

Do opposites attack? Resource interactions between an alien and native crayfish from the Lake Eyre Basin

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ABSTRACT

Context. Investigating resource competition between introduced and native species is important to understand the impacts of invasive species, not only on native species, but also with respect to the wider ecosystem. Within the Lake Eyre Basin, there is concern that feral populations of the tropical *Cherax quadricarinatus* are outcompeting the basins' native crayfish species, the temperate–subtropical *Cherax destructor*. **Aims.** This study sought to observe the behavioural and inter-specific food competition between juvenile *C. quadricarinatus* and *C. destructor* under experimental conditions to inform whether *C. quadricarinatus* has the potential to outcompete native *C. destructor* populations. **Methods.** Interactions were quantified by establishing a behavioural intensity score, dominance score and recording the total time in possession of the food resource in a range of interspecific and intraspecific experimental pairings at 26°C. **Key results.** *Cherax quadricarinatus* had a significantly higher dominance ($z = -2.276$, $P = 0.023$) and behavioural intensity score ($t = 4.723$, $P < 0.001$) than did *C. destructor*, but there was no difference between the two species for time in possession of the food resource ($z = -1.334$, $P = 0.182$). **Conclusions and implications.** These results have significant ecological implications because the capacity of *C. quadricarinatus* to displace *C. destructor*, a keystone species, has the potential to irreversibly alter ecosystem function in invaded habitats.

Keywords: aquarium experiment, behavioural study, *Cherax destructor*, *Cherax quadricarinatus*, competition, crayfish behaviour, invasion ecology, species interactions.

Introduction

Human pressures and alterations to the environment create novel pathways that allow species to spread beyond their historical range and invade previously isolated habitats. Such locally alien organisms can pose a significant threat to freshwater ecosystems, which are already extremely vulnerable to biodiversity loss because of many other anthropogenic pressures, including water resource development and climate change (Dudgeon *et al.* 2006). Although the potential impacts of species invasions are inherently complex, investigating resource interactions affords an opportunity to understand potential trophic interactions and disturbances of invasive species.

Keystone species have a disproportionately high effect on ecosystem function in proportion to abundance (Valiente-Banuet *et al.* 2015). Within freshwater ecosystems, ecosystem engineers, defined as species that create, destroy or significantly modify a habitat, can hugely affect other species through altering water quality, nutrient content and organic matter (Gallardo *et al.* 2016). Decapods, such as crayfish, are generalist omnivores that typically act as both ecosystem engineers and keystone species within their natural ecosystem (Strayer 2010). Locally alien crayfish species can therefore cause significant and irreversible alterations to functions and the interactions among the species within an invaded ecosystem (Gherardi *et al.* 2011; Twardochleb *et al.* 2013).

The red-claw crayfish (*Cherax quadricarinatus*), native to northern Australia and Papua New Guinea, is a species with significant invasive potential in Australia. Its attractive features, large maturing size and high flesh to size ratio have made it a sought-after

species within the international aquarium and aquaculture trades. The robust and adaptable *C. quadricarinatus* is a formidable invasive species, with feral populations recorded across the globe originating from escapees of aquarium and aquaculture activities (Twardochleb *et al.* 2013). Recently, feral populations of *C. quadricarinatus* have been identified within the Lake Eyre Basin (LEB) of central Australia (Leland *et al.* 2012; Kingsford *et al.* 2014). This range expansion is theorised, as in the case of the international examples, to be the combined result of aquaculture escapees, private dam stocking escapees and fishing bait escapees, and there is a growing awareness of the threats posed by this species as an invasive (Leland *et al.* 2012). The appearance of *C. quadricarinatus* in the LEB is particularly concerning because of the biologically unique nature of the basin's catchments. Unlike many other aquatic ecosystems globally and within Australia, rivers and wetlands of the LEB are largely untouched by invasive species, with other recorded invasive species being fish, namely, sleepy cod (*Oxyeleotris lineolata*), goldfish (*Carassius auratus*) and mosquito fish (*Gambusia affinis*; Kingsford *et al.* 2014; Sternberg and Cockayne 2018).

The LEB is a highly arid environment and the survival of many of its species, both aquatic and terrestrial, rely on periods of high productivity, associated with large flows after unpredictable and uncommon rainfall events (Arthington and Balcombe 2011; Kingsford *et al.* 2014; Lake Eyre Basin Ministerial Forum 2017). Rarely being the result of local rainfall, these massive flows often originate from monsoonal rainfall in northern Queensland. From there, floodwaters make their way south through the Cooper and Diamantina–Georgina catchments, an event known as a 'dry flood' (Kingsford 2017). Characterised by a 'boom and bust' ecology, isolated waterholes sustain aquatic biodiversity within the LEB during the dry 'bust' period. Here, specialised endemic aquatic species, such as the endangered Cooper Creek catfish (*Neosiluroides cooperensis*), survive until the next significant flow event fills the river channels, connecting previously isolated waterholes (Arthington and Balcombe 2011; Arthington *et al.* 2019). During the contrasting 'boom' periods, large numbers of wetland birds migrate towards the LEB to feed and reproduce following the significant increase in biomass of aquatic organisms (Arthington and Balcombe 2011; Arthington *et al.* 2019). This high concentration of endemic aquatic species, and importance to Australia's wetland birds, contributes to the high conservation value of the LEB (Kingsford *et al.* 2014; Kingsford 2017). Unlike the neighbouring Murray–Darling Basin, Australia's other extensive dryland basin system, the LEB is mostly unregulated, resulting in the preservation of the unique biodiversity that relies on 'boom and bust' ecology (Costelloe *et al.* 2003; Kingsford *et al.* 2014; Kingsford 2017; Lake Eyre Basin Ministerial Forum 2017).

Both published and unpublished observations have identified *C. quadricarinatus* populations within the LEB

(Kingsford *et al.* 2014). *C. quadricarinatus* has the ability to grow to almost twice the weight and twice as fast as the only native crayfish species in the LEB, the blue-claw crayfish (*Cherax destructor*). Crayfish dominance is highly affected by size, with larger individuals overpowering smaller specimens (Moore 2007). Consequently, there is concern that this obvious size advantage will allow *C. quadricarinatus* to outcompete and displace the native *C. destructor* species within the LEB (Masser and Rouse 1997; Moore 2007). This feature may be particularly relevant in terms of food resource competition, because both species are opportunistic omnivores that inhabit the same ecological niche. The replacement of a keystone native species with a larger, more aggressive, faster-growing invasive species has the potential to affect all species within the given ecosystem (Carpenter *et al.* 1985). There is concern that this interaction may pressure the unique refuge ecosystems of the LEB during the vulnerable 'bust' period when resources are limited (Kingsford *et al.* 2014).

Anecdotal records have recounted some form of interaction between invasive *C. quadricarinatus* and native *C. destructor* within the LEB, with a noted reduction in *C. destructor* numbers when *C. quadricarinatus* is present (Kingsford *et al.* 2014; Lake Eyre Basin Ministerial Forum 2017; G. King, unpubl. data). However, there has not previously been any formal research or monitoring effort dedicated to assessing the nature of this interaction. This study investigated behavioural and inter-specific food competition between the locally alien *C. quadricarinatus* and the native *C. destructor* under experimental conditions. The primary objective of this study was to examine the dynamics between the two species to better understand their likely behavioural interactions in the field, and to determine whether *C. quadricarinatus* has the potential to outcompete or exclude *C. destructor* populations. We hypothesised that *C. quadricarinatus* would exhibit significantly more aggressive behaviours than would *C. destructor* and be more dominant in interactions (Hypothesis 1). We also hypothesised that this higher aggression and dominance would translate to *C. quadricarinatus* being in possession of a food resource for significantly longer than would *C. destructor* (Hypothesis 2).

Materials and methods

Study species

Cherax destructor is a wide-spread medium-sized Australian crayfish species, with an average maturing occipital carapace length (OCL, measured from the rostrum's tip to the end of the carapace) of 200 mm. Although native to the temperate–subtropical areas of central and eastern Australia, its natural range spans across all states and territories except for Tasmania and Western Australia (Nguyen *et al.* 2004). As a result of a continuing decline in native habitat and fragmented

native populations, *C. destructor* was listed as a vulnerable species by the IUCN in 1996 (Crandall 1996). Popular in aquaculture farming and as recreational fishing bait, *C. destructor* has been introduced to areas outside its natural range and can now be found in all states and territories in Australia and has introduced populations internationally (Lopez *et al.* 2019). A versatile species, *C. destructor*, can inhabit a wide range of ecological niches, ranging from semi-arid temporary water systems of the LEB to the cooler, more permanent southern Australia waterbodies (Nguyen *et al.* 2004).

Cherax quadricarinatus of the tropical northern Australia and Papua New Guinea is the larger of the two species but rarely grows to an OCL longer than 350 mm. *C. quadricarinatus* has similarly been heavily farmed both nationally and internationally for human food production (Souty-Grosset *et al.* 2006). Escapees have established feral populations internationally, with populations having been recorded in Costa Rica, Mexico, Africa and Thailand (Bortolini *et al.* 2007; Azoifeifa-Solano *et al.* 2017; Petersen *et al.* 2017; Chaichana and Wanjit 2018; Douthwaite *et al.* 2018). Although being native to northern Australia, *C. quadricarinatus* has been identified as far south as Lake Ainsworth in New South Wales and within the biologically significant LEB (Leland *et al.* 2012; Kingsford *et al.* 2014). This range change is theorised, like the international examples, to be the result of aquaculture escapees from both commercial and private establishments in the area (Leland *et al.* 2012).

Experimental design

Crayfish collection

Forty individuals of each species were purchased from local and online suppliers, with 24 individuals of each species being included in the experiments. Any crayfish with visible parasites, missing limbs, visible injuries, or that had recently moulted were excluded from the experiment. All crayfish were sexed, because sex influences crayfish behaviour and must be controlled for in behavioural experiments (Moore 2007). Crayfish were sexed on the basis of the presence of genital papillae at the base of the bottom set of legs on males. Females lack this feature and instead have ovary openings at the base of the third set of legs. All crayfish used in the experiments were juveniles, ranging in size from an OCL of 23 to 32 mm. This choice came down to experiment practicality, with juvenile crayfish being easier to source. There is no evidence to suggest that this would affect the behaviour of the crayfish when carapace lengths differ no more than 20% (Moore 2007).

Crayfish housing

Crayfish were individually housed in 15-L opaque aquaria, each containing one PVC pipe for shelter (100-mm length, 45-mm inside diameter), a sand substrate of 2-cm depth

and 5 L of rainwater. All aquaria were housed in a controlled laboratory environment, with crayfish being exposed to a natural (uncontrolled) photoperiod of an average 11 h of daylight. Water temperature was maintained at 26°C, with *C. quadricarinatus* originating from the tropical north, and *C. destructor* from cooler subtropical–temperate habitats; this is the mid-range of optimal temperature for both species (Masser and Rouse 1997).

During a 1-week acclimation period, crayfish were fed a mixture of bottom-feeder shrimp pellets (API, America), cooked zucchini and raw green prawns 3 times per week. Crayfish were isolated for at least 7 days to allow the natural dominance state of the crayfish to reset after an agonistic interaction (Schneider *et al.* 1999; Moore 2007). Because the aquaria did not contain any form of filtration, a water change was completed the day after feeding to remove any uneaten food. After the experiment, all crayfish were observed for 1 week, with any crayfish that moulted during this period being excluded from the experiment (Gherardi *et al.* 2011).

Competition experiment

After the acclimation period, all crayfish were starved for 7 days to standardise food motivation. After this starvation period, the OCL of each crayfish was measured. Crayfish pairs were then established, comprising size- and sex-matched *C. destructor* and *C. quadricarinatus*, including, in total, 12 inter-specific pairs (comprising six male and six female pairs), 6 *C. destructor*-only pairs (three male and three female pairs) and 6 *C. quadricarinatus*-only pairs (three male and three female pairs; see Supplementary material Table S4). Dominance among crayfish individuals is highly dependent on individual carapace size; therefore, OCL size difference was limited to 10% (Hudina *et al.* 2016; Lopez *et al.* 2019; see Table S4). Although chelae size also plays a role in dominance among crayfish individuals, it was impossible to control for this variation because of the inherent differences between the species. *C. quadricarinatus* has skinnier chelae than does *C. destructor*, an anatomical feature that is particularly evident in adult individuals. Therefore, juvenile crayfish individuals were preferred, allowing a chelae width and length difference of less than 20% (Moore 2007).

Interactions between pairs took place in 60 × 30 × 30-cm aquaria divided into three sections by opaque dividers. The aquaria contained 2 cm of gravel substrate and were held at a constant temperature of 26°C. A food resource (2-cm cube of raw green prawn tissue and 2-cm cube of cooked zucchini) was wrapped in flyscreen and secured to the bottom of the middle compartment, thus allowing the food resource to be interacted with without being manipulated or consumed (Lopez *et al.* 2019). The crayfish were separately placed in each of the end compartments and allowed 15 min to acclimatise to the new aquaria conditions before interacting with each other and the food resources (Fig. 1).

After the acclimation period, the opaque dividers were removed, and the crayfish pair were allowed to interact

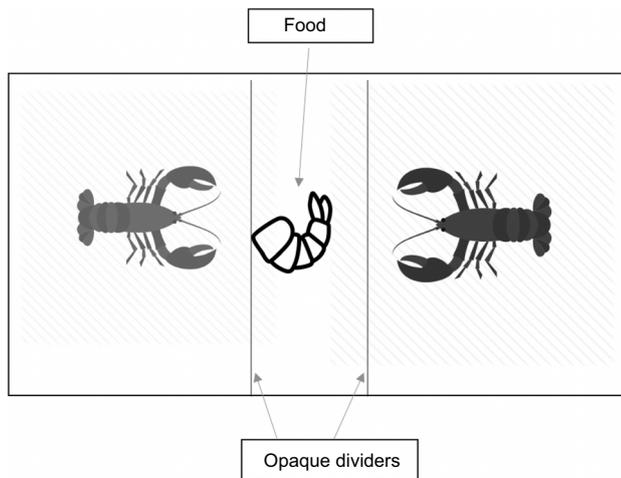


Fig. 1. Experimental trial set-up where *C. destructor* and *C. quadricarinatus* were placed on either side of an opaque divider, which was removed after an acclimation period to allow interactions with each other and the food resource.

with each other and the food resource for 20 min. The whole interaction was video recorded with all persons removed from the laboratory to prevent observer effects. Each experiment occurred at night between 1900 and 2400 hours, illuminated with a red light that is a spectrum that crayfish cannot detect (Dalosto et al. 2015). After the experimental period, the two individuals were returned to their separate aquaria and fed. This experiment was conducted once with each pair.

Behavioural observations

Each recorded experiment was viewed, and the interactions were recorded following the procedures of Dalosto

et al. (2015) and Moore (2007). The amount of time an individual spent within 1 cm of the food resource without the competitor was considered 'time in possession of the food resource' (TPFR) and was regarded as an individual's capacity to dominate a food resource. The number of agonistic bouts, in which both individuals were initiated in a fight lasting at least 10 s, was also recorded. The individual that retreated first was identified as the loser, with the crayfish that won the most of these interactions identified as the winner (Dalosto et al. 2015). All interactions were scored through the behavioural ethogram presented in Table 1 (modified from Moore 2007). Additional behaviours that were recorded for further analysis are shown in Table 2. For inter-specific interactions only, the dominance score was calculated for each individual of a pair by the number of contests the individual won divided by the total number of contests between the two contestants. The behavioural intensity score (BIS) for each individual was calculated through the sum total of the associated score for each behaviour observed during the interaction trial, as shown in Table 1.

Data analysis

For intra-specific interactions, there were not enough trials to ensure statistical robustness. Therefore, no analysis was conducted. Instead, the average of the measured variables (Table 2) was calculated in Microsoft Excel (ver. 16.29.1, Microsoft Corporation, see <https://www.microsoft.com>). For inter-specific pairs, the differences between individuals in the 'dominance score' and 'time spent in possession of the food resource' variables were analysed using the non-parametric Wilcoxon signed-ranks test (Quinn and Keough 2002).

Differences between the BIS of the individuals in the inter-specific pairs were analysed using a paired *t*-test, because all normal distribution assumptions were met. All analyses were

Table 1. Ethogram of agonistic behaviours, their behaviour intensity score (BIS) and behaviour type modified from Moore (2007).

Behaviour	Description	Score	Behaviour type
Tail flip	Rapid contraction of the abdomen, which results in the quick backwards retreat	-2	Submissive
Retreat	Slow backwards retreat through the movement of the legs	-1	Submissive
Ignore	Ignoring or exhibiting non-aggressive behaviours in response to agonistic displays from the opponent	0	Neutral
Non-aggressive approach	Slowly approaching the opponent without agonistic displays	+1	Dominant and Aggressive
Aggressive approach	Aggressive approach with the flicking of the antennae	+2	Dominant and Aggressive
Cheliped raise	Spread and raise of chelipeds towards the opponent	+2	Dominant and Aggressive
Cheliped punch	Boxing, pushing or touching of close chelae onto the opponent's body or limbs. Chelae not used to grasp the opponent	+3	Dominant and Aggressive
Active chelae strike	Active strike and grabbing or holding of the opponent with opened chelae. It can involve attempts to overturn the opponent	+4	Dominant and Aggressive
Unrestrained	Unrestrained fighting by pulling opponents limbs and body. Involves multiple active chelae strikes	+5	Dominant and Aggressive

Table 2. List of behaviours and trial metrics that were recorded for each crayfish pair interaction.

Food resource	Agonist interaction	Individual
FRCI: the first individual to make contact with the food resource	Contest initiator: the first individual to initiate a contest	The type and number of submissive or aggressive behaviours performed by an individual will be recorded and given a score (Table 1). Accumulative score of an individual's agonist behaviours will be used to calculate their behaviour intensity score (BIS; Table 1)
Food latency time: the time from the beginning of the trial to the first contact with the resource	Fight latency time: the time from the beginning of the trial to the first contest	
TPFR: the time each individual spends in possession of the food resource	Contest length: the length of an individual contest	
	Winner: the winner of an individual contest	
	Loser: the loser of an individual contest	

conducted in SPSS (ver. 25.0, IBM Corporation) with the significance level set to $\alpha = 0.05$.

Results

Intra-specific interactions

Cherax quadricarinatus in intra-specific pairs spent an average of 40% of the time in contest, averaging 5.3 contests per pair (Table 3). The maximum intensity reached was unrestrained fighting (+5), with an average contest latency time of 121.7 s (Table 3). *C. quadricarinatus* pairs had an average combined time in possession of the resource of 1.3%, with a latency time of 142 s. By contrast, none of the six *C. destructor* pairs engaged in contests, with the maximum level of agonistic behaviour reached of active chelae strike (+4; Table 3). On average, however, the *C. destructor* pairs reached the food resource twice as fast as the *C. quadricarinatus* at 61.2 s and spent an average of 61.2% of the total trial time in possession of the food resource (Table 3).

Inter-specific interactions

In the inter-specific pairs, *C. quadricarinatus* specimens were ~3.5 times more dominant than were the *C. destructor*

Table 3. Intra-specific interactions average contest and resource competition variables (± 1 s.e.) for *C. quadricarinatus* and *C. destructor* during a 20-min interaction trials, averaged from six trials for each species.

Variable	<i>C. quadricarinatus</i>	<i>C. destructor</i>
Average contest latency time \pm s.e. (s)	121.7 \pm 75.2	N/A
Range of contest latency time \pm s.e. (s)	23–492 \pm 75.2	N/A
The average percentage of total time spent in contest \pm s.e.	40.7 \pm 10.7	0
The range percentage of total time spent in contest \pm s.e.	19.7–75.5 \pm 10.7	0
The average number of contests per pair \pm s.e.	5.3 \pm 0.8	0
Highest level of agonistic behaviour reached	+5	+4
The average food latency time \pm s.e. (s)	142 \pm 121.51	61.2 \pm 28.9
The range of food latency time \pm s.e. (s)	0–743 \pm 121.51	30–193 \pm 28.9
The average percentage of total time spent in possession of the food resource \pm s.e.	1.3 \pm 1.2	61.2 \pm 7.7
The range percentage of total time spent in possession of the food resource \pm s.e.	0–7.25 \pm 1.2	7.6–75.3 \pm 7.7

specimens, with the Wilcoxon signed-rank test identifying this as a significant difference ($z = -2.276$, $P = 0.023$; Fig. 2, see Supplementary material Table S1). With an average of 2.5 contests per pair, *C. quadricarinatus* won 4 times as many contests as did *C. destructor* (Table 4). The maximum number of fights conducted by a pair was nine, with a minimum of one fight per pair. *C. quadricarinatus* individuals were significantly more aggressive, with a BIS ~7 times higher than that of their *C. destructor* opponents ($t = 4.723$, $P < 0.001$; Fig. 3, Table 4). On average, *C. destructor* possessed the food resource 6 times longer than did *C. quadricarinatus* (Fig. 4, Table 4); although this was not a significant difference ($z = -1.334$, $P = 0.182$). On occasions when *C. destructor* was able to take possession of the food resource, it did so almost twice as fast as did *C. quadricarinatus* (Table 4).

Cherax destructor displayed significantly more submissive and neutral behaviours, identified as tail flip ($z = -2.527$, $P = 0.012$), retreat ($z = -2.083$, $P = 0.037$) and ignore ($z = -2.032$, $P = 0.042$), than did their *C. quadricarinatus* opponents (Fig. 5). Comparatively, *C. quadricarinatus* performed significantly more aggressive behaviours, identified

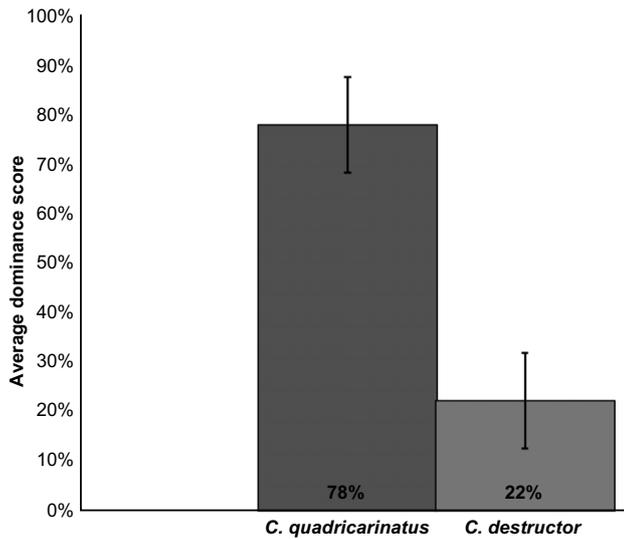


Fig. 2. The dominance score percentage (± 1 s.e.) of *C. quadricarinatus* (dark grey) and *C. destructor* (light grey) averaged over 12 inter-specific interaction trials.

as active chelae strike ($z = -2.955, P = 0.003$), cheliped punch ($z = -2.680, P = 0.007$) and aggressive approach ($z = P = 0.012$) (Fig. 5). The frequency of the behaviours of unrestrained combat and non-aggressive approach was not significantly different between the species (Fig. 5).

Discussion

Invasion of an alien crayfish into a large and highly intact river basin poses significant threats to global pursuits to protect freshwater ecosystems and their assemblages from invasive species. The translocation of *C. quadricarinatus* to the LEB has become a significant concern to the scientific and general community over the recent decade, particularly in relation to its interactions with the native *C. destructor*

Table 4. Inter-specific interactions average contest and resource competition variables (± 1 s.e.) for *C. quadricarinatus* and *C. destructor*, during a 20-min interaction trials, averaged from 12 trials.

Variable	<i>C. quadricarinatus</i>	<i>C. destructor</i>
The average number of contests won	2 \pm 0.35	0.5 \pm 0.19
The average behavioural intensity score range	14–169 \pm 12.3	–20–36 \pm 4.7
The average food latency time (s)	9 min 32 s \pm 1 min 46	5 min 46 s \pm 1 min 53
The average percentage of total time spent in possession of the food resource (%)	0–8.83 \pm 0.8	0–66.67 \pm 5.9

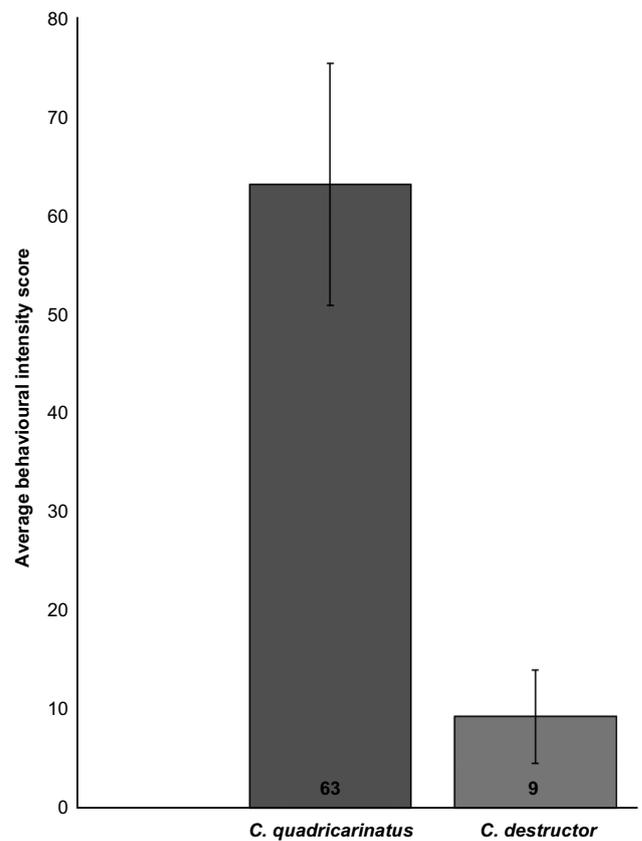


Fig. 3. The average behavioural intensity score (BIS; ± 1 s.e.) of *C. quadricarinatus* and *C. destructor* during 12 inter-specific interaction trials.

(Kingsford et al. 2014; Firm et al. 2015; Schmarr et al. 2016). Unpublished data by King, as well as the Lake Eyre Basin Ministerial Forum (2017), has located established *C. quadricarinatus* populations within the three major catchments of the Queensland segment of the LEB, the Diamantina, Georgina and the Cooper catchments. Sites with *C. quadricarinatus* detected had an observed reduction in *C. destructor* captured compared with sites where *C. quadricarinatus* was not detected, with the Lake Eyre Basin Ministerial Forum (2017) classifying *C. quadricarinatus* as a high-risk invasive. The results of our study suggested that where *C. quadricarinatus* has established populations within the LEB, it may pose a risk to the native *C. destructor* through its aggressive and dominant behaviours, although the mechanisms enabling *C. quadricarinatus* to dominate *C. destructor* may be more complex than originally thought.

In accordance with Hypothesis 1 that *C. quadricarinatus* will show significantly more aggressive behaviours than does *C. destructor* and will also be more dominant, the invasive *C. quadricarinatus* displayed more aggressive behaviours leading to a higher dominance than for the native

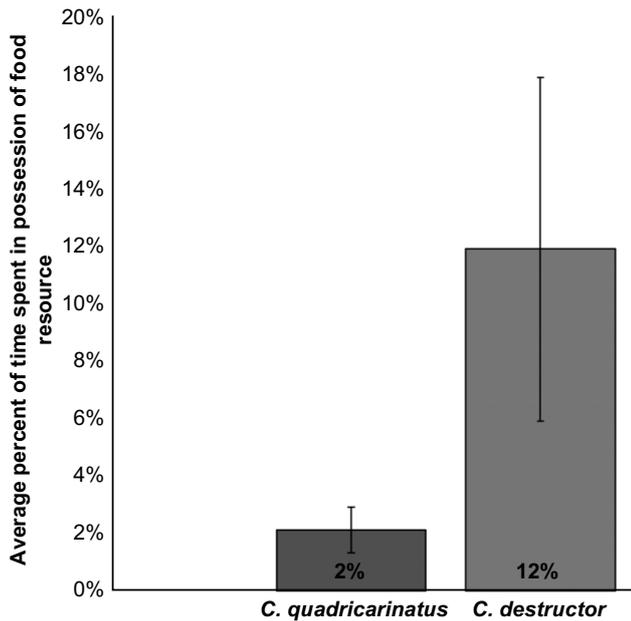


Fig. 4. The average amount of time, as a percentage of the 20 min, that *C. quadricarinatus* and *C. destructor* crayfish spent in possession of the food resource during the 12 inter-specific trials (± 1 s.e.).

C. destructor in experimental interactions, supporting this hypothesis. However, this clear dominance did not result in a higher resource-holding capacity, with *C. destructor* possessing the food resource for a longer, albeit statistically non-significant, time. This result does not support the predictions of Hypothesis 2 that *C. quadricarinatus* will possess a food resource for significantly longer than does the *C. destructor* during laboratory-based pairwise trials.

Cherax quadricarinatus and *C. destructor* interaction dynamics

Dominance

Dominance, defined here as the ability to win more agonistic contests, is one of the many factors that contribute to the displacement of endemics by invasive species (Moore 2007). For crayfish, in particular, dominance plays an essential role in the success of an invasive species within a habitat that already contains a native crayfish species (Thomas Lorenz *et al.* 2019). This dominance can translate into the possession of food resource, shelter and territory, all of which enhance an individual's chance of survival (Moore 2007). The results of this study indicated that the trend for invasive crayfish species to be more dominant than their native counterparts, as was also indicated in a meta-analysis by Twardochleb *et al.* (2013), extends to the interactions between the invasive *C. quadricarinatus* and the native *C. destructor* in the LEB. The results of this study indicated that *C. destructor* is likely to be a submissive, almost placid, contestant. The placid behaviour of

C. destructor was highlighted in the intra-specific trials, where same-species contestants behaved in a communal nature, choosing to share the resource rather than fight for it. This starkly contrasts to the behaviour of *C. quadricarinatus* in the intra-specific trials, which displayed a high motivation to establish dominance through aggression. The intra-specific trials further pronounced the behaviours observed in the inter-specific trials, particularly that of *C. destructor*, which had no recorded fights.

The behaviour of *C. destructor* contrasts with the findings of Lynas *et al.* (2007), where *C. destructor* won significantly more interactions during contests with *Cherax cainii*. Lynas *et al.* (2007) linked this result to the larger chelae of *C. destructor*, than that of *C. cainii*, a physiological characteristic that is closely linked to crayfish dominance (Moore 2007). Although precise chelae size was not used in the size matching of individuals within this study, all crayfish pairs had a chelae-size difference of less than 20%, a degree which Moore (2007) reported would not significantly affect dominance in crayfish. This decision was made as *C. quadricarinatus* generally has thinner chelae than does *C. destructor*; therefore, it was not possible to match individuals on the basis of both chelae and carapace size. A carapace size match was prioritised over chelae, because this was determined to play a larger role in determining dominance (Moore 2007; see Table S4).

The results of this study, and that of Lynas *et al.* (2007), suggested that crayfish dominance varies across species. Although a species may be submissive in one situation with one opponent species, it may be dominant in another interaction with a different species. This pattern of behaviour appears to be the case with *C. destructor*, which has a varied level of dominance depending on the opponent species. This pattern further unfolds when comparing the results of Lynas *et al.* (2007) and Lopez *et al.* (2019). Lopez *et al.* (2019) similarly undertook behavioural interactions between carapace size-matched *C. destructor* (the invader) and a native crayfish species. Contrasting to the results of Lynas *et al.* (2007), the native crayfish species, *Euastacus dharawalus*, was much more aggressive, with *C. destructor* taking on a submissive role. Many factors could contribute to this variation in behaviour, including differences in the species physiological makeup, including body and chela ratio and differences in neurochemistry and motivation (Moore 2007). A notable factor that may also influence such behavioural variations is the invaded species' historic interactions with the invader. Lopez *et al.* (2019) collected both invaded and invader from the same creek system. Invaded specimens that are already familiar with the invader may exhibit more aggressive behaviours than one that is naïve to the invasive species (Moore 2007). A meta-analysis by Twardochleb *et al.* (2013) showed that, overall, crayfish that are invasive are more likely to display aggressive and dominant behaviours; this was linked to the enhanced competitive ability of many invasive crayfish species,

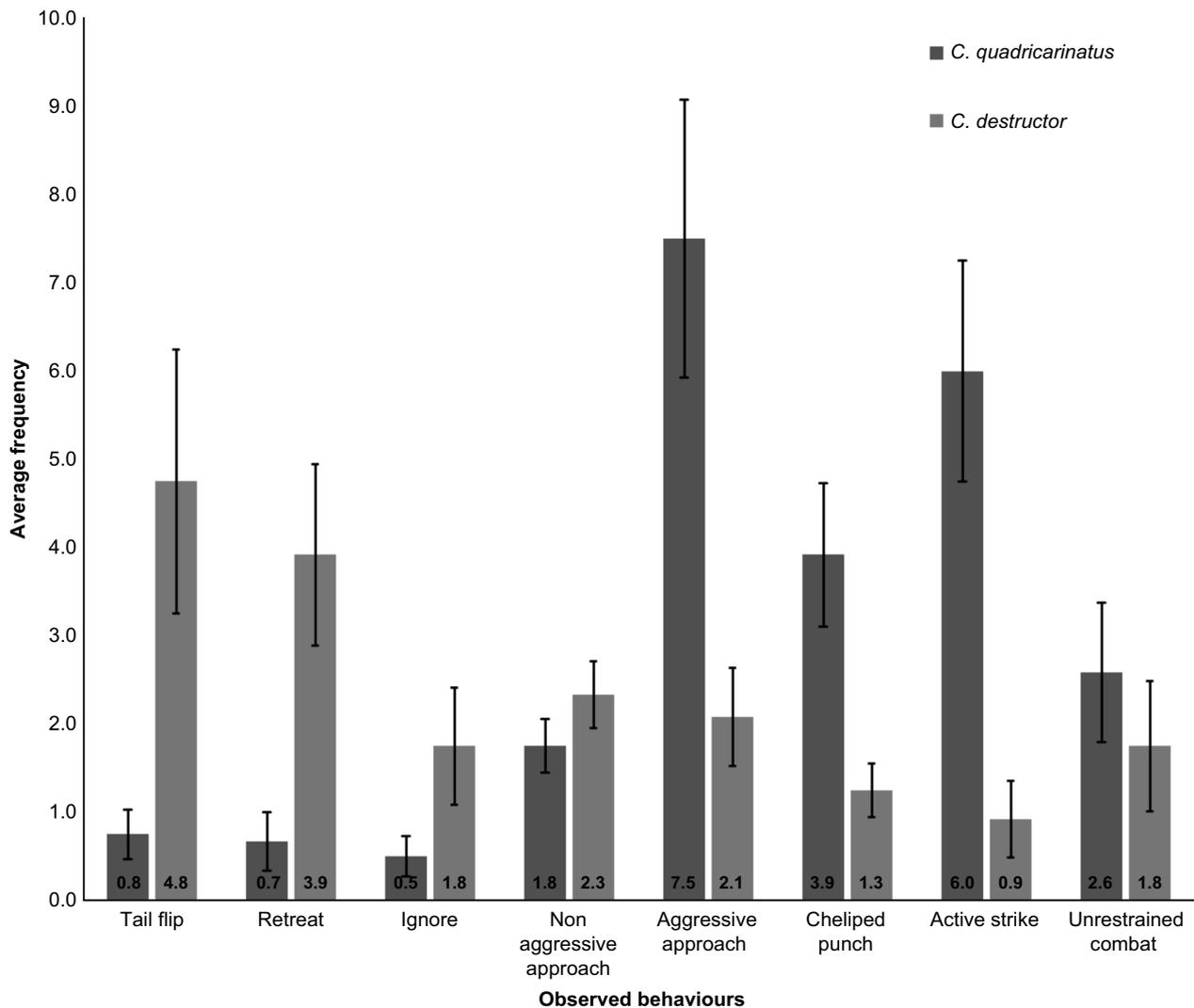


Fig. 5. The average number of times each identified submissive or aggressive behaviour was observed (± 1 s.e.) during the 12 inter-specific trials.

although deviations from this trend are present, as can be observed with the behaviour of *C. destructor*.

Agonistic behaviours

Similar to patterns in dominance, invasive crayfish species generally exhibit more agonistic behaviours than do their native contestants (Dalosto *et al.* 2015). As was the case with dominance, this trend extends to the interactions between *C. quadricarinatus* and *C. destructor* observed in this study, with *C. quadricarinatus* exhibiting predominately agonistic behaviours and *C. destructor* exhibiting predominately submissive behaviours. Because dominance and the performance of agonistic behaviours are closely linked, this was not unexpected.

On average, *C. destructor* performed tail flips 6 times more than did *C. quadricarinatus* during the inter-specific trials.

Tail flips have been identified as a significant indication of a crayfish's submission during agonistic interactions (Moore 2007). Although tail flips are common in laboratory studies and do not always indicate the termination of further contests, fights in wild conditions rarely end in a tail flip, with the fight breaking up and the submissive individual retreating before the fight intensity warrants a hasty escape (Bergman and Moore 2003). The tendency for invasive crayfish to display more aggressive behaviours than does native crayfish during inter-specific interactions was highlighted in the meta-analysis of the impact of invasive crayfish by Twardochleb *et al.* (2013), although it was also noted that the link between more aggressive behaviours and a decline in native crayfish populations was highly variable within the literature.

Resource-holding capacity

Although many studies have concluded that invasive crayfish species are more aggressive and dominant, directly increasing their resource-holding capacity (such as *Procambarus clarkii* in studies by Dalosto *et al.* 2015), this was not observed in the inter-specific interactions performed in our study (Gherardi *et al.* 2011; Twardochleb *et al.* 2013). In particular, the high aggression of *C. quadricarinatus* did not translate to a high resource-holding capacity. This surprising result is not the consequence of an inadequate food source that one species prefers, because preliminary trials testing appropriate food resources found that both species were attracted to, and consumed, the chosen food resource of a raw green prawn and cooked zucchini cube. Similar results were found in a study by Lopez *et al.* (2019), in which *C. destructor* had a significantly higher resource-holding capacity than did the more aggressive *E. dharawalus*. In this case, the role of *C. destructor* was reversed from that of the current study, with it being the invasive species within native habitat of *E. dharawalus*.

In the intra-specific trials conducted here, the readiness of *C. quadricarinatus* to fight with its own species was surprising because multiple studies have labelled it as gregarious, and it is often farmed happily in high densities (Masser and Rouse 1997; Bortolini *et al.* 2007). We suspect that this social nature does not extend to periods when food availability is low and, after the initial contest to determine social hierarchy, *C. quadricarinatus* might be a more social species. The disconnect between crayfish aggression and resource-holding capacity observed here would suggest that, rather than aggression being the main indicator of the ability to acquire an essential resource, some other factors may be at play. Factors involving the establishment of an invasive crayfish species may be much more complex than variables such as aggression and resource-holding capacity. In both the inter-specific and intra-specific trials, *C. destructor* spent more time in possession of the food resource. This suggests that *C. destructor* may have a higher food motivation, prioritising food possession over the assertion of dominance, than does *C. quadricarinatus*, which instead has a high fight drive, prioritising the assertion of dominance over resource possession (Lopez *et al.* 2019). This would explain the polar opposite reactions of the two species within the intra-specific trials in relation to food and agonistic interactions.

Additional factors

Environmental factors such as temperature may affect species behaviour, with temperature effects driving metabolic responses (Díaz *et al.* 2004; Tattersall *et al.* 2012). This response to temperature is likely to vary among species depending on climatic preferences. In this instance, the study observed two species hailing from different climates and temperature preferences (Nguyen *et al.* 2004; Souty-Grosset *et al.* 2006). Recorded optimal temperature range varies in the literature for both species, although generally,

C. destructor is described as having an optimal survival range of 15–32°C, with a preferred temperature of 25°C, whereas *C. quadricarinatus* had an optimal range of 22–31°C with a preferred temperature of 28°C (King 1994; Verhoef *et al.* 1998; Verhoef and Austin 1999; Meade *et al.* 2002). Owing to time constraints, it was not possible to conduct this experiment under a variety of temperatures. Instead, 26°C was chosen as within the optimal thermal range of both species and between their preferred temperatures (King 1994; Verhoef *et al.* 1998; Verhoef and Austin 1999; Meade *et al.* 2002).

Juvenile specimens were exclusively used in this study, owing to both availability and financial constraints. Whereas this does allow a foundation to be laid in behavioural dynamics between *C. destructor* and *C. quadricarinatus*, more robust studies in the future should include a variety of OCL sizes, with an emphasis on mature specimens. This, particularly if paired with multiple experiment temperatures, will allow for results that more closely mimic that of the variable nature of the LEB.

Conclusions

This study has demonstrated that where *C. quadricarinatus* is present within the LEB, it is likely to pose a significant threat to *C. destructor* populations because of its higher dominance and readiness to perform agonistic behaviours. *C. quadricarinatus*' aggressive behaviour resulted in its dominance over the more submissive native *C. destructor*; however, this did not translate to dominance over a food resource at 26°C. The results suggested that *C. quadricarinatus* may well be affecting the *C. destructor* population within the Lake Eyre Basin, but that this interaction is not food-based competition. Instead, *C. quadricarinatus* may be more driven by territory establishment than food resources, which would explain why the presence of *C. quadricarinatus* within the Lake Eyre Basin has resulted in an observed reduction of *C. destructor* numbers (G. King, unpubl. data). The ability of *C. quadricarinatus* to grow substantially bigger than its native competitor only increases its ability to exclude *C. destructor*. This is of particular concern during the 'bust' periods within the Lake Eyre Basin when habitat is reduced to small remnant pools, reducing the amount of available territory and leaving the *C. destructor* with no escape from its aggressive invaders. Further research is needed to confirm which factors are contributing to the exclusion of *C. destructor* by *C. quadricarinatus*.

Supplementary material

Supplementary material is available [online](#).

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Data availability. Data are available from the authors upon reasonable request.

Conflicts of interest. Samantha Capon is an Associate Editor of *Marine and Freshwater Research* but did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practise when handling manuscripts submitted by an editor to this journal. *Marine and Freshwater Research* encourages its editors to publish in the journal and they are kept totally separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

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