

Aggressive interactions between three species of freshwater crayfish of the genus *Cherax* (Decapoda: Parastacidae)

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(Received 26 September 2006; in final form 3 January 2007)

Abstract

The freshwater crayfish, *Cherax destructor* Clark, native to southeastern Australia, was first introduced to farm dams in southwestern Western Australia in 1932. The geographic range of the crayfish in Western Australia has increased substantially since then, and in recent years it has become established in natural waterways where it co-occurs with species of freshwater crayfish endemic to southwestern Australia, *Cherax cainii* and *Cherax quinquecarinatus*. The potential for competitive exclusion of these endemic species by *C. destructor* was investigated through laboratory experiments measuring aggressive behaviour. Body mass and species were found to be important factors governing aggressive dominance between *C. cainii* and *C. destructor*, with *C. cainii* winning significantly more interactions only when they were larger in body mass than their opponent. In trials between *C. quinquecarinatus* and *C. destructor* of similar body mass, there was no difference between the number of interactions 'won' by the two species. The implications for natural populations are discussed.

Keywords: Crayfish, introduced species, aggression, dominance, interference competition, *Cherax*

Introduction

Translocation of crayfish beyond their natural range typically results in deleterious impacts such as predation on and competition with indigenous species (i.e. Holdich 1987; Horwitz 1990; Elvey et al. 1996; Gerardi and Holdich 1999; Gerardi in press), alteration to food webs resulting in changes to nutrient and energy flow (i.e. Holdich 1987; Nyström et al. 1999), and the introduction of diseases (i.e. Horwitz 1990; Gerardi and Holdich 1999; Vogt 1999). Aquatic biota are particularly vulnerable to introduced species owing to their relative ease of dispersal (Lodge et al. 1998; Beisel 2001) and the strong affinity of humans for water as a result of commerce, transportation or recreation (Uzio et al. 2001; Gerardi and Daniels 2004). Of the introduced aquatic species, crayfish

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are amongst the most commonly studied (Holdich 1987; Gerardi and Holdich 1999; Lodge et al. 2000; Stucki and Romer 2001; Usio et al. 2001; Gerardi and Daniels 2004).

The potential for introduced crayfish to replace an indigenous species has been recognised by Capelli and Munjal (1982), Butler and Stein (1985), Momot and Leering (1986), Söderbäck (1991), and Vorburger and Ribic (1999), for example. A number of mechanisms have been invoked to explain species replacements, including reproductive interference (Capelli 1982; Capelli and Munjal 1982; Butler and Stein 1985), differential susceptibility to predation (Donato and Lodge 1993; Mather and Stein 1993), and the transmission of disease (Vogt 1999). Competitive exclusion has been cited most often to explain species replacements detected in Europe and North America (e.g. Bovbjerg 1952, 1970; Aiken 1965; Capelli 1982; Butler and Stein 1985). Under competitive exclusion two, geographically sympatric, non-interbreeding populations sharing ecological attributes cannot coexist indefinitely; eventually the population with the superior competitive ability will displace the other (Cole 1960; Hardin 1960). The potential for interspecific competition may be exacerbated when congeneric species are introduced, due to an increased chance of ecological similarities leading to a substantial overlap in the use of resources (Franke and Janke 1998). Ultimately, the species with the most efficient access or utilisation of resources will displace/replace the other (Pianka 1974). Where aggressive crayfish are involved (Söderbäck 1991; Vorburger and Ribic 1999), interference competition likely plays a key role in species replacements (Bovberg 1970; Usio et al. 2001), with aggressive ability aiding in the procurement of food, shelter and mates (Bergman et al. 2003).

Although Australia does not have a history of introductions of crayfish from overseas, intra-continental transfers have occurred (Horwitz and Knott 1995; Lynas et al. 2004, 2006 in press); notably of the species *Cherax destructor* Clark into southwest Western Australia (Austin 1986; Morrissy and Cassels 1992; Horwitz and Knott 1995; Austin and Knott 1996) and Tasmania (Elvey et al. 1996), and *Cherax quadricarinatus* von Martens into the Kimberley region of Western Australia (Horwitz 1990; Curtis and Jones 1995; Doupé et al. 2004; Morgan et al. 2004; Lynas et al. in press). In this article we focus on aggressive interactions between the species *C. destructor* (the yabby) and two southwest Australian endemic species *Cherax cainii* Austin (smooth marron) and *Cherax quinquecarinatus* (Gray) (gilgie). The geographic range of *Cherax destructor* naturally extended from the southeast into central Australia (Riek 1967), and in 1932 the species was translocated without authorisation into Western Australia (Morrissy and Cassels 1992). Currently, the distribution of *C. destructor* in the State is from the Hutt River in the north to Esperance in the southeast, with isolated occurrences further inland, such as along the railway line to Cue, and in a creek system near Leonora (Figure 1; Lynas et al. 2004, 2006; Beatty et al. 2005). Despite their range expansion to-date, little research has been undertaken to ascertain the possible ecological impacts of the introduced crayfish in Western Australia.

An inherent dominance of the introduced over the indigenous species has been found in many species of freshwater crayfish. Dominant crayfish, as determined through agonistic contests in laboratory studies, tend to be the species expanding their range and competitively excluding and displacing indigenous crayfish in the field (i.e. Penn and Fitzpatrick 1963; Capelli 1982; Capelli and Munjal 1982; Butler and Stein 1985; Söderbäck 1991; Giasu and Dunham 1999). Consequently, we addressed the question of whether *C. destructor* is dominant over the endemic crayfish species in aggressive interactions through laboratory-based experiments designed to elucidate (1) whether *C. destructor* was dominant over (a) *C. cainii* and (b) *C. quinquecarinatus*, and (2) the



Figure 1. Map of *C. destructor* distribution across Australia, showing both their natural and introduced ranges. Distributions are not necessarily continuous and represent best current information. There are likely to be other occurrences which have not yet been discovered.

influence of body mass and sex in the aggressive behaviour of *C. destructor*, *C. cainii* and *C. quinquecarinatus*

Methods

Aggression trials

Aggression trials were conducted between individual specimens of *C. cainii* or *C. quinquecarinatus* with individual *C. destructor* to determine aggressive dominance. All trials were conducted in circular tanks of area 2.8 m^2 with 5 cm of sand covering the floor of the tank. Trials were conducted at night under a red lamp, with observations being made continually through a 2 h period.

Aggressive behaviour was assessed by observing and recording outcomes of agonistic interactions, being the head-on encounter between individuals resulting in the retreat of one individual. The categories recorded were those defined by Bøvbjerg (1953), as follows:

- **Fight** - a bilateral aggressive interaction where individuals strike out at each other, often leading to interlocking of chelae. An individual was awarded a 'fight' when the other animal was forced to retreat.

Table I. Treatment details for aggressive interaction experiments

Treatment	Sex	Replication
<i>C. cainii</i> > <i>C. destructor</i>	Male	5
<i>C. cainii</i> < <i>C. destructor</i>	Male	5
<i>C. cainii</i> = <i>C. destructor</i>	Male	5
<i>C. cainii</i> = <i>C. destructor</i>	Female	5
<i>C. cainii</i> > <i>C. destructor</i>	Female	5
<i>C. cainii</i> < <i>C. destructor</i>	Female	3
<i>C. quinquecarinatus</i> = <i>C. destructor</i>	Male	5
<i>C. quinquecarinatus</i> = <i>C. destructor</i>	Female	5

- **Strike** - a unilateral aggressive interaction whereby one individual strikes out at the other with a chela, causing the retreat of the adversary.
- **Threat** - a unilateral aggressive interaction where one animal rapidly approaches the other with chelae outstretched as if to strike, resulting in the retreat of the opponent.
- **Avoidance** - the retreat of one crayfish despite no obvious aggressive display by the other.

The number and types of interaction displayed by each individual during the 2 h observation period were recorded. Only tactile aggression was quantified in these experiments. For each species, the number of aggressive interactions won was determined by the number of fights, strikes and threats plus the number of avoidances by the other species.

To distinguish body mass from species effects, heterospecific pairs of differing body mass combinations were tested (Table I). Interactions between *C. cainii* and *C. destructor* involved either individuals of similar body mass (25 ± 5 g) or a 40% difference in body mass. Gerardi and Daniels (2004) considered that similar-sized individuals were those within 6 g body mass of each other. Interactions between *C. quinquecarinatus* and *C. destructor* involved only individuals of similar body mass (20 ± 5 g) owing to the comparatively small adult size of *C. quinquecarinatus*. Within all treatments, only individuals of the same sex were set against each other in an aggressive interaction, and all treatments were replicated (Table I). Each individual was used only once; a total of 76 animals were utilised. Due to the unexpected deaths of two large female *C. destructor*, only three replicates were possible of the *C. cainii* < *C. destructor* (female) treatment.

Data analysis

Repeated measures ANOVA was used to test for differences in the number of aggressive interactions recorded between *C. cainii* and *C. destructor*, with respect to species, body mass and sex. A post hoc least significant range test was used on the number of tension contacts won, where a significant interaction was found. To test for statistical significance between the number of tension contacts won by *C. quinquecarinatus* compared with those won by *C. destructor* of similar body mass, a paired two-tailed t test was used. Homogeneity of variances prior to statistical analysis was determined by a Cochran's Test (ANOVA) or F-test (t test) and the appropriate transformation applied to achieve equality of variances.

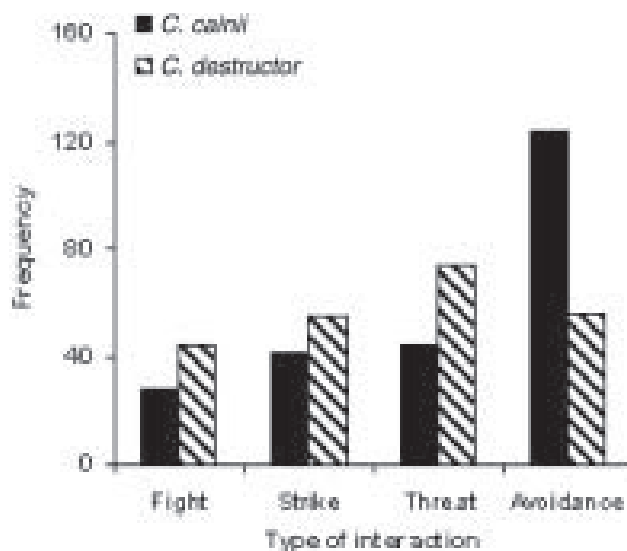


Figure 2. The frequency of recorded interactions between *C. destructor* and *C. cainii* for each type of aggressive behaviour ($n=28$).

Results

Trials involving *C. cainii*

The most common type of interaction for *C. cainii* and *C. destructor*, summed over all aggression trials ($n=28$), was avoidance and threat, respectively (Figure 2). The least common contact for both species was the fight. The mean number of interactions by *C. destructor* and *C. cainii* over all trials was not significantly different (repeated measures ANOVA; $df=1$, $F=3.09$, $p=0.092$). Similarly, no significant difference was detected in the mean number of aggressive interactions recorded between the body mass classes (repeated measures ANOVA; $df=2$, $F=2.85$, $p=0.08$) or sexes (repeated measures ANOVA; $df=1$, $F=0.11$, $p=0.74$). There was no interaction between species and sex (repeated measures ANOVA; $df=1$, $F=0.47$, $p=0.50$) or species, body mass and sex (repeated measures ANOVA; $df=2$, $F=1.65$, $p=0.22$).

The interaction between species and body mass, however, was significant with respect to the number of aggressive interactions won by *C. cainii* and *C. destructor* (repeated measures ANOVA; $df=2$, $F=6.88$, $p=0.005$; Figure 3). When *C. destructor* were larger ($p<0.05$, $df=2$, 22) or equal in body mass to *C. cainii* ($p<0.05$, $df=2$, 22) they won a significantly higher number of interactions (Figure 3). Alternatively, when *C. destructor* were of smaller body mass than *C. cainii*, the latter won a significantly higher number of interactions (Figure 3; $p<0.05$; $df=2$, 22).

There was no significant difference in mean body mass between *C. cainii* (28.8 g) and *C. destructor* (27.9 g) used in similar-sized trials (one-way ANOVA; $df=19$, $F=0.04$, $p=0.85$). However, there was a significant difference in chela length (one-way ANOVA; $df=19$, $F=6.30$, $p=0.02$), with *C. cainii* of similar body mass having longer chela (6.10 cm) than *C. destructor* (5.60 cm).

Trials involving *C. quinquecarinatus*

The most common type of interaction recorded in trials between *C. destructor* and *C. quinquecarinatus* was threat and avoidance, respectively (Figure 4). Threat was the least

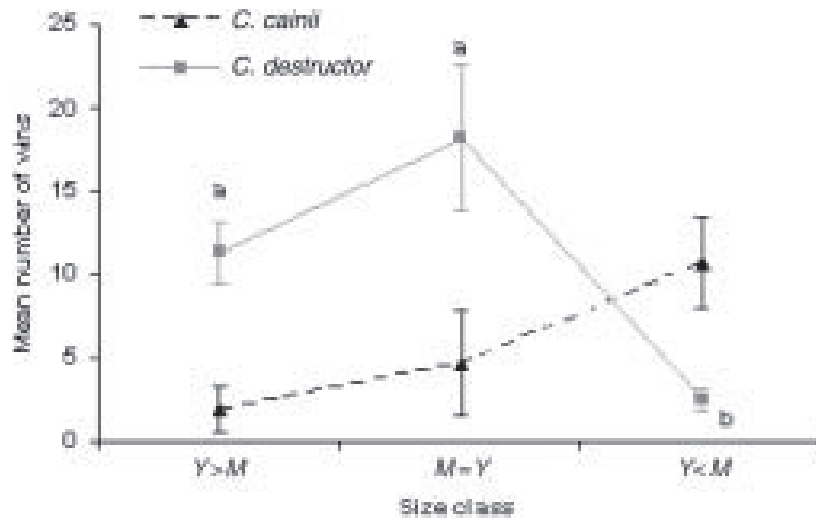


Figure 3. The interaction between species and size in relation to the mean number of aggressive interactions won (mean \pm SE) by *C. cainii* and *C. destructor* ($n=28$). Letters denote equal means determined using the least significant range test (Y > M, *C. destructor* 40% larger than *C. cainii*; M = Y, *C. cainii* same size as *C. destructor*; Y < M, *C. destructor* 40% smaller than *C. cainii*).

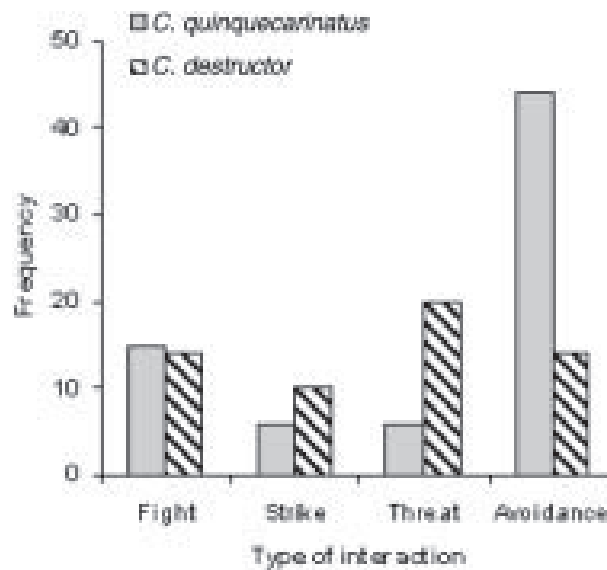


Figure 4. The frequency of recorded interactions between *C. destructor* and *C. quinquecarinatus* for each type of aggressive behaviour ($n=10$).

common contact recorded for *C. quinquecarinatus* whilst for *C. destructor* it was the strike (Figure 4). The mean number of aggressive interactions won by *C. destructor* (8.8) was not significantly different from the number won by *C. quinquecarinatus* (4.1) (two-tailed paired t test; $df=9$, t critical = 2.26, $p=0.22$). Furthermore, the proportion of interactions won by male (0.46) and female (0.74) *C. destructor* when in trials with *C. quinquecarinatus* of similar body mass was not significantly different (one-way ANOVA; $df=1$, $F=1.36$, $p=0.28$).

For individuals used in trials between *C. quinquecarinatus* and *C. destructor* there was no significant difference in mean body mass (one-way ANOVA; $df=19$, $F=3.55$, $p=0.08$) or chela length (one-way ANOVA; $df=19$, $F=0.40$, $p=0.53$).

Discussion

We conclude that body mass is an important factor affecting success in aggressive interactions. We used body mass as a surrogate for animal size: in a study of 1 469 specimens of *C. cainii* from southwest Western Australia, Bennet-Chambers (Curtin University, unpublished data) recorded a correlation of 98.7% between occipital carapace length (cm) and body mass (g). Similar studies reported elsewhere also found size to be a governing factor in dominance order in crayfish (e.g. Bøvbjerg 1953, 1956; Lowe 1956; Horwitz 1980; Rabeni 1985; Momot and Leering 1986; Vorburger and Ribí 1999; Usio et al. 2001). In trials between *C. cainii* and *C. destructor* of similar body mass, species also influenced dominance outcomes, with *C. cainii* winning a number of interactions and exhibiting aggressive behaviour, especially when they were of a larger body mass than *C. destructor*. This contradicts Shipway's (1951) conclusion that *C. cainii* do not display aggressive tendencies towards each other or other species. Nevertheless, *C. destructor* won a significantly greater number of interactions.

Crayfish of similar body mass used in the current study had species-specific variability in chela size which likely influenced dominance outcomes. In contests between individuals of differing size, larger animals would be equipped with larger defence appendages (Hartnoll 1974; Stein 1976). Individuals with larger claws have been found to dominate those with smaller chelae (Stein 1976; Snedden 1990; Garvey and Stein 1993; Rutherford et al. 1995). However, Gherardi and Daniels (2004) found an introduced species with significantly shorter chelae, *Procambarus darkii* (Girard), to be aggressively dominant over similar-sized, endemic crayfish *Procambarus acutus acutus* (Girard). Longer chelae, however, do not necessarily confer advantage in aggressive interactions. *Cherax destructor* of similar body mass to *C. cainii* had relatively wider, but shorter, chelae and won a greater number of aggressive interactions, suggesting that dominance is perhaps influenced more by chela width than chela length in these species. In trials using *C. quinquecarinatus* of similar body mass to *C. destructor*, chela length, chela width, and ultimately aggressive behaviour, were comparable. In aggression contests between *C. quinquecarinatus* and a native crayfish of temporary wetlands in southwestern Australia *Cherax preissi* (Erichson), the koonac, the largest interspecific correlation coefficients occurred when dominance order was ranked with either chela length or chela width (Horwitz 1980). Chela width may play an important role in head-on contests of this type because width of the chela would be more obvious visually to the opposing crayfish than chela length.

In species with differing adult sizes, the age of similar-sized heterospecific crayfishes may also differ, and would likely influence dominance outcomes (Momot and Leering 1986). Since *C. destructor* grow and mature faster than *C. cainii* (Morrissey et al. 1984), *C. destructor* specimens used in similar-sized trials would be at a greater stage of maturity than *C. cainii*. *C. destructor* with a body mass around 30 g is a sexually mature adult, while a 30 g *C. cainii* is still a juvenile. Consequently, only immature *C. cainii* were used in similar-sized aggression trials in the present study. In the North American crayfish, *Pacifastacus leniusculus* and *O. virilis*, the state of sexual maturity of the opponents affected the outcome of aggressive behaviour contests (Momot and Leering 1986).

In the current study, males and females of all species showed comparable tendencies for aggressive behaviour, with no significant differences detected between the proportion of interactions won by males and females. However, in order to derive meaningful conclusions regarding aggressive dominance between sexes, trials involving both males and females need to be conducted. Bøvbjerg (1953, 1956) suggested that male crayfish are more aggressive than females. Studies on aggressive dominance and hierarchies in societies of vertebrates

suggest that male and female aggressiveness tends to be more equal in animals where sexual dimorphism is minimal (Lowe 1956). *Cherax cainii* show some sexual dimorphism in chela width and shape, with males having wider, more robust chelae than females (Bennet-Chambers, Curtin University, unpublished data). Further, male *C. destructor* have both larger body mass and larger chelae compared with females (Lake and Sokol 1986). The fact that chelae size alone does not determine aggressive dominance is evident in the results that aggressive tendencies in males and females were not significantly different in any of the freshwater crayfish species studied, despite males having larger chelae. It is more likely that a number of factors work in concert to determine aggressive dominance in parastacid crayfish, including body size, species and level of innate individual aggression.

To what extent the artificial, simplified laboratory experiments of aggressive behaviour are applicable to natural environments requires careful consideration (Capelli and Munjal 1982; Gerardi and Daniels 2004). Aggressive interactions in the current study were investigated in a simplified homogenous environment lacking refuges under rocks, logs and/or vegetation, leaving the animals unable to avoid the intense contacts that were noted in laboratory trials. This contrasts with natural habitats, and consequently the frequencies of interactions presumably were increased by confining the specimens to a limited space in the experimental chambers. Nevertheless, the aggressive behaviours observed in the present study likely reflect those occurring in nature (Bovberg 1956; Horwitz 1980). However, the value of laboratory experiments is the ability to control different factors likely to affect aggressive interactions, such as size and sex.

Can species replacement between introduced and endemic crayfish species be predicted from the results of aggressive interactions reported here? While competition is widely accepted as a significant force responsible for shaping the ecologies of species and natural communities over evolutionary time (Franke and Janke 1998; Byers 2000), the phenomenon can be extremely difficult to demonstrate unequivocally, leading to some ambiguity over the role that competition plays in species invasions (Byers 2000). Lodge (1993) suggested that the effects of competition may be underestimated because they are more difficult to quantify than impacts associated with climatic and environmental change. Furthermore, there are other mechanisms than can result in species replacements including differential predation, reproductive interference and transmission of disease. Indeed, all of these factors may operate in concert to cause species replacements (Söderback 1995).

Acknowledging these caveats, it is pertinent to discuss likely outcomes concerning interactions between the three species in the field based on their biological and life history characteristics. It is likely, for example, that *C. destructor* will have an advantage over *C. cainii* when they co-occur in natural habitats. Not only are they more aggressive to *C. cainii* of a similar body mass as shown here, but they are also more tolerant of environmental fluctuations (Holdich and Lowery 1988), have a stronger burrowing ability (Morrissy et al. 1984; Holdich and Lowery 1988), grow considerably faster, have a short life cycle, higher fecundity and, under suitable conditions, can breed year-round (Morrissy et al. 1984; Beatty et al. 2005). In contrast, *C. cainii*, attaining a larger size than *C. destructor* (Riek 1967), mature slowly and have a single springtime breeding season (Morrissy 1983; Beatty et al. 2003). There is considerable asynchrony in the breeding cycles of these species, with *C. destructor* releasing juveniles and reaching maturity earlier than *C. cainii*. Therefore, *C. destructor* would have the size advantage when juveniles of both species come into contact in natural systems. Although individuals of similar body mass of *C. destructor* and *C. quinquecarinatus* showed similar tendencies in aggressive behaviour in laboratory trials, in natural environments where the introduced species attains a much larger

size, they would have a size and aggressive advantage over the endemic *C. quinquecarinatus*. Consequently, larger specimens of *C. destructor* would be capable of controlling access to limiting resources such as food and suitable shelter sites where microhabitats of the two species overlap.

Furthermore, when *C. destructor* and *C. cainii* co-occur in sympatry in natural habitats, *C. destructor* may dominate food resources over *C. cainii* juveniles. Beatty (2006), for example, reported an overlap in the use of food resources between sympatric *C. cainii* and *C. destructor* at certain times of the year. In the Hutt River during summer, both *C. cainii* and *C. destructor* preyed predominantly on the mosquitofish *Gambusia holbrooki*, with *C. destructor* showing a dietary shift towards herbivory in winter (Beatty 2006).

Given that the dominance of crayfish species identified in laboratory trials tends to support evidence of displacement patterns occurring in the field (Capelli 1982; Capelli and Munjal 1982; Butler and Stein 1985; Söderbäck 1991; Guiasu and Dunham 1999), the results from the present study do not bode well for the continuing survival of native crayfish of southwest Western Australia in competition with introduced *C. destructor*. This is particularly true given current climatic trends in the southwest: as a result of the increasing drying climate and reduced rainfall, groundwater levels are decreasing (Allan and Haylock 1993). Given that *C. destructor* are burrowing crayfish adapted to long-term population survival in fluctuating environments of impermanent waters (Morrissy et al. 1984), they are likely at an advantage (Lynas et al. in press). The life-history traits of *C. destructor* would also allow the successful colonisation of disturbed habitats and areas which have undergone anthropogenic modification, such as many of the rivers of southwestern Australia (Lynas et al. in press). This effectively enables yabbies to become the most abundant crayfish species in many of the freshwater systems throughout its translocated range in southwestern Australia (Beatty et al. 2005). Consequently, there is a strong case for establishing a comprehensive study to reveal the current status of *C. destructor* in Western Australia, and particularly concerning interactions with native species in natural populations.

Acknowledgements

We acknowledge, with gratitude, assistance from Dr Craig Lawrence (Department of Fisheries, Government of Western Australia), and Drs Kyle Armstrong and Jane Prince (School of Animal Biology, The University of Western Australia). Funding was provided by the School of Animal Biology, The University of Western Australia. The map was compiled by Lisa Chandler (School of Animal Biology, The University of Western Australia). Dr Marilyn Bennet-Chambers is thanked for unpublished information on smooth marron.

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