



Freshwater decapod (*Aegla longirostri*) uses a mixed assessment strategy to resolve contests



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How animals decide to withdraw from a contest has puzzled researchers for years. Currently, four models try to explain how this decision is made: war of attrition (WOA); cumulative assessment (CAM); opponent-only assessment (OOA); and sequential mutual assessment (SAM). Although their predictions differ, they must be simultaneously tested to infer which model best describes contests. Herein, we identified the traits related to the resource-holding potential (RHP) in the decapod *Aegla longirostri*, and used these traits to test the predictions of each model. We identified which morphological/performance traits affect contest outcome, related these traits to the contest duration of male dyads, and tested the differences in aggressive acts (claw grabs). We tested the models using pairs of random and RHP-matched opponents. Additionally, we performed contests where RHP-matched opponents could communicate before the contest ('previewed'), and contests where the focal animal would only communicate with one individual and fight another unseen individual afterwards ('unseen'). In comparing these groups we tested whether information was being exchanged. The best predictor of contest outcome included a combination of cephalothorax length and claw height, and claw grabs increased with opponent similarity. Contest duration increased with loser's cephalothorax length and decreased with winner's cephalothorax length in random pairs, and winners spent more time in claw grab than losers. These findings refute WOA and OOA. In RHP-matched pairs, no relation was found and contests with previewed opponents were shorter than contests with unseen opponents, both results suggest SAM. However, the time spent in claw grab did not differ between previewed and unseen opponents. We argue that SAM is cognitively complex, and mutual assessment without comparison of RHP could be a better explanation. Furthermore, claw grab is important in contest resolution. Thus, the costs inflicted may suggest a mixed assessment strategy for *A. longirostri*'s contests.

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Animals use agonistic behaviours during contests to secure access to limited resources (e.g. food, mates, shelter; Hardy & Briffa, 2013). Theory dictates that, as resource becomes more valuable (e.g. scarcer; Grant, Gaboury, & Levitt, 2000), contests get longer and more intense (Maynard Smith & Price, 1973). However, even intense contests rarely result in severe injuries and/or death (Maynard Smith, 1976). Most contests are settled by a decision of one of the contestants to withdraw from the contest (i.e. the loser). This decision is based on the benefits and costs of persisting in the

contest (Kokko, 2013). The benefits are related to resource value (e.g. Doake & Elwood, 2011), whilst the costs are related to increased predation risk, energy and/or injuries accrued during the contest (Briffa & Sneddon, 2010). Thus, contest duration and increasing escalation can be seen as the interaction between the willingness to pay the costs (e.g. the resource value) and the ability to pay the costs (i.e. fighting ability, energy reserves; Elwood & Arnott, 2012).

When contestants perceive the resource equally, the individual with the highest fighting ability (resource-holding potential, RHP; Parker, 1974) usually wins the contest. The RHP is often associated with body size, in which large animals are stronger and better at inflicting injuries (Archer, 1988). Other traits can also be considered as correlates of RHP (reviewed in Arnott & Elwood, 2009), but weapon size and/or strength can be particularly influential in affecting the chances of winning a contest among taxa with developed weaponry (vertebrates: Clutton-Brock, Albon, Gibson, & Guinness, 1979; Lailvaux, Herrel, Vanhooydonck, Meyers, &

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Ircshick, 2004; arthropods: Pomfret & Knell, 2005; Seebacher & Wilson, 2006, 2007; Sneddon, Huntingford, Taylor, & Orr, 2000). Weapons can be used to inflict injury in the opponent (Lailvaux et al., 2004) and/or can signal the RHP of the bearer (Hoffmann & Schildberger, 2001; Hughes, 1996). Alternatively, weapons can affect contest outcome by being energetically demanding to wield (Matsumasa & Murai, 2005). Therefore, weaponry has to be accounted for when investigating which traits relate to the RHP.

Understanding how animals decide to retreat from a contest is the goal of assessment models. Currently, assessment models can be classified into three main groups based on the relationship between RHP and the withdrawal decision: self-assessment (SA), opponent-only assessment (OOA) and mutual assessment (sequential mutual assessment, SAM) (Elwood & Arnott, 2012). The SA models dictate that animals do not (or cannot) assess their opponents RHP, and thus, the decision to give up is based solely on their own RHP. The SA is further subdivided in war of attrition models (WOA; Mesterton-Gibbons, Mardens, & Dugatkin, 1996; Payne & Pagel, 1996, 1997) and the cumulative assessment model (CAM; Payne, 1998). These models make different predictions regarding how costs are accrued during a contest (Kokko, 2013). The WOA models assumes that costs accrue because of the animal's own actions (e.g. energy spent, time invested; Mesterton-Gibbons et al., 1996), whereas CAM assumes that, alongside with the costs of the animal's own actions, costs are also accrued through the opponents' actions (e.g. injuries), and that with a higher RHP, animals inflict costs at a higher rate (Payne, 1998).

The OOA represents the opposite of the SA models, and predicts that the decision to give up is based solely on the opponent's RHP (Elwood & Arnott, 2012). However, OOA is not a theoretical model, and it is considered very unlikely to occur (for a discussion see Elwood & Arnott, 2013). Nevertheless, since there is evidence for OOA (e.g. Reddon et al., 2011), we considered it during data analysis. Lastly, the SAM model assumes that animals assess their opponents' RHP and their own, basing their decision to withdraw on both RHPs (Enquist & Leimar, 1983).

Despite the predictions of the assessment models having been tested in a wide range of species (see Hardy & Briffa, 2013), these have rarely been fully supported by empirical data (Arnott & Elwood, 2009; Briffa & Elwood, 2009). This has two explanations: (1) difficulty in identifying RHP traits (Stuart-Fox, 2006); (2) the exclusion of one model does not corroborate the other models (Junior & Peixoto, 2013). Thus, all models have to be tested simultaneously. Taylor and Elwood (2003) showed that the relationship between contest duration and the RHP of both opponents can be used to discriminate between the assessment models, since they make different predictions regarding the relation between contest duration and RHP (Table 1). Alternatively, contest dynamics and structure can be used to differentiate WOA from CAM/SAM: WOA predicts that the behaviours of both contestants are matched in type, frequency and intensity, whereas CAM and SAM predict that

behaviours are unmatched between contestants (Payne, 1998). Thus, by analysing the differences in the behavioural acts performed by winners and losers, we could provide more evidence to distinguish between WOA and CAM/SAM models.

Although SAM and CAM models suggest two distinct forms of assessment, they make the same predictions when opponents are not matched for their RHP (Briffa & Elwood, 2009). The best way to distinguish between SAM and CAM is using data from contests between RHP-matched opponents. In this scenario, SAM and CAM make contrasting predictions (Fawcett & Mowles, 2013). Still, the evidence for SAM in RHP-matched pairs is based on a nonsignificant relation between contest duration and RHP, which reduces inference power (Table 1; Arnott & Elwood, 2009). Alternatively, performing contests between RHP-matched opponents that have interacted using chemical/visual/mechanical cues (previewed opponent), and comparing to contests between RHP-matched opponents that have not interacted in any way (unseen opponent), can be a solution for this issue (Arnott & Elwood, 2009). Since SAM predicts that there is information exchange between the opponents and CAM does not, different predictions are made (Table 1). Because of information exchange, we can also expect that individuals would use less aggressive acts during the contests with previewed opponents than with unseen opponents. By comparing contests duration and aggressive acts between these two conditions, inference can be made with two sources of evidence, thus allowing more robust inference (Briffa & Elwood, 2009; Table 1).

Decapod crustaceans are excellent models to study animal contests. They fight readily in laboratory conditions even in the absence of obvious resources (Ayres-Peres, Araújo, & Santos, 2011), and their interactions in controlled environments reflect their interactions in natural environment (Bergman & Moore, 2003; Fero & Moore, 2008; Parra, Barria, & Jara, 2011). In addition, decapods have been shown to use extensive chemical signalling in aggressive contexts (Breithaupt, 2011; Briffa, 2013), and contests tend to be longer and more intense in the absence of chemical cues (Katoh, Johnson, & Breithaupt, 2008). Such extensive use of chemical communication suggests that some sort of information is being exchanged during the contest (i.e. SAM). Conversely, the ubiquitous use of their highly developed claws during contests (Sneddon et al., 2000) suggests that injuries are being inflicted on their opponents (Figure S1 in Dennenmoser & Christy, 2013), which suggests CAM. Through empirical testing, Smallegange, Sabelis, and van der Meer (2007) investigated the assessment models in shore crabs (*Carcinus maenas*), but their results could not distinguish between SAM and CAM. Lastly, Briffa (2013) states that swimming crab contests do not fully fit SAM predictions regarding contest structure, since there is no clear pattern of escalating phases. These contrasting evidences highlight the need for more studies on decapod contests.

The goals of our study were (1) to determine which traits relate to the RHP of the freshwater decapod *Aegla longirostri* (Anomura) and (2) to test the predictions from WOA, CAM, SAM and OOA

Table 1
Predictions of the assessments models^a

	War of attrition	Cumulative assessment	Sequential mutual assessment	Opponent-only assessment
Relation between RHP and contest duration in random pairings	Loser—Positive relation Winner—Weak positive or no relation	Loser—Positive relation Winner—Negative relation	Loser—Positive relation Winner—Negative relation	Loser—No relation Winner—Negative relation
Relation between RHP and contest duration in RHP-matched pairings	Positive	Positive	No relation	Negative
Difference in contest duration between previewed and unseen opponent	No difference	No difference	Shorter contests with previewed opponents	Shorter contests with previewed opponents

RHP: resource-holding potential.

^a Adapted from Arnott and Elwood (2009).

models by analysing data from random contests, RHP-matched pairs, previewed and unseen opponent contests, thus assessing whether one of the models explains how *A. longirostri* decides to withdraw from a contest.

METHODS

Study Organism, Capture, Housing and Measuring

Aegla longirostri has a marked sexual dimorphism, with males having larger bodies and larger claws than females (Colpo, Ribeiro, & Santos, 2005). During contests, males use mostly their left claw for grabbing, striking and pulling (Ayres-Peres et al., 2011), since it is larger than the right claw (Colpo et al., 2005). The use of chemical cues has already been reported during sexual interactions (Palaoro, Ayres-Peres, & Santos, 2013) similar to what has been found for crayfish (Breithaupt, 2011). Thus, the use of chemical cues during contests is thought to be important because of the ecological/behavioural similarity that aeglids share with crayfish (Burruss, Gangloff, & Siefferman, 2013), a more thoroughly studied group (Breithaupt, 2011).

We captured 115 adult males of *A. longirostri* in two first-order streams (29°40'13"S; 53°45'44"W and 29°39'49"S; 53°44'34"W) in southern Brazil, and transported them to the laboratory. We accommodated all aeglids in individual aquaria (2 litres) for 1 week prior to experimentation to eliminate the effects of prior experiences (Moore, 2007). All aquaria had constant aeration, 2 cm of gravel, and ad libitum food composed of decaying leaves taken from the stream (Cogo & Santos, 2013). We measured all individuals according to their cephalothorax length (Fig. 1a), claw length

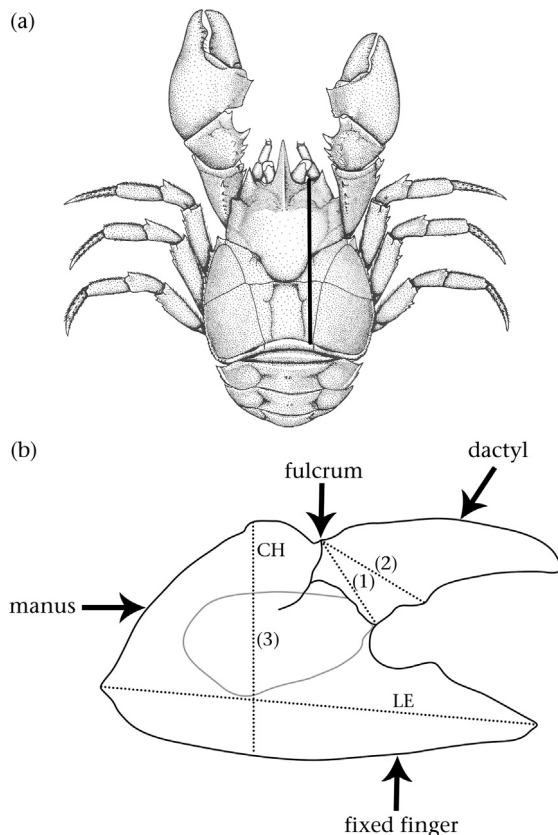


Figure 1. (a) Representation of a male *Aegla longirostri* adapted from Bond-Buckup (2003). Line denotes cephalothorax length. (b) Schematic representation of the left claw of *A. longirostri*. LE: claw length; CH: claw height; (1): dactyl height; (2): distance from the fulcrum to the first tubercle; (3): apodeme.

(Fig. 1b), claw height (Fig. 1b), height of the dactyl (Fig. 1b) and distance between the fulcrum and the tubercle (Fig. 1b), using a digital calliper (precision: 0.01 mm), and apodeme area (Fig. 1b) as described in Dennennmoser and Christy (2013). We used the height of the dactyl, the distance between the fulcrum and the tubercle, and apodeme area to calculate the index of closing force.

The index of closing force is a measure of the claw's strength (Dennennmoser & Christy, 2013). The claw closing force is determined by the mechanical advantage of the claw dactyl and the cross-sectional area of the muscle that moves the dactyl. This muscle is attached to a flat cuticular apodeme, which is attached to the dactyl and longitudinally bisects the manus (proximal area of the claw; Fig. 1b; Dennennmoser & Christy, 2013). To calculate the mechanical advantage, the height of the dactyl is divided by the distance between the fulcrum (i.e. point where the dactyl flexes; Fig. 1b) and the first tubercle in the dactyl (Dennennmoser & Christy, 2013; Fig. 1b). The muscle cross-sectional area is calculated as the area of the apodeme, which is highly correlated with the muscle cross-sectional area (Warner & Jones, 1976; Fig. 1b). By multiplying the values for mechanical advantage and muscle cross-sectional area, we get the index of closing force of that claw, which is correlated to the force produced by the claw (Levinton, Judge, & Kurdziel, 1995). Since calculating the muscle cross-sectional area requires euthanizing the individuals (or at least removing both claws), we chose a more parsimonious protocol. We used 20 individuals that perished during pilot studies of this and other experiments (i.e. were already available in the scientific collection of the laboratory, voucher number UFSM-C 249) to calculate the muscle cross-sectional area. We then regressed their muscle cross-sectional area with their claw height. The correlation was high for the left claw ($R^2 = 0.9623$; Fig. 2). Thus, we used the equation from that regression ($y = -0.3701 + 0.0804 \times x$) to calculate the muscle cross-sectional area of the left claw of all the individuals used in our experiment. With the extrapolated muscle cross-sectional area, we multiplied it by the individual's mechanical advantage to get the index of closing force of the left claw. We did not perform the same procedure for the right claw because of its low use during contests (Ayres-Peres et al., 2011) and the low correlational value ($R^2 = 0.7974$), which could lead to spurious results. Therefore, we used cephalothorax length, claw length, claw height and the index of closing force as the morphological and performance traits possibly related to the RHP (see below).

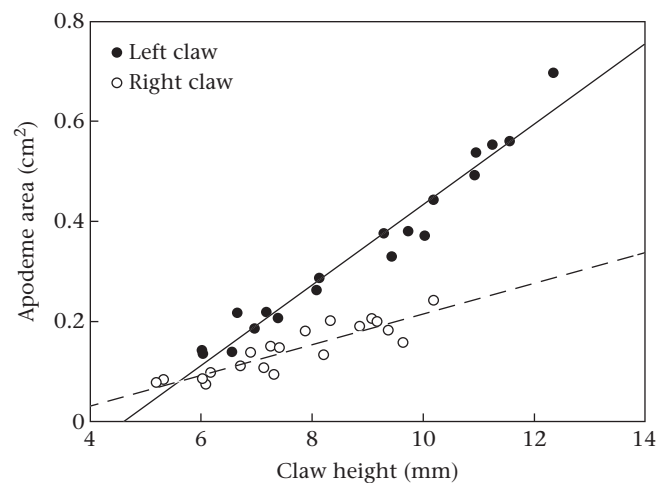


Figure 2. Relation between claw height and the apodeme area for the left claw (black circles) and the right claw (open circles). The straight line represents the regression line for the left claw ($R^2 = 0.9623$), and the dashed line represents the regression for the right claw ($R^2 = 0.7974$).

Experimental Set-up

We assigned the individuals to four different treatments. First, we paired 28 individuals randomly ($N = 14$ pairs; random treatment). Second, we paired 32 individuals according to the RHP traits, with a maximum difference of 10% between the individuals ($N = 16$ pairs; RHP-matched treatment). Third, we paired 18 individuals using the same criteria as the RHP-matched treatment, but allowed the opponents to interact visually and chemically during the acclimation period (see below; $N = 9$ pairs; previewed opponent treatment). Finally, we arranged 27 individuals in triads according to their RHP traits. In this treatment, the focal animal could interact visually and chemically with one individual during acclimation, and perform the contest with the other individual that was not seen during the acclimation (see below; $N = 9$ triads; unseen opponent treatment).

We performed all interactions in an aquarium ($21 \times 15 \times 13$ cm) divided in three sections using removable dividers. Both dividers were opaque and nonperforated in the random treatment and in the RHP-matched treatment. The previewed opponent treatment had both translucent and perforated dividers to allow chemical/visual communication between the opponents during acclimation. Lastly, the unseen opponent treatment had one opaque and nonperforated divider (i.e. the real opponent could not be seen or smelled during acclimation), and one translucent and perforated divider (i.e. the opponent that could interact visually/chemically with the focal individual during the acclimation period). Therefore, in the unseen opponent treatment, the focal individual would be accommodated in the middle, and the opponents in the extremities behind the dividers. We accommodated the individuals in the aquarium, and left them to acclimate to the new conditions for 20 min. Afterwards, we lifted the dividers (and removed the extra individual in the unseen opponent treatment) and left the individuals to interact for an additional 20 min. The contests were recorded at night with a Sony Handycam HDR-CX560[®] positioned 30 cm vertically above the aquarium, and four incandescent red light bulbs (40 W) positioned equidistantly around the aquarium. We used red lights because crustaceans have low sensitivity for this wavelength (Turra & Denadai, 2003). After the contest, we returned the individuals to their previous individual aquaria, and observed them for 1 week prior to returning them to the natural environment. In case any animal died or moulted, we excluded them from the analysis to avoid biasing the results (Moore, 2007). Ten of the 115 captured individuals died, and we discarded them from the analysis. This mortality rate can be explained by the high metabolic demand of aeglids compared with other decapods (Dalosto & Santos, 2011). Thus, some individuals brought to the laboratory might be stressed due to the environmental conditions during collection (e.g. mild droughts, highly fluctuating temperatures) and may die during acclimation. However, aeglids can rapidly recuperate their high population densities (Bueno et al., 2014), and thus, our field samplings do not impact the population significantly. No individuals were injured during the interactions.

To calculate contest duration, we summed the duration of the first three bouts. A bout was initiated when one individual approached to within one body length of the opponent and the opponent did not flee. The bout was deemed finished when the individuals did not interact for 5 s after they had backed away or fled from each other (Goessmann, Hemelrijk, & Huber, 2000). We did not use a minimum aggressive level to determine a bout, since that could bias the results through analysing fights rather than contests (Elwood & Arnott, 2013). We used only the first three bouts because fight durations are longer when individuals have limited space to flee, such as in an aquarium (Bergman & Moore, 2003). Therefore, contest duration could be overestimated if we

had used all bouts. Besides, aeglids may not form a clear dominance relationship (winner–loser) in only one bout (Ayres-Peres et al., 2011; Palaoro et al., 2013). Hence, using only the first bout could have affected our analysis of which traits are associated with the RHP due to the lack of clear dominance. The winner was deemed the individual that did not flee in the majority of the three bouts, whereas the one that fled was deemed the loser. To analyse aggressive acts, we counted the number of claw grabs and the time spent in claw grabs performed by both winners and losers. We used only claw grabs as a proxy for aggressiveness due to their conspicuous and ubiquitous use in aeglid contests (Ayres-Peres et al., 2011). In addition, noncontact and contact phases of aeglid contests are not distinguished, and the individuals do not perform any visual display. Since only contact behaviours are conspicuous enough to be accurately assessed (Ayres-Peres et al., 2011), we evaluated only the claw grabs to avoid biasing the results.

Determination of Traits Associated with RHP

To test which traits are associated with the probability of winning a contest, we performed logistic regressions using cephalothorax length, claw length, claw height and the index of closing force as explanatory variables and winner/loser (i.e. 1 or 0) status as the response variable. Prior to testing, we performed a data modification (e.g. Junior & Peixoto, 2013; Kemp, 2000) to avoid pseudoreplication. First, since the claw is positively correlated with body size (Colpo et al., 2005), we performed three linear regressions using each claw variable separately (claw length, claw height, index of closing force; response variables) with cephalothorax length as an explanatory variable to obtain values of claw morphology and performance regardless of body size. Then, we extracted the standardized residuals from each analysis, and used the residual values throughout the study. Second, we randomly selected focal males from all four treatments. If the focal male won the contest, we assigned him a value of 1, and if he lost, we assigned a value of 0 ($N = 48$ focal males). Third, we calculated the difference in cephalothorax length, residual claw length, residual claw height and residual index of closing force between focal males and their opponents. By doing this, we expected that focal winners would have higher values than focal losers.

More than one trait can be related to the probability of winning a contest (Briffa et al., 2013). Thus, we used the Akaike's Information Criterion corrected for small samples (AICc) to select the most parsimonious hypotheses of which traits are related to the RHP (see Results, Table 2). Using all available hypotheses can be considered only an explorative analysis (Symonds & Moussalli, 2011), and would need further confirmatory analysis (Dochtermann & Jenkins, 2011). Therefore, we tested only nine hypotheses (Table 2). Since we have a priori knowledge to generate meaningful hypotheses, we were able to use this evidence for inference rather than only generating further hypothesis (Symonds & Moussalli, 2011).

Four of our hypotheses related each trait alone with the probability of winning a contest (i.e. 1 or 0), since there is evidence that these traits (cephalothorax length, claw length, claw height and index of closing force) alone can affect contest outcome (Table 2; Moore, 2007). Our next three hypotheses combined cephalothorax length with one of the claw measurements (claw length, claw height and index of closing force), since the claw morphology/performance may only be important when body size is matched (Table 2; Sneddon, Huntingford, & Taylor, 1997). Next, we tested whether only the claw was important using all claw traits and their interactions without considering the cephalothorax length (Table 2). In our last hypothesis, we tested whether all traits are important using the full model (i.e. cephalothorax length and all claw traits; Table 2). We did not test hypotheses with only two claw

Table 2

Model comparisons using AICc scores from logistic models to examine RHP-related traits in *Aegla longirostri*

Model	AICc	Δ_i	df	w_i
Cephalothorax length+residual claw height ^a	58.1	0	3	0.443
Cephalothorax length ^b	58.9	0.8	2	0.2981
Cephalothorax length+residual index of closing force ^a	60.6	2.4	3	0.1329
Cephalothorax length+residual claw length ^a	60.6	2.6	3	0.1217
Cephalothorax length+residual claw length*residual claw height*residual index of closing force ^c	67.6	10.2	9	0.0027
Residual claw length ^b	71.3	13.3	2	<0.001
Residual claw height ^b	71.5	13.6	2	<0.001
Residual index of closing force ^b	72	14.1	2	<0.001
Residual claw length*residual claw height*residual index of closing force ^d	74.2	16.9	8	<0.001

AICc: Akaike's Information criterion value corrected for small samples; Δ_i : difference in the AICc value between of the most parsimonious model and model i ; w_i : Akaike weight of model i . These models are based on the difference of each trait between a focal male (chosen randomly) and his opponent regressed with the probability of winning a contest ($N = 48$).

^a Model tested the importance of cephalothorax length and one claw measurement.

^b Model tested the importance of each trait alone.

^c Model tested the importance of the claw (using all claw traits and their interactions) without considering cephalothorax length.

^d Model tested the importance of all traits using the full model.

traits because it would be difficult to provide arguments that only two dimensions are important without isolating the other experimentally. We used the cut off rule of $\Delta \leq 2$ to distinguish between the most parsimonious candidates (Burnham & Anderson, 2002), and used the traits contained in these models in the remaining analyses. In addition, to test the importance of claw grabs during contests, we performed a generalized linear model with a quasi-Poisson error structure and a log link. We used the number of claw grabs performed by the winner as the response variable and the difference in the traits identified in the previous analysis ($|\text{winner} - \text{loser}|$) as the explanatory covariables.

Distinguishing among WOA, OOA and SAM/CAM Models

We performed a multiple linear regression following Taylor and Elwood's (2003) suggestion, using the data from the random treatment. We used contest duration as the response variable and each morphological/performance trait identified in the previous analysis of both winners and losers as explanatory covariables. Afterwards, we compared our results to the predictions of each model (Table 1). We performed a two-tailed permutation paired t test to test whether the behaviours of the opponents were matched. We tested the difference between the time spent in claw grab by winners and losers using the data from RHP-matched treatment. We did not use the data from the random pairs because of an excessive number of zeros.

Distinguishing between SAM and CAM Models

We performed three different tests to distinguish between these two models. First, we used the data from the RHP-matched treatment to perform a multiple linear regression using contest duration as the response variable, and each morphological/performance trait identified in the RHP analysis of both winners and losers as

explanatory co-variables. We then compared our results to the predictions of each model (Table 1).

Next, we used the data from the previewed opponent treatment and the unseen opponent treatment. We compared the contest duration of these two treatments using a two-tailed permutation t test. Finally, we compared the time spent in claw grab by winners with a two-tailed permutation t test using the same treatments from the prior analysis. We did not perform tests with losers because of an excessive number of zeros, which would bias the analysis. We performed all analyses in the R environment (R Development Core Team, 2013). For the AIC analysis, we used the 'bbmle' package (Bolker & R Development Core Team, 2013).

Ethical Note

All individuals were sampled, maintained and returned to the natural environment under license from IBAMA (Instituto Brasileiro do Meio Ambiente), number 14180–1, granted on 4 December 2007 and according to the applicable statutes (Federal law number 5197, of 3 January 1967; Resolutions: number 16 of 4 March 1994 and number 332 of 13 March 1990).

RESULTS

Summary of the Contests

All contests resulted in physical contact between the opponents. All individuals fought using the same body posture during the contests, with the right claw bent downwards (i.e. the tip of claw pointed towards the substrate of the contest aquarium) and the left claw extended forward trying to grasp the opponent.

Traits Related to the RHP

The model that considered cephalothorax length and claw height was the most parsimonious model. The model that considered only cephalothorax length was the second most parsimonious (Table 2). Thus, we adopted cephalothorax length and residual claw height as proxies of RHP in our study. The number of claw grabs decreased as the difference in cephalothorax length increased (GLM: $\chi^2_{1,28} = 16.56$, $P = 0.012$; Fig. 3) but did not increase/decrease significantly as the difference in residual claw height increased (GLM: $\chi^2_{1,27} = 0.034$, $P = 0.9$).

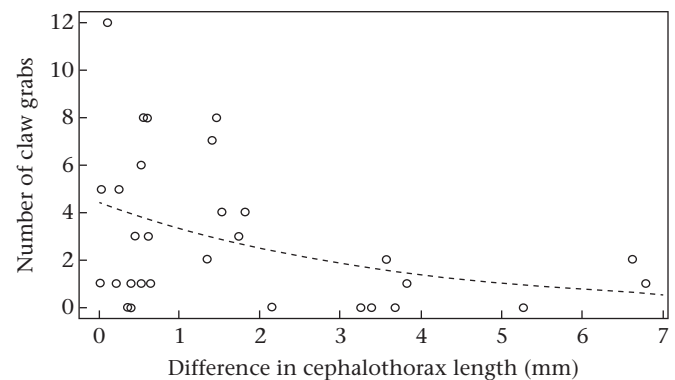


Figure 3. Relation between the difference of cephalothorax length ($|\text{winner} - \text{loser}|$) and the number of claw grabs performed by winners in contests of *Aegla longirostri* ($\chi^2_{1,28} = 16.56$, $P = 0.012$). The dashed line represents the generalized linear model with quasi-Poisson error structure and a log link.

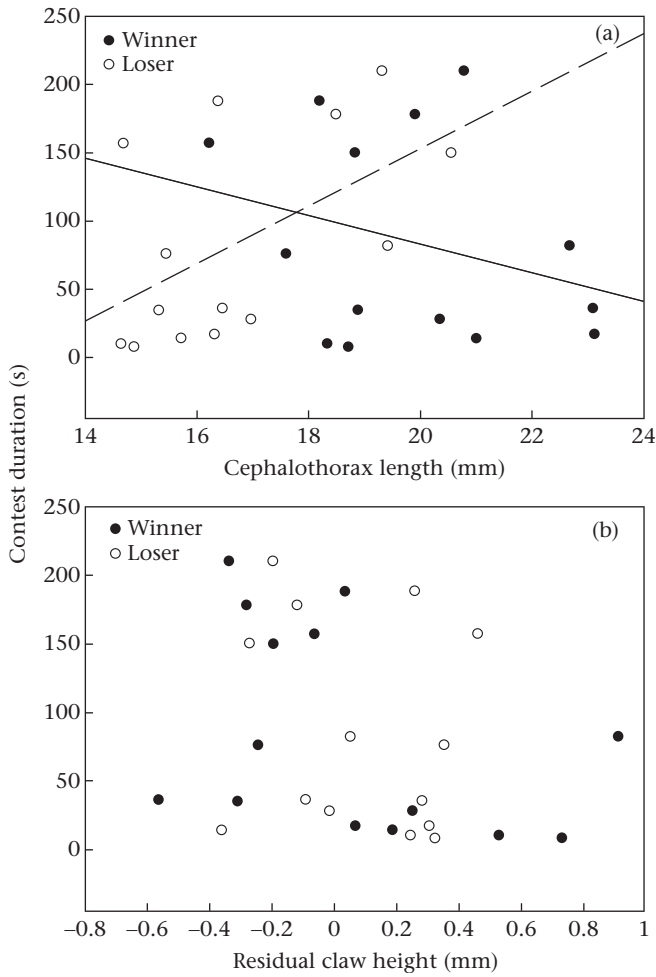


Figure 4. Relation between contest duration and (a) cephalothorax length and (b) residual claw height for random pairings. Straight line represents the regression for winners (black circles), and the dashed line represents the regression for losers (white circles). The regression lines are depicted only when the relationship was significant.

Distinguishing between WOA, OOA and SAM/CAM Models

In random pairings, contest duration increased significantly with loser’s cephalothorax length (Fig. 4a, Table 3) and decreased significantly with winner’s cephalothorax length (Fig. 4a, Table 3). Residual claw height was not significantly correlated with contest duration for losers (Fig. 4b, Table 3) or winners (Fig. 4b, Table 3). Additionally, winners spent significantly more time in claw grab than losers (permutation paired *t* test: $t_{15} = -2.705$, $P = 0.02$; Fig. 5).

Table 3
Multiple linear regression results using contest duration as response variable and cephalothorax length and residual claw height of both winners and losers as explanatory covariables in *Aegla longirostri*

Treatment	Effect	Slope	df	F	P
Random pairings	Winner cephalothorax length	-17.696	1	5.387	0.045
	Winner residual claw height	-55.908	1	2.759	0.131
	Loser cephalothorax length	32.783	1	11.41	0.008
	Loser residual claw height	63.802	1	0.699	0.424
	Residual	—	9		
RHP-matched pairings	Winner cephalothorax length	1.268	1	0.002	0.964
	Winner residual claw height	18.289	1	0.127	0.728
	Loser cephalothorax length	-10.958	1	0.141	0.715
	Loser residual claw height	54.315	1	1.175	0.312
	Residual	—	11		

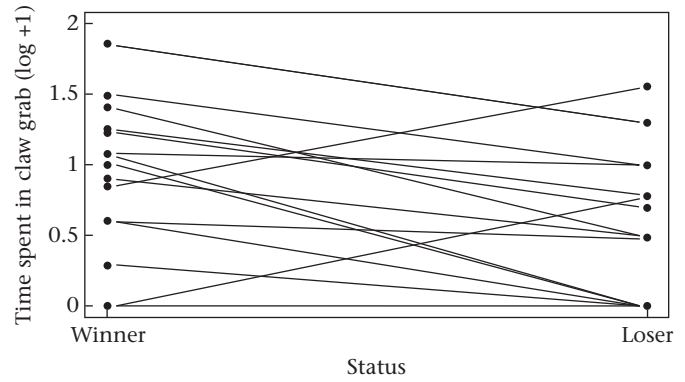


Figure 5. Time spent by winners and loser in claw grab ($\log x + 1$). A permutation paired *t* test showed that winners spent more time in claw grab than losers ($t_{15} = -2.705$, $P = 0.02$). Lines connect the individuals of each pair.

Distinguishing between SAM and CAM Models

In RHP-matched pairings, contest duration was not significantly correlated with cephalothorax length or residual claw height for losers or winners (Fig. 6a, b, Table 3). Contests were significantly shorter in the previewed opponent treatment than in the unseen opponent treatment (two-tailed permutation *t* test: $t_{14} = -2.005$, $P = 0.046$; Fig. 7). However, the time spent in claw grab by winners

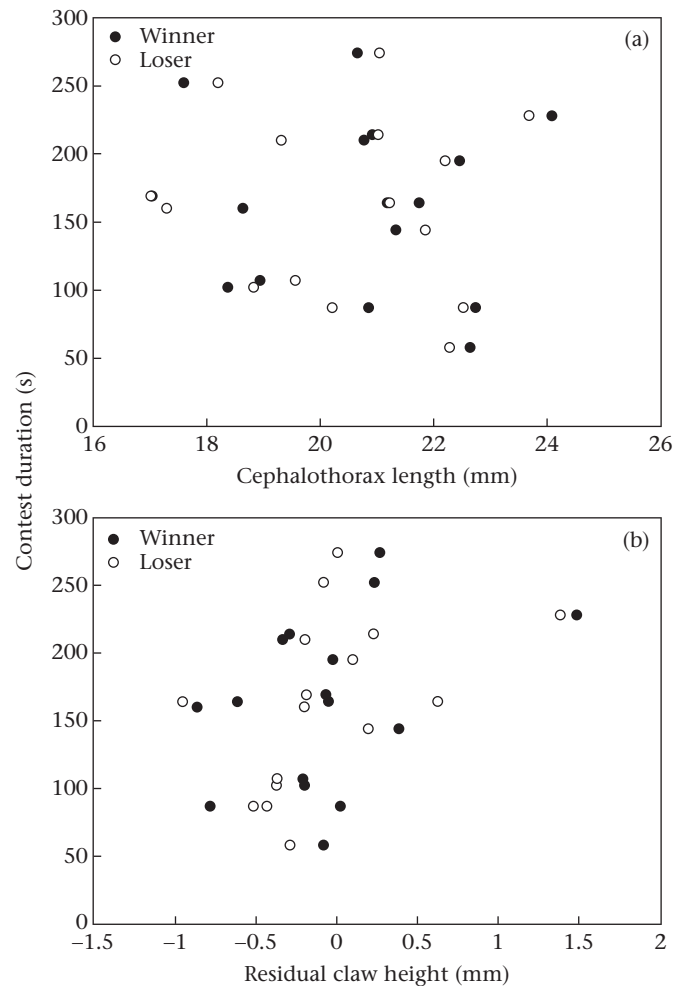


Figure 6. Relation between contest duration and (a) cephalothorax length, and (b) residual claw height for both winners (black circles) and losers (white circles) for RHP-matched pairings. The regression lines were not plotted due to non-significance.

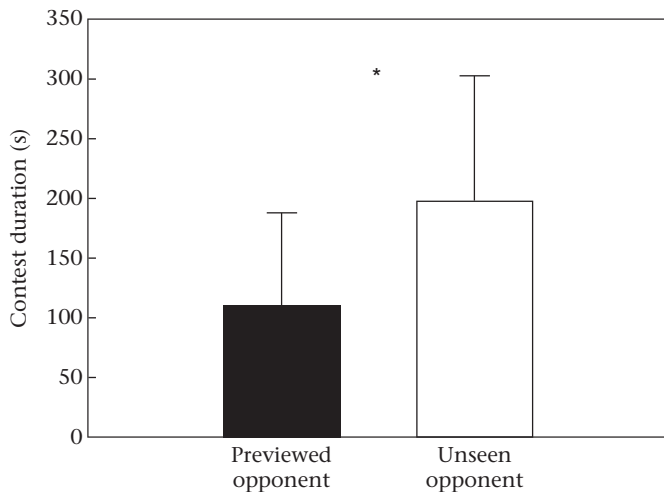


Figure 7. Mean contest duration (\pm S.D.). Black bar denotes the previewed opponent treatment (focal individual could interact visually/chemically with the opponent during acclimation). White bar denotes the unseen opponent treatment (focal individual would interact visually/chemically with one individual during the acclimation, and interact physically with other individual afterwards). Asterisk (*) denotes significant difference between the treatments (two-tailed permutation t test; $t_{14} = -2.005$; $P = 0.046$).

did not differ between the treatments (two-tailed permutation t test: $t_{12} = 0.4$, $P = 0.69$).

DISCUSSION

Herein, we show how *A. longirostri* make decisions during contests using four sources of information. First, we found that body size and weaponry can influence contest outcome. The effect of body size on contest outcome is well known and studied across several taxa (reviewed in [Arnott & Elwood, 2009](#); [Briffa & Sneddon, 2010](#)), where large body size is related to dominance. However, the effect of weaponry may vary depending on the type of contest. Contests divided in noncontact and contact phases may show different relations between weaponry and contest outcome depending on which part is being analysed. [Rudin and Briffa \(2011\)](#) showed in the beadlet anemone, *Actinia equina*, that weaponry (acrorhagi) was only important when the contest escalated to physical contact. On the other hand, decapods use their claws in almost all contests, whether by displaying them in the noncontact phase or using them to grab opponents ([Briffa, 2013](#)). Most of our analyses did not demonstrate a relatively high importance of the claw (i.e. no significant correlations with contest duration) in *A. longirostri*'s contest. Nevertheless, we found that as similarity between opponents increased, more claw grabs were performed by the winner ([Fig. 3](#)). In addition, even in shorter contests (i.e. previewed opponents), the claw grabs were necessary to resolve the contest. Therefore, weaponry is important in defining contests in *A. longirostri*, especially when individuals are size matched.

[Sneddon et al. \(1997\)](#) showed that claw length is a better predictor of winning a contest than is body size. In our analysis, claw height, not length, was a better predictor of contest outcome when combined with body size. This peculiarity may be related to different uses of the claw. The species studied by [Sneddon et al. \(1997\)](#), *C. maenas*, uses its claws for both visual displays (i.e. meral spread) and for grabbing other crabs ([Sneddon et al., 1997](#)), whereas *A. longirostri* only uses its claw for grabbing and striking opponents ([Ayres-Peres et al., 2011](#)). The use of a claw to display a signal may favour longer fingers and a smaller manus ([Fig. 1b](#)), whereas the use as a weapon favours shorter fingers and a larger manus. This occurs because shorter fingers would increase the

mechanical advantage of the claw, and the larger manus would have more space for the closing muscle, resulting in increased closing force ([Dennennmoser & Christy, 2013](#)). Crabs would then have claws that favour both signalling and fighting (i.e. a mix between the two claw shapes), and aeglids would have claws that favour fighting only. Therefore, claw height may be a better predictor of contest outcome than claw length in species that use their claws mainly as weapons rather than for signalling.

In the subsequent analyses, we investigated the relationships of contest duration and RHP traits to discriminate whether *A. longirostri* losers decided to withdraw based on SA, SAM or OOA. We also analysed differences in aggressive levels to further increase the robustness of our inferences. In random pairs, the contest duration increased with loser's RHP and decreased with winner's RHP. This refutes WOA and OOA as possible explanation models for contests in *A. longirostri* ([Table 1](#)). In addition, there was no behavioural matching between winners and losers ([Fig. 3](#)), which provides further evidence for refuting WOA as a possible explanation model. The remaining two models, SAM and CAM, were analysed using three approaches. In the first approach, using RHP-matched pairs, we showed that neither the loser's RHP nor the winner's RHP correlated with the contest duration. This evidence suggests SAM. However, it is difficult to infer using nonsignificance as an argument ([Briffa & Elwood, 2009](#)). An alternative analysis, therefore, would be to examine the contest duration between previewed and unseen opponents.

In our second approach, we found that contests with previewed opponents were shorter than contests with unseen opponents. Since in both treatments the individuals could interact with an opponent during acclimation, this strongly suggests that information from the opponent was used in the decision to withdraw. In our third approach, we expected that the individuals would need less aggressive acts to define the contests due to the information exchange with previewed opponents. However, the time spent in claw grabs did not differ between previewed or unseen opponents. Although this finding was the opposite of what we expected, it supports both SAM and CAM models. These models differ only in their interpretation of the claw grab meaning. Under SAM assumptions, the claw grab can be interpreted as conveying information regarding the RHP of the individual. Under CAM assumptions, the claw grab conveys costs to the opponent. Thus, individuals exchange information (i.e. contests between previewed opponents were indeed shorter), but ultimately rely on the claw grab to resolve contests.

Two of our three sources provided evidence for SAM as the best model to explain decision making in *A. longirostri*. The extensive use of chemical cues during decapod contests may provide information regarding the sender, whether intentionally or not. Indeed, performing aggressive acts enhances the probability of urine release, which is the main pathway used for chemical communication in decapods ([Breithaupt & Eger, 2002](#)). In addition, aggressive acts are known to alter their opponent's behaviour only when coupled with urine release ([Breithaupt & Eger, 2002](#)). Lastly, contests without urine release tend to be longer and more intense than contests with urine release ([Katoh et al., 2008](#)). Thus, it is safe to conclude that individuals are using information from their opponents. However, 'true' mutual assessment would require the individual to compare both RHPs to make a decision, and that is a cognitively complex process ([Elwood & Arnott, 2012](#)). Crustaceans are used as models in neurobiology because of their lower neuronal complexity ([Herberholz, 2007](#)). Perhaps, a more parsimonious explanation would be that the chemical cues may affect the motivational state of the opponent. This would not require the comparison of RHPs, but rather, information about the opponent would reduce the motivation to persist in the contest ([Elwood & Arnott,](#)

2012). This process was called 'mutual assessment without comparison' by Elwood and Arnott (2012), and is less cognitively demanding than the 'true' SAM. Evidence for this comes from crayfish, where future winners release more urine than losers during contests (Breithaupt & Eger, 2002). By releasing more urine, winners could be reducing the motivation of the loser, thus reducing contest duration.

Although individuals conveyed information to their opponent, claw grabs were still necessary to resolve contests. Thus, information conveyed through chemical cues may be limited. Individuals may use claw grabs for two reasons: (1) as a social mechanism to ensure the honesty of the individual's RHP; (2) to inflict costs on the opponent. Using claw strength as a social mechanism has been shown in other decapods. For instance, the crayfish *Cherax destructor* has a high variability in force production (Walter, van Uitregt, & Wilson, 2011), which means claw size is not a reliable indicator of strength. This species uses visual displays of the claw to resolve some contests. However, to avoid losing to a larger but weaker opponent, males of *C. destructor* enter in physical contact in the majority of the contests to verify that the opponent is not bluffing its RHP (Walter et al., 2011). These trials of force are also used in another crayfish species (*Procambarus clarkii*), in which individuals interlock their claws and start pushing each other. The claw interlock phase has been shown to be important in contest resolution in this species (Ueno & Nagayama, 2012). Nevertheless, we must consider that both of these species use visual displays of the claw (i.e. the meral spread), whereas aeglids do not. Furthermore, at least in *C. destructor*, claw size is not a reliable indicator of strength, which is the opposite of aeglids. The apodeme area was tightly correlated with claw height (Fig. 2), meaning that claw height is indeed a good predictor of claw strength. Therefore, aeglids may not need to use their claw grabs as a social mechanism to ensure RHP's honesty, but rather to inflict costs on their opponents.

In the light of this evidence, we hypothesize that chemical cues released with urine lower the motivation of the loser to persist in the contest (i.e. lowers the threshold of the cost that the loser is prepared to pay; Elwood and Arnott's (2012) motivational model), and that claw strength may be needed to inflict costs on the opponents when individuals have similar RHPs. Future studies should try to decouple urine release and the costs inflicted by the claw. This can be done by blocking the decapod's urine release (Breithaupt & Eger, 2002) and altering the costs inflicted by the claw, perhaps by attaching rubber to the outer surface of the claw, which would lower the force of the claw grab felt by the focal individual, similar to what has been done to hermit crab shells (Briffa & Elwood, 2000).

In summary, we provide evidence that body size and claw strength alter contest outcome in *A. longirostri*. We also provide two sources of evidence suggesting that SAM is the best explanation model for *A. longirostri* contests. However, since SAM is cognitively complex, and decapods have a relatively simple nervous system (Herberholz, 2007), we suggest that chemical signalling may be lowering the loser's motivation to persist in a contest through 'mutual assessment without comparison'. In addition, we highlight the importance of the claw during decapod contests and suggest a possible mixed strategy including both chemical cues and the costs inflicted by claw grabbing. In this scenario, the loser would withdraw based on the information regarding the winner and his ability to inflict costs.

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References

- Archer, J. (1988). *The behavioural biology of aggression*. Cambridge, U.K.: Cambridge University Press.
- Arnott, G., & Elwood, R. W. (2009). Assessment of fighting ability in animal contests. *Animal Behaviour*, 77, 991–1004.
- Ayres-Peres, L., Araújo, P. B., & Santos, S. (2011). Description of the agonistic behavior of *Aegla longirostri* (Decapoda: Aeglidae). *Journal of Crustacean Biology*, 31, 379–388.
- Bergman, D. A., & Moore, P. A. (2003). Field observations of intraspecific agonistic behavior of two crayfish species, *Orconectes rusticus* and *Orconectes virilis*, in different habitats. *Biological Bulletin*, 205, 26–35.
- Bolker, B., & R Development Core Team. (2013). *bbmle: Tools for general maximum likelihood estimation*. R package version 1.0.13. Vienna, Austria: R Foundation for Statistical Computing <http://CRAN.R-project.org/package=bbmle>.
- Bond-Buckup, G. (2003). Família Aeglidae. In G. A. S. Melo (Ed.), *Manual de identificação dos Crustacea decapoda de água doce do Brasil* (pp. 21–116). São Paulo, Brazil: Editora Loyola.
- Breithaupt, T. (2011). Chemical communication in crayfish. In T. Breithaupt, & M. Thiel (Eds.), *Chemical communication in crustaceans* (pp. 257–276). New York, NY: Springer.
- Breithaupt, T., & Eger, P. (2002). Urine makes the difference: chemical communication in fighting crayfish made visible. *Journal of Experimental Biology*, 205, 1221–1231.
- Briffa, M. (2013). Contests in crustaceans: assessments, decisions and their underlying mechanisms. In I. C. W. Hardy, & M. Briffa (Eds.), *Animal contests* (pp. 86–112). Cambridge, U.K.: Cambridge University Press.
- Briffa, M., & Elwood, R. W. (2000). The power of shell rapping influences rates of eviction in hermit crabs. *Behavioral Ecology*, 11, 288–293.
- Briffa, M., & Elwood, R. W. (2009). Difficulties remain in distinguishing between mutual and self-assessment in animal contests. *Animal Behaviour*, 77, 759–762.
- Briffa, M., Hardy, I. C. W., Gammell, M. P., Jennings, D. J., Clarke, D. D., & Goubault, M. (2013). Analysis of animal contest data. In I. C. W. Hardy, & M. Briffa (Eds.), *Animal contests* (pp. 47–85). Cambridge, U.K.: Cambridge University Press.
- Briffa, M., & Sneddon, L. U. (2010). Physiological constraints on contest behaviour. *Functional Ecology*, 21, 627–637.
- Bueno, S. L. S., Takano, B. F., Cohen, F. P. A., Moraes, J. C. B., Chiquetto-Machado, P. L., Vieira, L. C. M., et al. (2014). Fluctuations in the population size of the highly endemic *Aegla perobae* (Decapoda: Anomura: Aeglidae) caused by a disturbance event. *Journal of Crustacean Biology*, 34, 165–173.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer.
- Burruss, E. D., Gangloff, M. M., & Siefferman, L. (2013). Trophic analysis of two subtropical South American freshwater crabs using stable isotope ratios. *Hydrobiologia*, 702, 5–13.
- Clutton-Brock, T. H., Albon, S. D., Gibson, R. M., & Guinness, F. E. (1979). The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Animal Behaviour*, 27, 211–225.
- Cogo, G. B., & Santos, S. (2013). The role of aeglids in shredding organic matter in Neotropical streams. *Journal of Crustacean Biology*, 33, 519–526.
- Colpo, K. D., Ribeiro, L. O., & Santos, S. (2005). Population biology of the freshwater anomuran *Aegla longirostri* (Aeglidae) from South Brazilian streams. *Journal of Crustacean Biology*, 25, 495–499.
- Dalosto, M. M., & Santos, S. (2011). Differences in oxygen consumption and diel activity as adaptations related to microhabitat in Neotropical freshwater decapods (Crustacea). *Comparative Biochemistry and Physiology A*, 160, 461–466.
- Dennemmoser, S., & Christy, J. (2013). The design of a beautiful weapon: compensation for opposing sexual selection on a trait with two functions. *Evolution*, 67, 1181–1188.
- Doake, S., & Elwood, R. W. (2011). How resource quality differentially affects motivation and ability to fight in hermit crabs. *Proceedings of the Royal Society B: Biological Sciences*, 278, 567–573.
- Dochtermann, N. A., & Jenkins, S. H. (2011). Developing multiple hypotheses in behavioral ecology. *Behavioral Ecology and Sociobiology*, 65, 37–45.
- Elwood, R. W., & Arnott, G. (2012). Understanding how animals fight with Lloyd Morgan's canon. *Animal Behaviour*, 84, 1095–1102.
- Elwood, R. W., & Arnott, G. (2013). Assessments in contests are frequently assumed to be complex when simple explanations will suffice. *Animal Behaviour*, 86(5), e8–e12.
- Enquist, M., & Leimar, O. (1983). Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, 102, 387–410.
- Fawcett, T. W., & Mowles, S. L. (2013). Assessments of fighting ability need not be cognitively complex. *Animal Behaviour*, 86(5), e1–e7.

- Fero, L., & Moore, P. A. (2008). Social spacing of crayfish in social habitats: what role does dominance play? *Behavioral Ecology and Sociobiology*, 62, 1119–1125.
- Goessmann, C., Hemelrijk, C., & Huber, R. (2000). The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties. *Behavioral Ecology and Sociobiology*, 48, 418–428.
- Grant, J. W. A., Gaboury, C. L., & Levitt, H. L. (2000). Competitor-to-resource ratio, a general formulation of operational sex ratio, as a predictor of competitive aggression in Japanese medaka (Pisces: Oryziidae). *Behavioral Ecology*, 11, 670–675.
- Hardy, I. C. W., & Briffa, M. (2013). *Animal contests*. Cambridge, U.K.: Cambridge University Press.
- Herberholz, J. (2007). The neural basis of communication in crustaceans. In J. E. Duffy, & M. Thiel (Eds.), *Evolutionary ecology of social and sexual systems: Crustaceans as model organisms* (pp. 71–88). New York, NY: Oxford University Press.
- Hoffmann, H. A., & Schildberger, K. (2001). Assessment of strength and willingness to fight during aggressive encounters in crickets. *Animal Behaviour*, 62, 337–348.
- Hughes, M. (1996). Size assessment via a visual signal in snapping shrimp. *Behavioral Ecology and Sociobiology*, 38, 51–57.
- Junior, R. S. L., & Peixoto, P. E. C. (2013). Males of the dragonfly *Diastatops obscura* fight according to predictions from game theory models. *Animal Behaviour*, 85, 663–669.
- Katoh, E., Johnson, M., & Breithaupt, T. (2008). Fighting behaviour and the role of urinary signals in dominance assessment of Norway lobsters, *Nephrops norvegicus*. *Behaviour*, 145, 1447–1464.
- Kemp, D. J. (2000). Contest behavior in territorial male butterflies: does size matter? *Behavioral Ecology*, 11, 591–596.
- Kokko, H. (2013). Dyadic contests: modelling fights between two individuals. In I. C. W. Hardy, & M. Briffa (Eds.), *Animal contests* (pp. 5–32). Cambridge, U.K.: Cambridge University Press.
- Lailvaux, S. P., Herrel, A., Vanhooydonck, B., Meyers, J. J., & Irschick, D. J. (2004). Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society B: Biological Sciences*, 271, 2501–2508.
- Levinton, J. S., Judge, M. L., & Kurdziel, J. P. (1995). Functional differences between the major and minor claws of fiddler crabs (*Uca*, family Ocypodidae, order Decapoda, subphylum Crustacea): a result of selection or developmental constraint? *Journal of Experimental Marine Biology and Ecology*, 193, 147–160.
- Matsumasa, M., & Murai, M. (2005). Changes in blood glucose and lactate levels of male fiddler crabs: effects of aggression and claw waving. *Animal Behaviour*, 69, 569–577.
- Maynard Smith, J. (1976). Evolution and the theory of games. *American Scientist*, 64, 41–45.
- Maynard Smith, J., & Price, G. R. (1973). The logic of animal conflict. *Nature*, 246, 15–18.
- Mesterton-Gibbons, M., Marden, J. H., & Dugatkin, L. A. (1996). On wars of attrition without assessment. *Journal of Theoretical Biology*, 181, 65–83.
- Moore, P. A. (2007). Agonistic behaviour in freshwater crayfish: the influence of intrinsic and extrinsic factors on aggressive encounters and dominance. In J. E. Duffy, & M. Thiel (Eds.), *Evolutionary ecology of social and sexual systems: Crustaceans as model organisms* (pp. 91–112). New York, NY: Oxford University Press.
- Palaoro, A. V., Ayres-Peres, L., & Santos, S. (2013). Modulation of male aggressiveness through different communication pathways. *Behavioral Ecology and Sociobiology*, 67, 283–292.
- Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, 47, 223–243.
- Parra, C. A., Barria, E. M., & Jara, C. G. (2011). Behavioural variation and competitive status in three taxa of *Aegla* (Decapoda: Anomura: Aegliidae) from two-community settings in southern Chile. *New Zealand Journal of Marine and Freshwater Research*, 45, 249–262.
- Payne, R. J. H. (1998). Gradually escalating fights and displays: the cumulative assessment model. *Animal Behaviour*, 56, 651–662.
- Payne, R. J. H., & Pagel, M. (1996). Escalation and time costs in displays of endurance. *Journal of Theoretical Biology*, 183, 185–193.
- Payne, R. J. H., & Pagel, M. (1997). Why do animals repeat displays? *Animal Behaviour*, 54, 109–119.
- Pomfret, J. C., & Knell, R. J. (2005). Sexual selection and horn allometry in the dung beetle *Euoniticellus intermedius*. *Animal Behaviour*, 71, 567–576.
- R Development Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reddon, A. R., Voisin, M. R., Menon, N., Marsh-Rollo, S. E., Wong, M. Y. L., & Balshine, S. (2011). Rules of engagement for resource contests in a social fish. *Animal Behaviour*, 82, 93–99.
- Rudin, F. S., & Briffa, M. (2011). The logical polyp: assessments and decisions during contests in the beadlet anemone *Actinia equina*. *Behavioral Ecology*, 22, 1278–1285.
- Seebacher, F., & Wilson, R. S. (2006). Fighting fit: thermal plasticity of metabolic function and fighting success in the crayfish *Cherax destructor*. *Functional Ecology*, 20, 1045–1053.
- Seebacher, F., & Wilson, R. S. (2007). Individual recognition in crayfish (*Cherax dispar*): the roles of strength and experience in deciding aggressive encounters. *Biology Letters*, 3, 471–474.
- Smallegange, I. M., Sabelis, M. W., & van der Meer, J. (2007). Assessment games in shore crab fights. *Journal of Experimental Marine Biology and Ecology*, 351, 255–266.
- Sneddon, L. U., Huntingford, F. A., & Taylor, A. C. (1997). Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behavioral Ecology and Sociobiology*, 41, 237–242.
- Sneddon, L. U., Huntingford, F. A., Taylor, A. C., & Orr, J. F. (2000). Weapon strength and competitive success in the fights of shore crabs (*Carcinus maenas*). *Journal of Zoology*, 250, 397–403.
- Stuart-Fox, D. (2006). Testing game theory models: fighting ability and decision rules in chameleon contests. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1555–1561.
- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multi-model inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65, 13–21.
- Taylor, P. W., & Elwood, R. W. (2003). The mismeasure of animal contests. *Animal Behaviour*, 65, 1195–1202.
- Turra, A., & Denadai, M. R. (2003). Daily activity of four tropical intertidal hermit crabs from southeastern Brazil. *Brazilian Journal of Biology*, 63, 537–544.
- Ueno, R., & Nagayama, T. (2012). Interlocking of chelae is a key factor for dominance hierarchy formation in crayfish. *Journal of Experimental Biology*, 215, 2841–2848.
- Walter, G. M., van Uitregt, V. O., & Wilson, R. S. (2011). Social control of unreliable signals of strength in male but not female crayfish, *Cherax destructor*. *Journal of Experimental Biology*, 214, 3294–3299.
- Warner, G. E., & Jones, A. R. (1976). Leverage and muscle type in crab chelae (Crustacea: Brachyura). *Journal of Zoology*, 180, 57–68.