

Research Article

Reversal of competitive dominance between invasive and native freshwater crayfish species under near-future elevated water temperatureStephanie Cerato¹, Andrew R. Davis¹, Daniel Coleman² and Marian Y.L. Wong^{1,*}¹Centre for Sustainable Ecosystems Solutions, School of Earth, Atmospheric and Life Sciences, University of Wollongong, Northfields Avenue, Wollongong NSW 2522, Australia²Crown Lands and Water, NSW Department of Industry, Level 0, 84 Crown Street, Wollongong NSW, 2500, AustraliaAuthor e-mails: stc378@uowmail.edu.au (SC), adavis@uow.edu.au (ARD), daniel.coleman@dpi.nsw.gov.au (DC), marianw@uow.edu.au (MYLW)

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Abstract

Biological invasions are a major cause of biodiversity loss and, coupled with climate change, will likely have detrimental impacts for native species and the functioning of ecosystems. To mitigate such impacts, it is important to elucidate the behavioural mechanisms underpinning interactions between invasive and native species. Here we examined how competitive interactions between invasive and native species are modified under conditions of near-future elevated water temperature using freshwater crayfish as a model system. Contest experiments between the native *Euastacus spinifer* and invasive *Cherax destructor* revealed that the competitive advantage of *E. spinifer* at current maximum temperatures (22 °C) was reversed at elevated near-future temperatures (26 °C), after controlling for relative body size. In addition, the native crayfish spent twice as long motionless at 26 °C than *C. destructor*, consistent with physiological challenges underpinning this competitive reversal. Most alarmingly, *E. spinifer* experienced significant mortality after fighting *C. destructor*, particularly at 26 °C. Mortality usually ensued two days post-contest even when *E. spinifer* had won. Mortality was rare when fighting conspecifics. Together, these results suggest that while *E. spinifer* is more likely to win contests under current conditions, it could suffer considerable impacts if climate change and the spread of invasive *C. destructor* continue unabated.

Key words: contests, invasive species, climate change, mortality, competition**Introduction**

Across the globe, it has become increasingly apparent that extinction rates of freshwater taxa parallel and often exceed those of terrestrial taxa (Ricciardi and Rasmussen 1999; Jenkins 2003; Sala et al. 2000; Pimm et al. 2014). Declines in freshwater biodiversity have been associated with multiple factors, including the rapid spread of invasive species leading to declines in native biota and ecosystem functioning (Dudgeon et al. 2006). Although the mechanisms underlying the impacts of invasive species on natives are varied, competitive exclusion of natives from key resources by aggressive invasive species appears to be a common theme (Holway 1999;

Juette et al. 2014) alongside direct predation (Case and Bolger 1991; Worthington and Lowe-McConnell 1994), habitat modification (Koehn 2004; Kimbro et al. 2009) and disease transmission (Du Preez and Smit 2013).

Freshwater systems are proving particularly vulnerable to climate change (Woodward et al. 2010) as well as to invasive species. Climate change is expected to negatively impact freshwater fauna as a result of fluctuations in water temperature, salinity and flow (Palmer et al. 2008; Whitehead et al. 2009; Pratchett et al. 2011). Additionally, climate change is likely to contribute to the successful establishment of invasive species in freshwater ecosystems (Hellmann et al. 2008; Rahel and Olden 2008). However, empirical studies investigating the interactive effects of climate change and invasive species on native species are rare, and as such, we are unable to predict how native freshwater fauna will fare in the future. This is especially alarming from a conservation standpoint, because many of these native freshwater taxa are already considered vulnerable, endangered or critically endangered (e.g. Gallardo and Aldridge 2013; Muhlfeld et al. 2014).

To examine how climate change may modulate the behavioural interactions between invasive and native freshwater fauna, we used freshwater crayfish as our model system. Freshwater crayfish are often the largest-bodied invertebrates in freshwater ecosystems representing the bulk of the biomass, and are ecosystem engineers (Hale et al. 2016; Hudina et al. 2016). Some species have been widely introduced into non-native catchments worldwide, including the common yabby, *Cherax destructor* (McCormack 2014; Scalici et al. 2009; Capinha et al. 2012) (Supplementary material Figure S1). In Australia, this species is native to the Murray-Darling river system in NSW but has since expanded beyond its native range largely owing to the stocking of farm dams to provide recreational fishing opportunities (Coughran et al. 2009; McCormack 2014; Figure S1). This species' high fecundity, rapid growth, protracted spawning period and wide thermal tolerance range (1–35 °C) contribute to its invasive capability (Beatty et al. 2005; Withnall 2000; Veselý et al. 2015). Although largely speculative, this species has been designated a Key Threatening Process to members of the native crayfish genus, *Euastacus*, of which 34 of over 50 taxa are considered endangered or critically endangered (McCormack 2015; IUCN 2018). To date, there has only been one study investigating the interactions between *C. destructor* and a member of the genus *Euastacus* (Lopez et al. 2019), which contrary to expectations demonstrated that the critically endangered native species, *Euastacus dharawalus* (Morgan, 1997) won more contests and was more aggressive than the invasive *C. destructor*. However, the simultaneous impact of climate change on the outcome of resource contests has yet to be assessed and given that many *Euastacus* taxa are cold adapted (Horwitz 1990), may indicate greater vulnerability of *Euastacus* species than is currently expected.

Here we tested the hypothesis that the outcome and intensity of interspecific contests between *Cherax destructor* and *Euastacus spinifer* (Heller, 1865), would be influenced by water temperature. We note that *E. spinifer* is currently listed as “Least Concern” on the IUCN Red List but investigating its interactions with *C. destructor* is important for providing insights into the potential role of climate change on *Euastacus* spp. as its range currently overlaps with that of *C. destructor* (Figure S1). Based on previous studies on crayfish contests, we predicted that i) *E. spinifer* would win more interspecific contests over resources and be more aggressive than *C. destructor* under current temperature regimes, but that ii) *C. destructor* would win more interspecific contests over resources and be more aggressive under near-future temperatures owing to its reported capacity to tolerate elevated temperatures (Seebacher and Wilson 2006). Given the unexpected deaths of crayfish following contests observed in the current study, we were able to further investigate the direct fitness consequences of interspecific contests under both temperatures. We compared the mortality rate of *E. spinifer* following contests with conspecifics versus *C. destructor* under current and near-future temperatures. We predicted that i) *E. spinifer* would suffer higher mortality following contests with *C. destructor* compared to contests with conspecifics, and ii) rates of *E. spinifer* mortality would be higher if they had contested under near-future temperatures than at current temperatures.

Materials and methods

The investigation was conducted between May 2016–January 2017 using *Euastacus spinifer* and *Cherax destructor* collected from farm dams and freshwater creeks in the Illawarra region of NSW, Australia. All specimens were captured using a combination of baited opera house traps, baited shrimp traps, baited rope techniques and by handheld nets. Once collected, individuals (*C. destructor*, N = 12; *E. spinifer* N = 12) were transported back to the Ecological Research Centre (ERC), University of Wollongong, NSW, where they were housed individually in recirculating freshwater aquaria (40 × 30 × 30 cm). The diet of both species while held in captivity consisted of vegetables and frozen fish meat. Each aquarium was lined with gravel with a PVC pipe for shelter. The occipital carapace length (OCL) of each crayfish was measured with callipers to the nearest 0.1 mm.

After 2 weeks acclimation, twelve *E. spinifer* – *C. destructor* pairs were created and randomly assigned to one of two temperature treatments (22 °C or 26 °C), creating 6 pairs per treatment. Temperatures were changed at a rate of 1 °C per day. A temperature of 22 °C corresponds with the current maximum annual temperature based on 2006–2016 mean hourly water temperature measurements recorded at the adjacent Cataract River gauge (Station number 2122323), and 26 °C corresponds to a 4 °C increase in the

maximum annual temperature expected at these latitudes by 2100 according to the B2 and A1B greenhouse gas emission scenarios (van Vliet et al. 2011).

Contests were then staged in a specialised observation aquarium (120 × 50 × 35 cm) that was divided into equal thirds using two opaque plastic dividers. A piece of shrimp was placed in the central compartment and the paired contestants introduced into the two end compartments for a 10-minute acclimation period. The dividers were then simultaneously lifted allowing the individuals to interact for 20-minutes. For each trial, contest outcome (defined by determining the first individual to tail-flick or flee from its opponent (Seebacher and Wilson 2006), contest intensity (number of aggressive acts) (Table S1 for ethogram) and the amount of time spent motionless were recorded (Gherardi et al. 2013). Individuals were placed back into their original housing aquarium following each trial and any subsequent mortality recorded.

During at least 12 days of rest, each individual was then gradually acclimated to the alternate temperature it had yet to be trialled at (at increments of ± 1 °C per 3 days) and each individual was trialled a second time at this alternate temperature paired with an unfamiliar individual as its new contestant. At the conclusion of the experiment we completed 12 interspecific contest trials conducted at 22 °C and 26 °C. In total, 5 new *E. spinifer* had to be collected during the course of the trials to replace individuals that had died following contests (making a total of 17 *E. spinifer* individuals used for inter-specific trials). Following the interspecific trials, intraspecific trials were conducted in the same manner but testing only pairs of *E. spinifer* under both temperatures. Twelve additional *E. spinifer* were caught for these trials and assigned into 6 contestant pairs, each fighting at 22 °C and 26 °C.

Statistical analyses

Normality of data was checked via visual inspections of QQ plots using RStudio. A Generalized Linear Mixed Model (GLMM) with binomial distribution and logit link function (lme4 package) was used to investigate the effect of species (categorical fixed effect) on outcome (win versus loss) of interspecific contests (binary response variable) under i) current (22 °C) and ii) near future (26 °C) temperatures. Trial ID was added as a random effect to control for the non-independence of individuals within a given pair of contestants. Another GLM with binomial distribution and logit link function was used to investigate the effect of relative body size of the individuals in each pair (categorical fixed effect) on the outcome (win versus loss) of interspecific contests (response variable) for *E. spinifer* and *C. destructor* separately, under i) current (22 °C) and ii) near future (26 °C) temperatures. Sample sizes did not permit the inclusion of both species and

relative size in a global model. Note that temperature was not included as a fixed effect in the models as the total number of wins and losses is identical under both temperatures.

For contest intensity and activity, General Linear Mixed Models (GLMM) were used to investigate the effects of temperature, species, relative size and an interaction between temperature and species. Contest intensity was expressed as the number of aggressive acts performed (log transformed) and activity was expressed as the number of seconds motionless during a trial. Crayfish ID and Trial were included as random factors in both models to account for multiple testing of individuals. The same tests were conducted to analyse intraspecific contests but without species as a fixed effect.

To investigate mortality, a Generalized Linear Model was used with temperature and type of contest (inter- or intraspecific) as fixed effects and mortality (yes or no) as binomial response variable.

Results

In interspecific trials, the average size of *Euastacus spinifer* was 122.1 mm (± 6.3 SE) and *Cherax destructor* was 121.2 mm (± 4.9 SE). In intraspecific trials, the average size of *E. spinifer* was 110.6 mm (± 4.48 SE). In interspecific trials, *E. spinifer* was the larger contestant in $N = 15$ trials and the smaller contestant in $N = 9$ trials. In all trials ($N = 24$), all crayfish of both species engaged in aggressive acts.

Interspecific contest dynamics

The native *E. spinifer* was more likely to win contests than *C. destructor* at low temperature (22 °C) (GLMM: Species $F_{1,11} = 5.431$, $P = 0.04$) (Figure 1a). At elevated temperature (26 °C) however, there was no significant difference in the likelihood of winning a contest between the species (Species $\chi^2_{1,11} = 0.379$, $P = 0.551$) (Figure 1a). Larger *E. spinifer* (relative to their contestant) were more likely to win contests than smaller *E. spinifer* (relative to their contestant) under low (GLM: Size $\chi^2_{1,10} = 8.318$, $P = 0.023$) and high ($\chi^2_{1,9} = 10.59$, $P = 0.032$) temperatures. Larger *C. destructor* (relative to contestant) also won more often at low (GLM: Size $\chi^2_{1,10} = 8.318$, $P = 0.023$) and high ($\chi^2_{1,10} = 3.94$, $P = 0.047$) temperatures than smaller *C. destructor*.

The intensity of aggression was unrelated to temperature (GLMM: $F_{1,18} = 1.07$, $P = 0.315$), species ($F_{1,3} = 2.44$, $P = 0.216$), relative size ($F_{1,19} = 0.78$, $P = 0.388$) or an interaction between temperature and species ($F_{1,5} = 1.622$, $P = 0.259$). The native *E. spinifer* spent similar amounts of time motionless as *C. destructor* at low temperature but spent over twice the amount of time motionless than *C. destructor* at high temperature (GLMM: Temperature*Species, $F_{19} = 76.09$, $P < 0.0001$) (Figure 1b). Relative size was also a significant predictor of time spent motionless, with smaller individuals spending more time motionless than larger individuals ($F_{120} = 6.43$, $P = 0.02$).

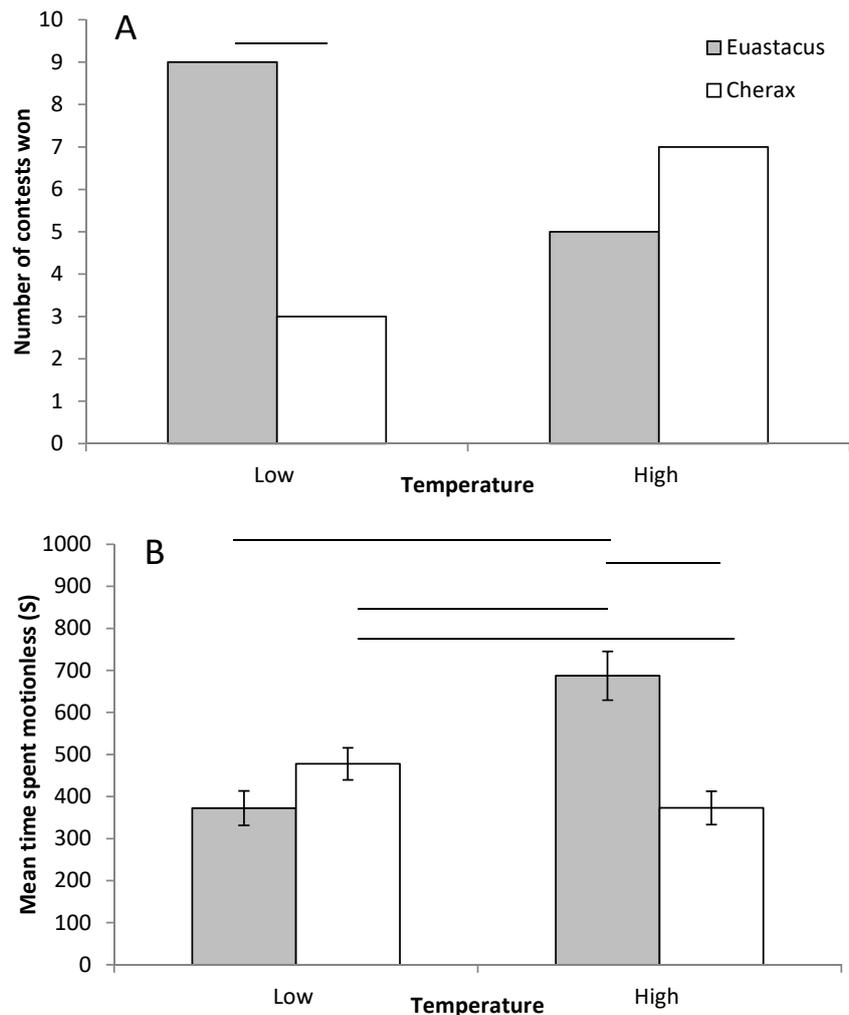


Figure 1. (A) Number of contests won by *Euastacus spinifer* (grey) and *Cherax destructor* (white) in relation to temperature (low = 22 °C; high = 26 °C) during interspecific contest trials; (B) mean time spent motionless (s) during contests by *Euastacus spinifer* (grey) and *Cherax destructor* (white) during interspecific contests at low (22 °C) and high (26 °C) temperatures. Bars represent means with standard errors. Horizontal lines join pairs that differ significantly based on Tukey's post hoc comparisons ($p < 0.05$).

Intraspecific contest dynamics

At both temperatures, individual *E. spinifer* were more likely to win if they were the larger of the pair (low: $\chi^2_{1,10} = 16.36$, $P < 0.001$; high: $\chi^2_{1,10} = 16.36$, $P < 0.001$). Contest intensity was unrelated to temperature (Temperature $F_{1,10} = 1.2$, $P = 0.299$) or the interaction between temperature and size (Temperature*Size $F_{1,8} = 0.22$, $P = 0.651$) but was significantly related to relative size with larger individuals being more aggressive than smaller individuals ($F_{1,8} = 28.9$, $P < 0.001$) (Figure 2). Time spent motionless was unrelated to temperature ($F_{1,6} = 2.07$, $P = 0.2$), relative size ($F_{1,9} = 4.45$, $P = 0.06$) or the interaction between temperature and size ($F_{1,9} = 1.32$, $P = 0.28$).

Mortality

Unexpectedly we observed deaths of *Euastacus spinifer* following interspecific contests. A total of 10 out of 17 individuals died (Table 1) whereas

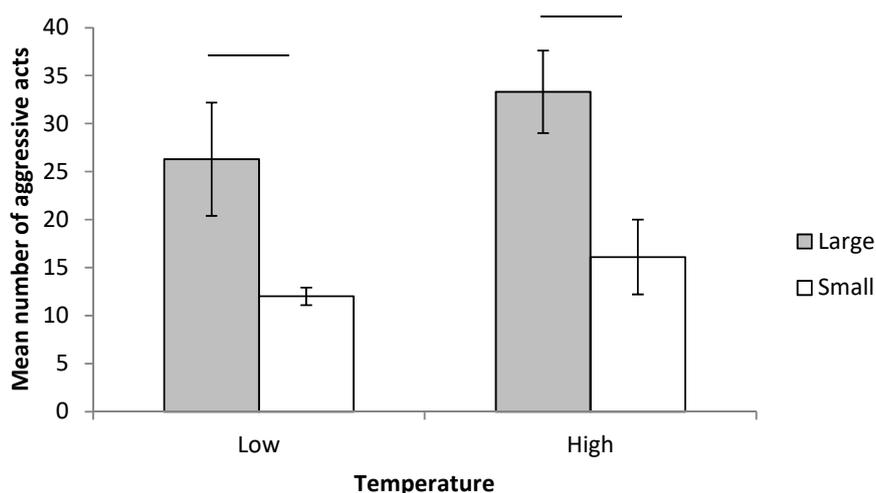


Figure 2. Mean number of aggressive acts given during intraspecific contests depending on the size (larger or smaller) of the contestant at low (22 °C) and high (26 °C) temperatures. Horizontal lines join pairs that differ significantly based on Tukey's post hoc comparisons ($p < 0.05$).

Table 1. *Euastacus spinifer* deaths following interspecific contest trials for first and second trials (randomised order of temperature presentation). Shown are the crayfish ID numbers, temperature at which they had fought prior to death, date of trial and death and associated number of days to death post-trial and the winner/loser status of the deceased individual. For the second trials, one individual (#8) was a new crayfish that had been collected to replace an individual that previously died after the first contest at 26°C. The remaining individuals in the second trial had all initially contested at 22°C.

First trials

Crayfish ID	Temperature of contest (°C)	Date of trial and death	No. days to death	Win/Loss
9	26	15/11, 17/11	2	Loser
12	26	16/11, 17/11	1	Loser
7	26	16/11, 28/11	12	Winner
8	26	17/11, 19/11	2	Loser
10	26	17/11, 21/11	4	Winner

Second trials

Crayfish ID	Temperature of contest (°C)	Date of trial and death	No. days to death	Win/Loss	Notes
4	26	5/12, 7/12	2	Loser	Fought @ 22 first trials
1	26	5/12, 7/12	2	Winner	Fought @ 22 first trials
8	22	5/12, 6/12	1	Winner	New crayfish
6	26	6/12, 8/12	2	Loser	Fought @ 22 first trials
5	26	7/12, 8/12	1	Loser	Fought @ 22 first trials

there were no deaths of *Cherax destructor* following inter-specific contests. Since one of the *E. spinifer* that died did so 12 days post-trial, we excluded this death from analyses as it may have occurred for reasons other than the trial. The remaining deaths occurred 1 day ($N = 3$), 2 days ($N = 5$) or 4 days ($N = 1$) after a trial (Table 1). Given that these crayfish had already been acclimated to laboratory conditions under stringent husbandry protocols, these deaths were therefore deemed to have occurred as a direct result of the trials themselves. Following intra-specific contests, only 1 *E. spinifer* died (1/12 individuals) (Table 1). In summary, *E. spinifer* were significantly more likely to die if they had fought *Cherax destructor* rather than a conspecific (Type of contest, $\chi^2_{1,34} = 4.831$, $P = 0.028$) (Figure 3a) and if they had fought at high temperature rather than low (Temperature, $\chi^2_{1,33} = 13.63$, $P < 0.0002$) (Figure 3b). There was no interaction between type of contest and temperature (Type*Temperature, $\chi^2_{1,32} = 0.069$, $P = 0.792$).

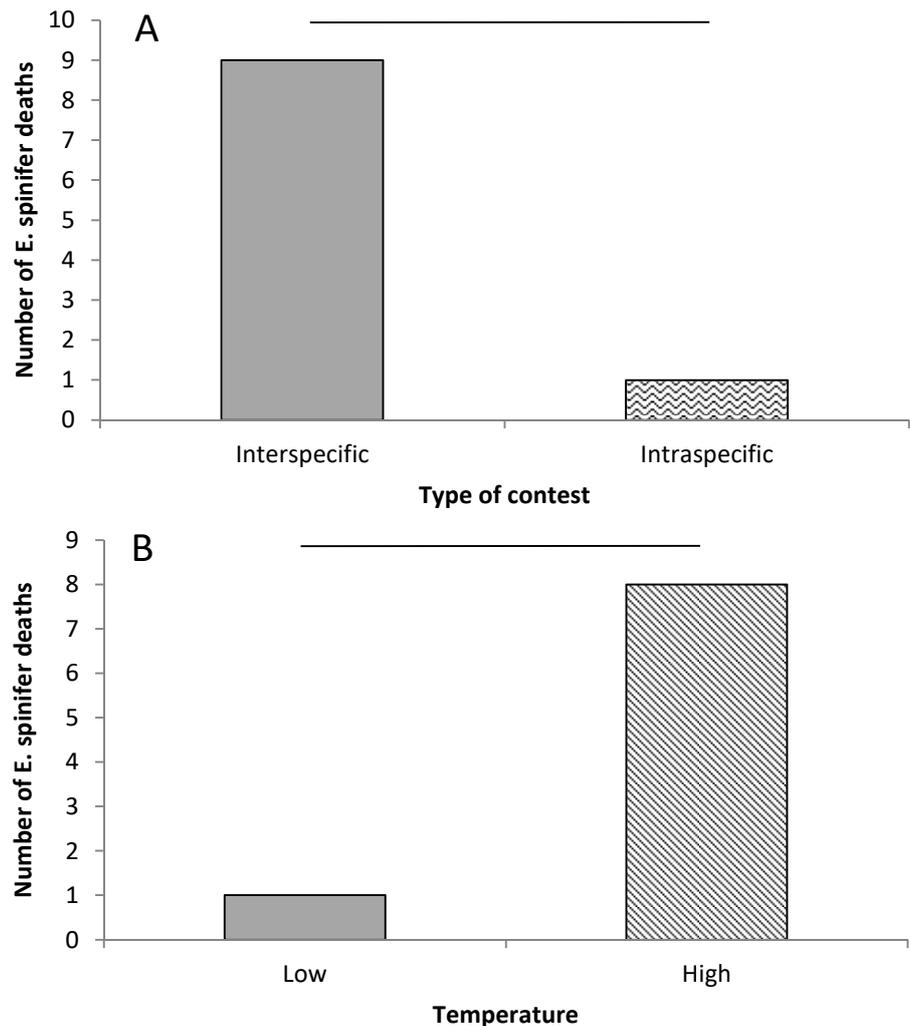


Figure 3. Number of *E. spinifer* that died within 0–4 days post-contest depending on (A) temperature and (B) type of contest. Included are deaths following first and second trials for each contest type. Horizontal lines join pairs that differ significantly based on Tukey’s post hoc comparisons ($p < 0.05$).

Discussion

Examining the behavioural mechanisms underpinning the interactions between native and invasive species under projected conditions of climate change is central to the management of species of conservation concern. Here, we show that while the native *Euastacus spinifer* was more likely to win a contest over food under current temperatures, it lost its competitive advantage against the warm-water tolerant *Cherax destructor* under the elevated temperatures anticipated in the near future. Further, contests appeared to exert a greater cost on *E. spinifer*, with higher mortality of the native after contests with *C. destructor* than after contests with conspecifics, even if *E. spinifer* had won the contest. Importantly, this was particularly apparent after contests at high temperature. These interesting results suggest that the alteration of aquatic habitats by climate change could yield non-lethal as well as lethal impacts on native *Euastacus* species, through the modification of the outcomes and costs of contests.

The increased time spent motionless by *E. spinifer* at high temperature during interspecific contests may represent an adaptive response enabling individuals to tolerate elevated temperature (Gherardi et al. 2013). However, *E. spinifer* did not spend more time motionless at high temperature during intraspecific contests, suggesting that contesting with *C. destructor* at high temperatures rather than contesting at high temperatures *per se* elicited the reduced activity. It is also unlikely that *E. spinifer* perceived *C. destructor* as a predator and hence reduced activity as a predator avoidance strategy (Stein and Magnusson 1976), since in many instances *E. spinifer* were actually larger than their opponents. Therefore, the results suggest that *E. spinifer* experienced unique physiological challenges when competing with *C. destructor* at high temperatures, and that the reduced activity that ensued likely resulted in the reversal of competitive dominance at high temperature. In contrast to the native species, *C. destructor* spent similar amounts of time motionless at both temperatures indicating that it experienced no particular physiological challenge from contesting with *E. spinifer* under elevated temperatures. These findings are in line with the fact that *E. spinifer* occupies freshwater systems colder than 24 °C (Coughran and Furse 2010) whereas the optimal thermal range for *C. destructor* has been reported to lie between 24–25 °C (Vesely et al. 2015), although it has been recorded in waters up to 35 °C (Withnall 2000). Interestingly however, individuals of *E. spinifer* did not show a reduction in the intensity with which they contested at high temperature despite the increase in time they spent motionless, demonstrating that they still had the capacity to fight. We speculate that this persistence in contest behaviour coupled with increased thermal stress produced the subsequent elevated mortality after contests with *C. destructor*.

Relative body size was a key predictor of contest outcome regardless of temperature, with larger individuals being more likely to win in both inter- and intraspecific trials. The key role of size asymmetry is not surprising and has been well documented in a range of decapod crustaceans (e.g. Vorburger and Ribic 1999; Nakata and Goshima 2003). In addition, body size was related to time spent motionless, with smaller crayfish spending more time motionless than larger crayfish during interspecific (but not intraspecific) contests. The fact that time spent motionless only varied between small and large crayfish during interspecific contests again highlights a contest dynamic that is unique to when *E. spinifer* engages with *C. destructor* (rather than with conspecifics). In terms of competitive interactions, this finding does not bode well for the success of the other *Euastacus* species which reach smaller average body sizes than *E. spinifer*, which is one of the larger members of this genus (McCormack 2012). As such, investigating the behavioural and physiological responses of other

smaller-bodied members of this genus would therefore represent an invaluable focus for future research.

Given that more *E. spinifer* died following contests with *C. destructor* and contests at high temperature, our study demonstrates the potentially lethal effects of contesting with heterospecifics when under thermal stress; which we had not anticipated. Deaths occurred typically within two days post-contest and are unlikely to be due to any other stressor as *E. spinifer* were acclimated to laboratory conditions without any mortality prior to the start of trials. Therefore, native crayfish species experienced both non-lethal (loss of resource) and lethal (mortality) effects of competition at high temperatures. Future work could involve monitoring stress levels (either from blood or water samples) before and after pair-wise contests under both temperatures, at low and high temperatures without contests, as well as between intra- and inter-specific contests at both temperatures, to more accurately determine whether the ultimate causes of mortality in *E. spinifer* were directly related to the cost of contesting versus temperature.

The wide thermal tolerance of *C. destructor* suggests that under near-future expected water temperatures this species is likely to continue spreading beyond its native range and into that occupied by *Euastacus* species. In addition, its apparent competitive dominance under higher temperatures as revealed in this study suggests that *Euastacus* species currently listed as endangered or critically endangered could face a real risk of extinction when the impacts of invasive *C. destructor* and climate warming act in concert. Further contest trials under altered temperatures that incorporate a greater range of *Euastacus* species and larger sample sizes are clearly needed, however, to reinforce the findings proposed here. Nevertheless, the important next steps would be to consider strategies that reduce the influx of this invasive species, such as the creation of barriers, education of the public and implementation of early detection. Further, maintenance of dispersal corridors, such as protected bushland, could allow *Euastacus* species to move and settle new habitats, as they will forage out of water, rather than being forced to compete with the invasive species, if colonisation of their waterways by *C. destructor* does occur. More generally, since climate warming is likely to magnify the effects of invasive species (Rahel and Olden 2008; Mainka and Howard 2010), there is an urgent need to consider ways to mitigate the impacts of climate change in order to ensure the persistence of native freshwater fauna with restricted thermal tolerances.

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Author contributions

MYLW and ARD conceived the project. SC and DC undertook field collections. SC collected laboratory data. MYLW analysed data, DC produced the figures and SC wrote the first draft. All authors edited the manuscript and agree on its submission.

Additional Information

Competing interests: The authors declare no competing interests.

Data Availability: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Map showing the relative distributions of *Euastacus spinifer* (black) and *Cherax destructor* (grey) in Australia. Records derived from the Atlas of Living Australia. <https://www.ala.org.au/>.

Table S1. Ethogram of observed contest behaviours of crayfish (adapted from Bergman and Moore 2003, and Gruber 2016).

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2019/Supplements/AI_2019_Cerato_etal_Table_S1.xlsx

http://www.reabic.net/aquaticinvasions/2019/Supplements/AI_2019_Cerato_etal_Figure_S1.pdf