of the opponents, mutilations, molt stage and sex (cf. Nakata and Goshima 2003; Gherardi and Cioni 2004), with male crayfish usually considered as more aggressive than females (e.g. Berry and Breithaupt 2010). Therefore, only intact adult intermolt male individuals were selected from stocks before the start of the experiments. All selected individuals were marked using waterproof paint and their weight (W), carapace length (CL) and right claw length (RCL) was measured. The greater size of *P. leniusculus* in source populations used to create stocks (cf. Souty-Grosset et al. 2006) resulted in greater average morphometric values for this species (mean  $\pm$  SD for *P. leniusculus* ( $N = 90$ ):  $W(g) = 34.973 \pm 21.021$ ,  $CL(mm) = 36.193 \pm 6.315$ ,  $RCL(mm) = 39.338 \pm 11.067$ ; for *O. limosus* ( $N = 96$ ):  $W(g) = 26.375 \pm 9.356$ ,  $CL(mm) = 32.150 \pm 4.491$ ,  $RCL(mm) = 34.593 \pm 7.098$ ). Out of all measured animals a selection of the crayfish was used in experiments: 54 individuals per species were put into the outdoor experiment, while another selection was transported to the laboratory for 3 weeks acclimatization to laboratory conditions (37 *P. leniusculus* individuals and 42 *O. limosus* individuals).

### Experimental design

We used two major experimental setups: (1) laboratory pair wise experimental setup and (2) outdoor group scale experimental setup. Pair wise experiments were performed at Alterra, Wageningen UR, The Netherlands, while group scale experiments were performed at Sinderhoeve experimental station, Renkum, The Netherlands.

#### *Pairwise experiments—general procedure*

Individuals were housed in 10 aquaria ( $100 \times 40 \times 40$  cm) filled with aerated water (communal tanks). Ten animals of one species were housed per aquarium, each animal separated from the other using dividers that allowed water circulation but prohibited physical contact. Animals were kept under controlled conditions (light regime 12 : 12 L : D, water temperature 19–21°C, pH 7.8–8.1) for three weeks prior to testing and were fed three times a week with fish pellets and peas.

As body size of contestants is an important predictor of agonistic success (e.g. Vorburger and Ribi 1999), to account for the effect of body size and mass pairs were matched so that differences between pair members did not exceed 10% for all three compared measurements (W, CL and RCL), as in other dyadic studies of crayfish interactions (e.g. Söderbäck 1991; Schroeder and Huber 2001; Alonso and Martinez 2006; Fero et al. 2007 etc.). Before the start of each laboratory trial, crayfish were kept in total isolation for 24 h during which each individual was kept in separate plastic tank with aerated water. No individual was used twice in the laboratory experiment setups within at least 7 days, which is within the range of the most frequent records of the time needed to eliminate the effect of prior agonistic experience, although this range could be species-specific (cf. Hemsworth et al. 2007).

*Experiment 1: pairwise interactions with shelter resource absent*

Agonistic interactions were staged in 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 as in the communal tanks (average values of water characteristics: T = 20.5°C, pH = 7.8). The aquarium was divided in two equal sized compartments by an opaque removable Plexiglas divider. In each trial, contestants were put in separate compartments of the tank and were allowed to acclimate for 5 min. Then the divider was lifted and the resulting interaction was videotaped for 15 min after which animals were returned to their compartment in the communal tanks.

The recordings of 25 interspecific and 32 intraspecific (16 for *P. leniusculus* and 16 for *O. limosus*) trials in total were analyzed using Observer XT program (Noldus Information Technology, Wageningen, The Netherlands). The following events were recorded (cf. Huber and Kravitz 1995; Gherardi and Cioni 2004): (i) total number of agonistic interactions per trial (agonistic interaction began when two individuals approached within one body length of each other and reacted to opponent's presence; agonistic interaction ended when the contestants were away from each other by a distance longer than one body length for at least 5 s); (ii) duration of each agonistic interaction per trial and cumulative time spent

interacting; and (iii) identity of initiator of agonistic interaction, initiator of physical interaction and its eventual winner. The winner was the individual that did not retreat or that retreated after the opponent displayed subordinate posture—either a body down posture or remaining motionless (cf. Bruski and Dunham 1987). Number and duration of agonistic interactions in conspecific pairs were compared to those in heterospecific dyads.

*Experiment 2: pairwise interactions with shelter resource present*

Shelter competition experiments were examined in three glass aquaria (65 × 40 cm) with the same substrate type, water level and water characteristics (temperature, pH) as in Experiment 1. One shelter was placed in each aquarium against the wall in the middle on the longer aquarium side. Before the start of each trial, two opaque Plexiglas dividers were placed to form two equal sized compartments, isolating both animals from shelter and from each other. Each individual was placed in its compartment and was left to acclimate for 10 min, after which dividers were removed and crayfish observed continuously for an hour. After the first hour, shelter occupancy was recorded hourly 8 times and again after 24 h. Shelter was considered occupied when the entire body of a crayfish was inside it at the time of recording.

A total of 27 trials were carried out with the following parameters recorded: (i) identity of shelter occupant and (ii) time needed until the first shelter occupancy. Parameter (ii) was recorded only if observed within continuous observation period in the first hour. To analyze whether obtained results were determined by the species-specific differences in shelter preference, the propensity to occupy shelter was additionally examined in a non-competitive environment. In such trials, only one individual was put into the aquarium containing one shelter and its tendencies to occupy shelter were recorded following the same procedure as described above. Altogether, 20 such trials were performed per species.

*Outdoor group scale experiments—general procedures*

Outdoor tanks (18 tanks; surface area 1 m<sup>2</sup>, volume 1 m<sup>3</sup>) were filled with a sand substrate 5 cm deep and

then filled with water to a depth of 1 m. Aeration was placed at the center of each tank and all tanks were covered with a mesh that prevented crayfish from escaping or potential predators from intruding. Water temperature (average  $\pm$  SD:  $8.98 \pm 2.15^\circ\text{C}$ ), oxygen saturation (average  $\pm$  SD:  $12.55 \pm 0.74$  mg/l), and pH (average  $\pm$  SD:  $7.91 \pm 0.25$ ) were measured constantly in three tanks using a SC1000 (Hach Lange, Tiel, The Netherlands) data logger. Tanks differed in shelter presence—half of the tanks contained no shelters, while a limited number of shelters were added to the other half. In the latter tanks, there were twice as many animals (6) as the available shelters (3).

Crayfish were added to each tank in densities of 6 crayfish/m<sup>2</sup>, which was at the lower end of density ranges used or observed by other authors in similar experimental settings (e.g. Holdich et al. 1995; Corkum and Cronin 2004; Davis and Huber 2007; Pintor and Sih 2009). This eliminated the potential higher injury frequency and unrealistically high number of *per capita* interactions that a combination of higher densities and confined space could elicit (Pintor et al. 2009), but was well within the wide density range observed in nature (between 0.1 and >20 animals/m<sup>2</sup> in both species; e.g. Guan and Wiles 1996; Haertel-Borer et al. 2005; Gherardi 2007) and therefore assumed injury levels and interaction frequencies were applicable to natural conditions. To compare the success of two crayfish species experiencing competition we used growth measurements calculated as the ratio between wet weight after the end of experiment and wet weight at the beginning of experiment (biomass change) across tanks. Biomass change was the only measured parameter of growth since no molts were detected during the course of 30 days experiment.

Injury level was defined as low intensity (antenna/one of walking appendages missing) or high intensity (a claw or more than one antenna/walking appendage missing). As injuries are often perceived as an indirect measure of the intensity of resource competition (Söderbäck 1995), their level and frequency was used to compare levels of competition in tanks with and without shelter.

### *Experiment 3: group scale interactions with limited shelter and without shelter*

Twelve tanks were used to host 6 individuals of either *P. leniusculus* or *O. limosus* (control tanks), while six

tanks were heterospecific with 3 *P. leniusculus* (PL mixed tanks) and 3 *O. limosus* individuals (mixed tanks).

Animals were sampled from captive populations exhibiting size differences (*t*-test CL:  $t_{(106)} = 5.021$ ,  $P \ll 0.001$ ; W:  $t_{(106)} = 4.248$ ,  $P \ll 0.001$ ) that in turn arose from differences already present between the two populations. *P. leniusculus* individuals were on average larger than *O. limosus* individuals, reflecting conditions in naturally occurring populations since *P. leniusculus* reaches up to 16 cm total length, while *O. limosus* grows up to 12 cm total length (Souty-Grosset et al. 2006). As a reflection of the size difference between species as observed in nature, all respective groups (PL controls, OL controls, PL mixed tanks, OL mixed tanks) differed significantly in both weight and carapace length (ANOVA CL:  $F_{(3,104)} = 8.526$ ,  $P < 0.001$ ; W:  $F_{(3,104)} = 6.834$ ;  $P < 0.001$ ). However, recorded differences were the result of differences between *O. limosus* and *P. leniusculus* controls rather than their differences in mixed tanks, as post-hoc Turkey's HSD test revealed no significant difference between species in mixed-species tanks (PL mixed and OL mixed) in either CL or weight ( $P > 0.05$  for all comparisons).

To reduce the effects of potential food competition, crayfish were fed in excess 3 times a week. After one month, all tanks were drained and one-time shelter occupancy and number of injuries, injury level and biomass change (see above) in (i) tanks with versus tanks without shelter, and (ii) mixed species populations versus conspecific populations were recorded and analyzed.

### Statistical analyses

Parametric tests (one-way ANOVA with post-hoc Turkey HSD test, *t*-test for independent samples) were used when the assumptions of normality of data and homogeneity of variance were met on either raw or transformed data. Log-transformations were used in the case of continuous data while square-root transformations were applied on count data. Where transformed data did not meet the assumptions necessary to use parametric analyses, their nonparametric analogues (Kruskal–Wallis ANOVA with post-hoc multiple comparisons of the average ranks, Mann–Whitney *U* test, Wilcoxon matched-pairs test) were used instead (cf. Zar 1996).

## Results

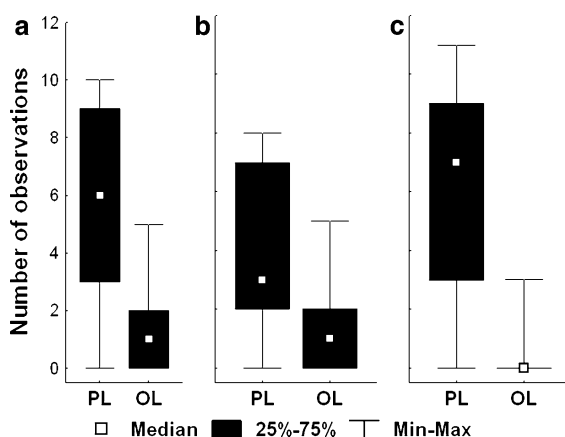
### Experiment 1: pairwise interactions with shelter resource absent

In heterospecific dyads *P. leniusculus* was clearly a dominant species, initiating significantly more agonistic interactions (Wilcoxon matched-pairs test:  $T = 22.5$ ,  $P < 0.001$ ; Fig. 1a) and physical contacts ( $T = 34$ ,  $P = 0.002$ ; Fig. 1b), and winning significantly more interactions ( $T = 6$ ,  $P \ll 0.001$ ; Fig. 1c).

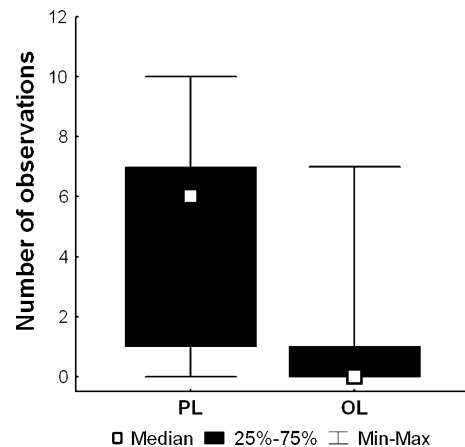
However, duration and number of agonistic interactions did not differ between *P. leniusculus* and *O. limosus* in conspecific and heterospecific dyads (duration of agonistic interactions: ANOVA  $F_{(2, 45)} = 0.743$ ,  $P = 0.481$ ; number of agonistic interactions:  $F_{(2, 45)} = 0.162$ ,  $P = 0.851$ ), meaning that time spent engaging in agonistic interactions and their number (absolute counts) was similar for both species and animals did not significantly change their behavior in these regards when facing heterospecifics as opposed to conspecifics.

### Experiment 2: pairwise interactions with shelter resource present

As there was no difference in time needed to occupy shelter in competitive and non-competitive trials for either species ( $F_{(3, 39)} = 1.342$ ,  $P = 0.275$ ), the



**Fig. 1** Counts and identity of **a** initiator of agonistic interaction, **b** initiator of physical contact and **c** interaction winner, in 25 heterospecific dyads of *P. leniusculus* (PL) and *O. limosus* (OL). PL initiated significantly more interactions and physical contacts than OL and was identified as interaction winner significantly more frequently



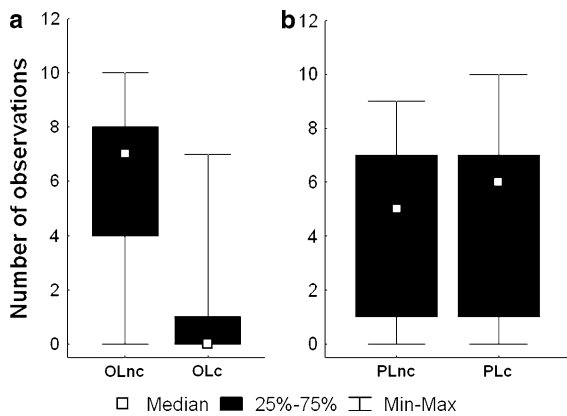
**Fig. 2** Frequency of shelter occupancy in competitive environment for *P. leniusculus* (PL) and *O. limosus* (OL). PL was significantly more frequently observed in shelter than OL

presence of a competitor did not increase the time needed to initially occupy shelter. Also, frequency of shelter occupancy did not differ between species in non-competitive environment (Mann–Whitney  $U$  test:  $U = 133$ ,  $P = 0.070$ ), which shows that *P. leniusculus* and *O. limosus* do not differ significantly in their tendency to occupy uncontested shelter. In competitive environment, however, *P. leniusculus* was significantly more frequently observed occupying the shelter than *O. limosus* ( $T = 43$ ,  $P = 0.002$ ; Fig. 2). This demonstrated that the dominance of *P. leniusculus* extends beyond the staged encounters and is also evident in direct competition for resources, in this case occupying a shelter.

Additionally, statistically significant differences in frequencies of shelter occupancy were recorded between *O. limosus* individuals in competitive versus non-competitive environment ( $U = 48.5$ ,  $P \ll 0.001$ ; Fig. 3a), while no such differences were observed for *P. leniusculus* ( $U = 259$ ,  $P = 0.813$ ; Fig. 3b). This suggests that *O. limosus* individuals were prevented from occupying a shelter by *P. leniusculus* individuals, while *P. leniusculus* occupied shelters at the same rate they would if heterospecific competitors were not present.

### Experiment 3: group scale interactions with limited shelter and without shelter

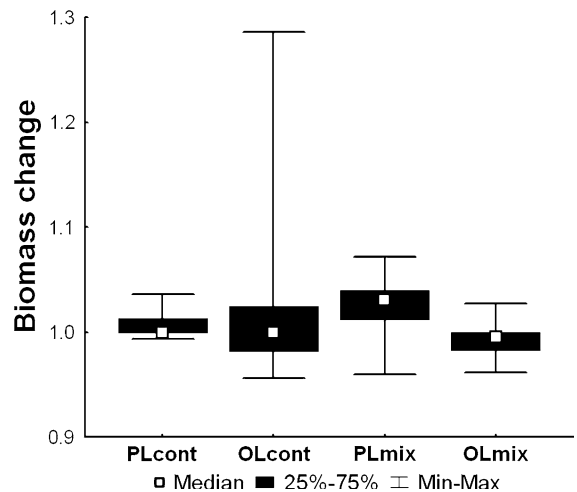
Injury levels and their frequencies were analyzed for 17 out of 18 experimental tanks, as in one *P. leniusculus*



**Fig. 3** Frequency of shelter occupancy of **a** *O. limosus* in non-competitive (OLnc) and competitive (OLc) environment and **b** *P. leniusculus* in non-competitive (PLnc) and competitive (PLc) environment. *O. limosus* individuals were much more frequently shelter occupants in a non-competitive environment, suggesting that they were prevented from occupying shelters by *P. leniusculus* individuals, which were in turn unaffected by competition

conspecific tank an individual was missing at the end of the trial. In conspecific *O. limosus* tanks none of the animals were injured neither in tanks with nor without shelter, while in *P. leniusculus* conspecific tanks 10% of animals suffered injuries all of which were exhibited in tanks containing shelter. The highest proportion of injuries was recorded in mixed species tanks where 22.2% of animals were injured, mostly in tanks containing shelters (16.7% of animals). All injuries in mixed species tanks were suffered exclusively by *O. limosus* individuals, while *P. leniusculus* individuals suffered no identifiable injuries either in tanks with or without shelter. Overall, limited shelter presence increased the number of injuries (i.e. competition intensity) since the majority of the recorded injuries (81.8% of all recorded injuries over all tanks and species) occurred in tanks containing limited shelter resource, while only 12.2% of all recorded injuries occurred in tanks without shelter resource.

When injuries were characterized, the highest proportion of low intensity injuries was recorded in mixed species tanks, where 22.2% of *O. limosus* individuals were missing an antenna; followed by a low proportion of low intensity injuries (3.3% of animals) in *P. leniusculus* conspecific tanks. High intensity injuries (missing claws) were recorded only in conspecific *P. leniusculus* tanks, albeit in a small proportion of individuals (6.7% animals).



**Fig. 4** Biomass change of *P. leniusculus* individuals in conspecific tanks (PLcont) and mixed species tanks (PLmix) and *O. limosus* individuals in conspecific tanks (OLcont) and mixed species tanks (OLmix) over all tanks (with and without shelter resource). In mixed species tanks biomass change of *O. limosus* significantly differed from biomass change of *P. leniusculus*. *O. limosus* was on average losing weight and with it the ability to effectively compete with *P. leniusculus*

Similar to laboratory experiments, one-time shelter occupancy recorded in the group scale experiments revealed that *P. leniusculus* was occupying the majority of shelters (66.7% of all available shelters in 3 mixed species tanks) in comparison to *O. limosus* (11.1% of all available shelters).

Significant change in weight (biomass change) was recorded between animals in conspecific and heterospecific tanks, both in tanks containing shelter (Kruskal–Wallis test:  $H_{(3, 52)} = 19.668$ ,  $P = 0.014$ ) and tanks without shelter ( $H_{(3, 47)} = 9.826$ ,  $P = 0.02$ ). Post-hoc multiple comparisons of the average ranks revealed that in both cases such results stem from differences in biomass change between *P. leniusculus* and *O. limosus* in mixed species tanks, and not from differences between conspecific tanks (Fig. 4).

## Discussion

Since crayfish species highly overlap in key resource needs and potential predators (cf. Gherardi 2007), competitive interactions between co-occurring crayfish invaders in contact zones may have long-term negative effects on at least one of the species. Our

results clearly demonstrate the competitive advantage of *P. leniusculus* over *O. limosus*. In staged encounters of interspecific pairs, *P. leniusculus* individuals initiated and won a higher number of interactions, and were therefore able to dominate agonistic interactions (fights) against their opponents without getting into more or longer fights, and thus without suffering greater costs of fighting. While these values did not change for *O. limosus* either, the one-sided outcomes of the fights suggest the existence of competitive advantage of *P. leniusculus*, due to the inability of *O. limosus* individuals to win contests. Since important determinants of dominance in crayfish (animal size, weight and claw length) were matched in paired individuals, as in other similar studies (cf. Söderbäck 1991; Vorburger and Ribi 1999; Breithaupt and Eger 2002; Fero et al. 2007; Martin and Moore 2008), we envision that the observed dominance of *P. leniusculus* over *O. limosus* can be attributed to some specific aspect of aggressive behavior of *P. leniusculus* individuals that imparts a notable advantage and determines the outcome. While at present we cannot rule out that some other physical attributes, such as chelar strength, are more important determinants of outcome in interspecies interactions than behavioral strategies, additional experiments aimed at providing a detailed analysis of relationships between such parameters and characteristics of interspecies combat are currently ongoing in our laboratories.

As expected, observed behavioral advantage in staged encounters translated into a significant advantage of *P. leniusculus* in shelter competition, which is consistent with the work of other authors on *P. leniusculus* interactions with native species (Vorburger and Ribi 1999; Usio et al. 2001) and on other species as well (e.g. Klocker and Strayer 2004). Shelter access may have higher fitness value than access to food (Bergman and Moore 2003), mainly because shelter ownership directly influences crayfish survival by lowering the risk of predation and cannibalism (Garvey et al. 1994; Söderbäck 1994; Hill and Lodge 1999) and is more likely to be a limited resource than food due to omnivorous nature of crayfish (Fero et al. 2007). Although both species showed similar shelter preference in a non-competitive environment, heterospecific competition significantly decreased shelter occupancy of *O. limosus*, while *P. leniusculus* was unaffected. Thus, for

*P. leniusculus* any fitness costs of competition were manifested only through fights, whereas *O. limosus* suffered not only costs of fights but also the shelter loss after losing fights. As resource acquisition and use is a good indicator of potential fitness consequences when facing competitive pressures (Fero et al. 2007), and its possession is usually proportional to the dominance status (e.g. Martin and Moore 2008), consequences of resource competition will be much more negative for *O. limosus* who suffered decreased shelter access and use, and would therefore experience an increased pressure by predators due to the larger exposure to them as demonstrated in previous studies (e.g. Garvey et al. 1994). Conversely, use and acquisition of shelter by *P. leniusculus* was not affected by the presence of *O. limosus*, suggesting no adverse effect from the presence of heterospecifics.

The effects observed in pairwise interactions were further corroborated by group-scale experiments. Observed dominance in shelter acquisition by *P. leniusculus* in dyads translated to a broader context of a group, with *P. leniusculus* occupying the majority of shelters in heterospecific tanks. Shelter competition also increased the frequency of injuries, with 81.8% of all recorded injuries across all tanks occurring in tanks containing limited shelter. Competition for shelter therefore incurred additional fitness costs to both species since injuries (i.e. appendage regeneration) represent additional energetic investment, which could reduce growth increment and affect intermolt duration in crayfish (Juanes and Smith 1995). Such energetic cost is higher for certain appendages (e.g. claws opposed to pereopods) and for larger crayfish due to reduced molting frequency, which makes claw loss a high fitness consequence, especially for large crayfish (Schroeder and Huber 2001). Also, antennal injuries can seriously affect crayfish behavioral outputs (Koch et al. 2006), including fighting ability (cf. Edsman and Jonsson 1996), therefore antenna loss represents further competitive disadvantage. When competing with conspecifics, *P. leniusculus* suffered high intensity injuries (claw loss) of low frequency, opposed to no injuries while in competition with *O. limosus*. Thus, resource competition with conspecifics was more intense for *P. leniusculus* at a given density than competition with *O. limosus* individuals. The greater risk of severe injuries, and injuries inflicted upon *O. limosus*, suggest that fighting is inherently more



costly when *P. leniusculus* is involved, and that such fights are probably not more frequent, but rather that they involve more injurious behaviors. Such behavioral patterns could explain a greater success of *P. leniusculus* in heterospecific fights, and also add another dimension to its competitive advantage over *O. limosus* in contact zones: not only is *P. leniusculus* able to outcompete *O. limosus*, but the injuries it inflicts can additionally reduce the fitness of the outcompeted species. High frequency of low intensity injuries exhibited solely on *O. limosus* in heterospecific pairs suggests that the injurious behavior is frequently present in such fights, but that *O. limosus* may be able to retreat from fights before suffering serious harm. This in turn may be a possible explanation how consistent dominance of *P. leniusculus* is achieved in heterospecific pairs observed in laboratory experiments.

Further evidence comes from observations of biomass change, i.e. the ratio of wet weight change after one month and at the start of experiment, which was used to measure the effects of competition. While in conspecific tanks there was no significant biomass change for any species regardless of the shelter presence, suggesting that competition did not affect the growth of individuals fed ad libitum, in heterospecific tanks significant difference in biomass change between both species occurred, with *O. limosus* suffering significant weight loss in the presence of *P. leniusculus*, even without shelter. While reasons for such weight loss in ad libitum conditions are not immediately obvious, it is likely that a combination of factors that lead to dominance of *P. leniusculus* could also lead to weight reduction in *O. limosus*. While food availability was not the limiting factor *per se*, competition for food in which one species is prevented from feeding cannot be ruled out even under ad libitum conditions if, for example food was patchily distributed, which is likely since crayfish were fed with randomly dispersed fish pellets. Since the results from Experiment 1 would suggest that *O. limosus* did not experience an increased number of interactions or time spent interacting, it was therefore either effectively prevented from taking food, or continued losses exhibited some other negative effect on its ability to attain and increase in weight. As crayfish often fight even in the absence of resources (Bovbjerg 1956; Bruski and Dunham 1987), direct competition for food may not be the main source of

weight loss in subordinate individuals. Rather, such effect may arise through a combination of high energetic demands that fights against *P. leniusculus* would incur, as well as constant flight responses (cf. Sneddon et al. 1999). Such disturbance may result in disruption in feeding behavior even if food is present in sufficient quantities, and as such lead to a reduced food intake that would consequently result in drop in body mass. Thus, resource monopolization is not a necessary prerequisite for competition between crayfish species to result in fitness differences among participants. The scale of the experiments provides substantial evidence that such processes may also occur when these two species meet in the field.

Size differential in outdoor group-scale experiments between larger *P. leniusculus* and smaller *O. limosus* individuals reflected the differences found in populations from which crayfish were sampled. As difference in body size has been repeatedly considered as a major determinant of dominance order in crayfish (Bovbjerg 1953; Vorburger and Ribic 1999), this difference in size could have contributed to the fight outcomes being skewed in favor of *P. leniusculus*, as well as prevalence of injuries, drop in biomass and shelter deprivation suffered by *O. limosus* in mixed-species tanks. In addition to these effects being likely to mimic those encountered in field conditions due to size differential of naturally occurring populations (Souty-Grosset et al. 2006), physical differences alone are unlikely to explain the exclusively unilateral results observed in the experiments given that there were no significant differences in size between species in mixed species tanks, and that all groups included at least 2 *P. leniusculus* individuals that were smaller than the largest *O. limosus* individual. The one-sided results provide some evidence that the observed consequences were thus less dependent on physical characteristics and more on species-specific differences. Results of group scale experiments indicate that *O. limosus* does not seem to possess any behavioral advantage to compensate for size differential of the dominant competitor. Further research into these phenomena is ongoing.

Based on our results, we expect that in existing or future contact zones interspecific competition has a potential to result in negative fitness consequences for *O. limosus*, a frequent loser of fights and suffering from loss of key resources, higher injury risk and consequent weight loss. Such effect of competition could decrease

not only the fitness of *O. limosus* individuals, but also their ability to regain resources and access to the preferred habitat at a later point. This may lead to decrease in their potential for further invasion and eventual displacement by the dominant opponent. At the same time, the costs of interspecific competition for *P. leniusculus* will be low, as demonstrated through its dominance in fights and resource acquisition, lower intensity of injuries in group scale experiments compared to its intraspecific groups, along with unchanged biomass regardless of the opponent identity or resource presence. It is thus unlikely that the invasion potential of *P. leniusculus* will be significantly affected by the presence of *O. limosus* based on competitive interactions alone. Several authors so far have recorded consistency of native crayfish replacement patterns by invaders in the field with laboratory studies which examined dominance in agonistic interactions (e.g. Capelli and Munjal 1982; Söderbäck 1991; Gherardi and Cioni 2004). However, since such relationship between field and laboratory observations might not always hold true (e.g. Maiwald et al. 2006), the prevalence of focal invaders in existing or future contact zones should not be inferred based upon experimental data alone.

While telling, direct competition is certainly not the only part of the story that determines successful invaders in a multiple-invaders scenario. Although competition is often regarded as an underlying mechanism of species displacement (Söderbäck 1995), other community structuring forces such as predation, parasitism and disturbance affect the outcomes of interspecific interactions (Gherardi 2002). Differential patterns of invasive species composition in the field suggest temporal and system-specific variability in biotic interactions Hill and Lodge (1994; 1999), governed by other factors besides species aggression, activity or size. Therefore, although aggression is often considered as a characteristics of successful invasive species (cf. Weis 2010), aggression will not always lead to success in competition while dominance will not always confer higher fitness, indicating that behavioral traits of invaders should be considered along with social context (Graham and Herberholz 2009) and characteristics of the invaded community, e.g. its niche opportunities (Shea and Chesson 2002). Therefore, this research is particularly suitable to be complemented by broad-scale field surveys in combination with in situ experiments in order to define the

relative role of identified mechanisms and their controlling factors.

The joint impact and consequences of multiple invaders presence on a community or ecosystem are often unknown and confounded by other forms of environmental change (Johnson et al. 2009). Our research highlights the importance of understanding interspecies interactions among invaders in efforts to control invasive species and conserve native fauna. Cumulative pressures by two competitively superior (more aggressive, fertile, resistant etc.) invasive species may raise the number of simultaneous negative interactions (Mills et al. 2004) with vulnerable native species, and it is essential to know what steps, and in what order, need to be taken to tackle this combined threat. We propose that assessment of interaction outcomes between invaders is crucial to understand the cumulative impact of multiple invaders on native species. Identifying the potential asymmetries in consequences of interspecies interactions can help to determine their current and future impact on the invaded ecosystem and consequently the actions necessary to control such threats. This is especially important for freshwater ecosystems, which have been heavily invaded by multiple invaders and also exhibit high degree of endemism and extinction rates. Assessments of this kind would therefore be especially relevant for local management efforts in freshwater habitats, and could help guide appropriate management decisions aimed at conservation and restoration of invaded ecosystems.

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