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Dishonest Signals of Strength in Male Slender Crayfish (*Cherax dispar*) during Agonistic Encounters

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ABSTRACT: Many animals resolve disputes without combat by displaying signals of potential strength during threatening displays. Presumably, competitors use each other's displays to assess their relative strengths, and current theory predicts that these signals of strength should generally be honest. We tested this prediction by investigating the relationships among morphology, performance, and social dominance in males of the slender crayfish *Cherax dispar*. Crayfish routinely use their enlarged front claws (chelae) for both intimidation and fighting, making this species ideal for studying the honesty of weapon size. We evaluated five competing models relating morphological and physiological traits to dominance during paired competitive bouts. Based on the best model, larger chelae clearly resulted in greater dominance; however, chela strength had no bearing on dominance. Thus, displays of chela size were dishonest signals of strength, and the enlarged chelae of males seemingly function more for intimidation than for fighting. In addition, an analysis of the performance of isolated chela muscle showed that muscle from male crayfish produced only half the force that muscle from female crayfish produced (236.6 ± 26.4 vs. 459.5 ± 71.6 kN m^{-2}), suggesting that males invest more in developing larger chelae than they do in producing high-quality chela muscle. From our studies of crayfish, we believe dishonest signaling could play a greater role in territorial disputes than previously imagined.

Keywords: signaling, weapon size, chela strength, dominance.

Animals routinely fight with conspecifics to resolve territorial disputes (Parker 1974). For organisms that possess specialized structures that function as weapons, fighting performance depends strongly on the ability of these structures to inflict injuries on rival combatants. However, aggressive interactions between animals are potentially costly because of the energy required to fight and the risk of injury or death (Maynard Smith and Harper 2003). Because of the inherent costs associated with escalating aggressive interactions, many animals resolve disputes without combat by signaling their own fighting potential and comparing this with the potential of their opponent (Parker 1974; Enquist and Leimar 1983; Maynard Smith and Harper 1988; Huntingford et al. 2000). Not surprisingly, weapons such as antlers, horns, and claws are often conspicuously displayed to rivals as a sign of the potential to impose fitness costs (Maynard Smith and Harper 2003). Signals that display the potential performance of weaponry could constitute an important component of many aggressive displays and reduce the occurrence of costly physical interactions. Indeed, substantial evidence indicates that animals use such specialized structures during aggressive encounters with conspecifics (e.g., Clutton-Brock 1982; Carrier et al. 2002), and these structures help to determine dominance (Brown and Bartalon 1986; Lappin and Husak 2005).

Theory predicts that animals should employ honest signals of resource holding potential during competitive interactions (Maynard Smith and Harper 1988; Dawkins and Guilford 1991) unless the cost of assessing the honesty of a signal is relatively great (Gardner and Morris 1989) and the cost of producing a deceptive signal is relatively small (Adams and Mesterton-Gibbons 1995). Signals of weaponry or potential strength should be physically or physiologically linked to competitive ability such that poor com-

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petitors cannot produce a signal equivalent to that of a good competitor (Zahavi 1975; Wiley 1983; Maynard Smith and Harper 1988). Not surprisingly, few clear examples of dishonest signals of fighting potential exist (Steger and Caldwell 1983; Caldwell 1986; Adams and Caldwell 1990; Backwell et al. 2000; Hughes 2000). Because dishonest signals are designed to go unnoticed, their detection is difficult for researchers and conspecifics alike. Assessing the honesty of signals requires (1) analyses of the relationship between the visual signal and fighting capacity and (2) measures of the physical performance of the displayed weaponry. Few studies have measured weapon performance directly (but see Sneddon et al. 2000; Lappin et al. 2006), and those that have indicate that weapons honestly signal the physical prowess of their bearers (Lappin et al. 2006). Gaping displays of adult male collared lizards (*Crotaphytus collaris*) were found to provide an honest and accurate index of biting performance by exposing the major jaw-adductor muscle complex to rivals (Lappin et al. 2006). Furthermore, biting force of male collared lizards predicted their access to females and their success in mating (Lappin and Husak 2005). These studies provide some of the best empirical evidence that displays of weapons honestly signal potential fighting performance.

In our studies, we discovered that males of the Australian slender crayfish (*Cherax dispar*) routinely used dishonest signaling of physical prowess during competitive interactions, suggesting that current theory may underestimate the prevalence of dishonest signals of strength in nature. We evaluated the honesty of competitive signaling by measuring both the size and the strength of the male's principal weapon in relation to his dominance. Male crayfish routinely use their enlarged front claws (chelae) for both intimidation and fighting, making these organisms ideal for studying the honesty of aggressive signals (fig. 1). During competitive interactions, we frequently observed males displaying their chelae to opponents, but direct physical contact occurred only in a small proportion of interactions. We evaluated five competing models relating morphological and physiological traits to dominance during the competition. Given that current theory predicts displays of weaponry to be honest signals of physical strength, we expected both chela size and strength to be good predictors of dominance during competitive interactions. In a dishonest signaling system, however, we should expect chela size to better predict dominance than chela strength alone, and male crayfish should invest more energy to develop larger chelae than they would to produce high-quality chela muscle. We evaluated this idea by comparing the force production of muscles taken from the chelae of male and female crayfish.

Figure 1: Male Australian slender crayfish (*Cherax dispar*) routinely engage in aggressive territorial fights when visual signals of chela size fail to resolve disputes. Photo by Anthony O'Toole.

Material and Methods

Australian slender crayfish (*Cherax dispar*) are highly territorial and aggressive animals (R. S. Wilson, unpublished observations) that inhabit creeks and swamps of the sand islands near southeast Queensland, Australia. We collected crayfish from the western creeks of North Stradbroke Island (27°29′S, 153°24′E) and immediately transported them to the Moreton Bay Research Station (University of Queensland) for our experiments.

To assess the honesty of weapon size as a signal of strength in this species, we determined the body size, chela size (right and left), chela strength (right and left), and dominance ability of 32 adult males. Body size was estimated as body length and body mass. Body length (the distance between the rostrum to the end of the tail) was measured with digital calipers (±0.1 mm), while body mass was measured with an electronic balance (±0.001 g). Because body mass and body length were highly correlated, we computed the residuals of body mass regressed onto body length (hereafter referred to as "condition").

Chela size was determined from images of the left and right chelae captured with a Panasonic digital camera and analyzed with morphometric software (SigmaScan 5.0, Systat, San Jose, CA). Five parameters were recorded from the digital images to measure the size of each chela: chela length, chela height, dactylus length, dactylus height, and propodus length. Because these variables were highly correlated, we used principal components (PC) analyses to derive a single measure of mean chela size for our analysis. A separate analysis was conducted for each chela. Both analyses yielded a principal component that described more than 90% of the variation in the five morphometric variables. For subsequent analyses, we used the mean of

PC scores for the two chelae; thus, chela size was characterized by a single variable (chela PC) that captured the vast majority of variation in the original chela dimensions. Slender crayfish possess two similarly sized chelae that differ in size only when one or both have been lost during combat or predator encounters and have regenerated. We used the average chela size for each crayfish because both chelae are simultaneously used during agonistic encounters.

Maximal chela strength was estimated as the force produced by the closing of the dactylus on the fixed propodus of the chela. Force measurements were recorded by a custom-built sensor that consisted of two metal plates (25 mm × 5 mm × 1 mm) separated by a third metal plate (4 mm thick) acting as a pivot; all three plates were mounted in a block of wood. The former two plates protruded 12 mm beyond the pivot plate, and each had a strain gauge (RS Electronics, Sydney) attached to it with epoxy resin. The outputs from each strain gauge were connected to a custom-made Wheatstone bridge each linked to a bridge amplifier (AD Instruments, Sydney). Output from the bridge amplifiers was monitored with a computerized recording system (PowerLab, AD Instruments). Each strain gauge was calibrated such that the voltage output from each bridge amplifier could be converted to newtons of force. When presented with the device, crayfish readily closed their chelae on the two plates carrying the strain gauges, enabling us to measure the force produced by the chela. The greatest force (the sum of both force transducers) produced by three to five grabs was measured for both chelae of each individual. Maximal forces of the left and right chelae were averaged to produce a single measure of chela force for our analyses.

Dominance was assessed during competitive bouts conducted in an experimental arena. The arena consisted of a plastic aquarium (0.30 m × 0.20 m × 0.10 m) containing natural creek water (pH 5.5) and a gravel substrate (1 cm). Water temperature was maintained at 20°C. The observation tank was initially separated into two sections with plastic dividers. Before each bout, one crayfish was placed on each side of the divider. After a 2-min period, the divider was removed and the behavior of each crayfish was observed and recorded for 10 min. Based on preliminary trials, we developed a scoring system that represented dominance during our staged encounters. The two most prevalent and easily recognized behaviors were "fights" and "chases." Fights were defined as two animals facing each other with each attempting to hold and unbalance the other. Crayfish typically used their chelae to push their opponent and to take hold of the adversary's chelae. Eventually, one of the contestants would move away, and the remaining animal was scored as the winner of the fight. In a chase, one of the animals would turn and retreat immediately without engaging in a fight, and the remaining animal was scored as the winner of the chase. We awarded 2 points for victory in a fight and 1 point for victory in a chase. No animals were physically harmed during any of these encounters. Our experimental design provided not only quantitative measures of dominance for randomly paired crayfish but also a complete ranking of all 32 crayfish in our sample. To achieve this ranking, we used a competitive tournament in which animals were randomly divided into eight groups of four individuals each. All individuals within each group competed against one another in three successive bouts. These bouts were equivalent to encounters between randomly paired males, and dominance scores from a subset of these bouts were analyzed independently (see "Analyses of Dominance Scores").

Analyses of Dominance Scores

We evaluated five competing models relating morphological and physiological traits to dominance (fig. 2). Models were fit by path analyses conducted with AMOS 5.0 (SPSS, Chicago). Each model was fit to two sets of data. First, we analyzed variation in the dominance score calculated from a single bout during round 1, in which each individual had been paired uniquely and randomly (single score). Second, we analyzed variation in the overall dominance score for the tournament (total score). Because these two scores were highly correlated ($t = 5.57$, $r^2 = 0.51$, $P < .00001$), our conclusions did not depend on which score was analyzed.

After fitting each model, we calculated the second-order Akaike Information Criterion ($\mathrm{AIC_C}$):

$$\mathrm{AIC_C} = \chi^2 + 2K + \frac{2K(K+1)}{N-K-1}, \tag{1}$$

where χ^2 is the χ^2 goodness of fit, K is the number of estimated parameters, and N is the sample size (Burnham and Anderson 2002). Models were ranked based on their values of $\mathrm{AIC_C}$, after which these values were rescaled as simple differences between the $\mathrm{AIC_C}$ value for each model and that of the model with the lowest value (differential $\mathrm{AIC_C}$). Akaike weights were used to assess which model was most likely to be correct. The Akaike weight is the normalized likelihood that a model fits the data better than any other model in the set. The normalized likelihoods of the five models were very similar for analyses of single scores and total scores; in fact, the rankings of the five models were identical (table 1). The residual scores of the best model did not deviate grossly from normality (Shapiro-Wilk tests: $P = .12$ and $P = .50$ for analyses of total scores and single scores, respectively), indicating that our data met this assumption of the path analysis.

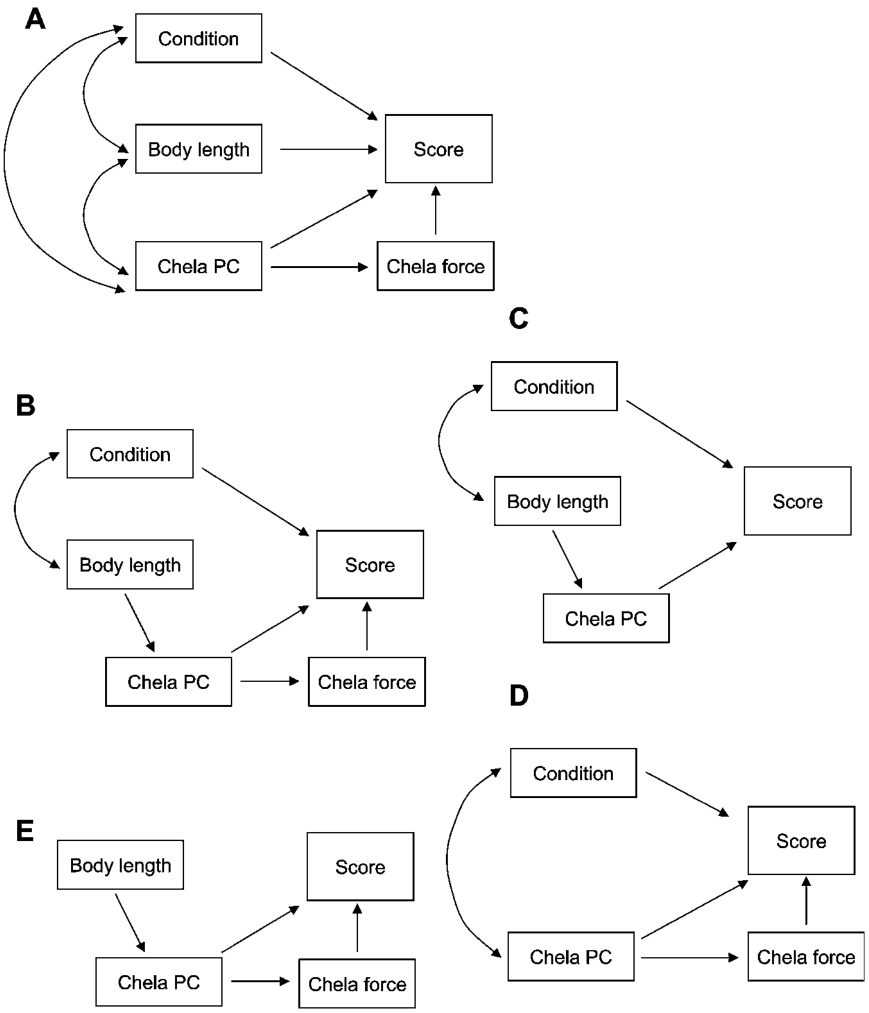

Figure 2: Five path models relating morphological and physiological characteristics of male Australian slender crayfish (*Cherax dispar*) to their dominance during competitive bouts.

Isolated Muscle Performance

We compared the in vitro performance of chela muscle from males ($N = 8$) and females ($N = 8$) of *C. dispar.* Crayfish were humanely killed before dissection. The propodal process was removed to free the dactyl from the rest of the propodus while leaving the chela closer muscle intact. Dissection was performed at 20°C in an aerated saline solution (Elrick and Charlton 1999) with pH of 7.4 and the following composition (in mM): 205 NaCl, 5.4 KCl, 2.7 $MgCl_2$, 10 glucose, 10.0 HEPES buffer, 13.5 $CaCl_2$. The dactyl was clamped in a crocodile clip attached to a force transducer (Dynamometer UF1, Pioden Controls), and the propodus was clamped in a crocodile clip attached to a servomotor (V201, Ling Dynamic Systems). The muscle preparation was placed inside a temperature-controlled Perspex bath, with circulating saline solution saturated with air and maintained at 20° ± 0.5°C.

A series of twitches were used to determine the stimulation amplitude and muscle length that generated the greatest isometric twitch force. Stimuli of 1.5 ms in duration were delivered via two parallel platinum wire electrodes placed on either side of the muscle. A 200-ms train of stimuli was then delivered to the muscle to elicit a tetanic contraction, and the frequency of stimulation was adjusted to maximize the height of the tetanus (90–100 Hz). A resting period of 5 min was provided between each tetanic response. The experimental apparatus was controlled, and data were collected using the Testpoint software package (Keithley, Cleveland, OH). Data were then exported and analyzed in Microsoft Excel. The maximal

Table 1: Comparison of path models describing the relationships among morphological traits, physiological performance, and total score of dominance

Model	Relevant figure	χ^2	df	K	AIC$_C$	δ_i	w_i
Chela size, force, and indirect effect of length	2*E*	1.305	2	12	41.73	.00	.9064 (.9368)
Condition, chela size, and force	2*D*	.045	1	13	46.27	4.54	.0936 (.0632)
Condition, chela size, and indirect effect of length	2*C*	33.35	2	12	73.77	32.04	.0000 (.0000)
Condition, length, chela size, and force	2*A*	.608	2	18	89.22	47.50	.0000 (.0000)
Condition, chela size, force, and indirect effect of length	2*B*	33.96	4	16	102.23	60.50	.0000 (.0000)

Note: The rightmost column lists the Akaike weight of each model (i.e., the likelihood that a particular model best describes the data); for comparison, Akaike weights of the analyses of single scores are listed in parentheses. For each model, we list the χ^2 goodness of fit, the degrees of freedom (df), the number of parameters (K), the Akaike Information Criterion (AIC$_C$), the differential AIC$_C$ (δ_i), and the Akaike weight (w_i).

force produced by each muscle was corrected for propodus size, enabling us to compare muscle quality/stress between genders. Maximal quality/stress was calculated as the maximal force divided by the mean muscle cross-sectional area, assuming that muscle density was 1,060 kg m^{-3}. Such a calculation makes no attempt to account for the highly pennate nature of the chela muscle; nevertheless, this calculation should indicate the relative difference between genders because we found male and female chela muscles to have similar pennation.

Results and Discussion

We found that a model describing the direct and indirect effects of chela size was more than 90% likely to provide the best description of the data (table 1). In this model, larger chelae clearly resulted in greater dominance (fig. 3*A*). However, chelae strength had no bearing on dominance (fig. 3*A*), indicating that chela size was often a dishonest signal of strength and that the enlarged chelae functioned more for intimidation than for fighting. Across a variety of taxa, weapon size appears to predict fighting capacity or resource holding potential better than body size does (reviewed in Andersson 1994; but see Sneddon et al. 2000). Despite the close relationship between weapon size and dominance among males of *Cherax dispar*, the dishonest signals of strength that we observed contrast with several recent studies demonstrating a strong relationship between the performance of a weapon and the dominance of its bearer (Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2006; Lappin et al. 2006). For example, Lappin et al. (2006) showed that in adult male collared lizards (*Crotophytus collaris*), the breadth of the jaw muscles, which are actively displayed to competitors by jaw gaping, is a strong predictor of bite force. Furthermore, performance of the lizards' principal weapon (i.e., biting strength) predicted dominance better than head size alone (Lappin and Husak 2005). Similarly, the biting performance of males of the lacertid lizard *Gallotia galloti* accurately predicted dominance during staged encounters with conspecifics (Huyghe et al. 2005).

Although large chelae do not accurately reflect the potential strength of male crayfish, large chelae could still enhance dominance via other functions. For example, they could enhance the ability to push during agonistic interactions or could decrease susceptibility to grabbing. To discover whether chela strength determines dominance during the escalation of territorial disputes, we analyzed 10 bouts from the main competition in which competitors were matched for size and engaged in active physical combat. We found no difference in mean chela size between winners and losers ($F = 2.97$, $P = .12$), but winners had significantly greater chela strength than did losers ($F = 8.64$, $P < .01$). Taken together, these results suggest that chela strength partially determines dominance during physical interactions when bluffing does not occur. When weapons were size matched between pairs of shore crabs (*Carcinus maenas*), Sneddon et al. (2000) also found that winners possessed major and minor chelae that exerted greater force than chelae of losers. Thus, although male crayfish could win disputes merely by displaying their larger chelae, they might also test the honesty of the signal by escalating the conflict to physical interactions. However, the large chelae of dominant males could also have other functions during competitive bouts or predator encounters that are not related to the potential to impose injuries on an opponent. Although current theory predicts that the assessment of weapon performance should depend on characteristics that are available to function as signals, this is clearly open to routine corruption when assessment of

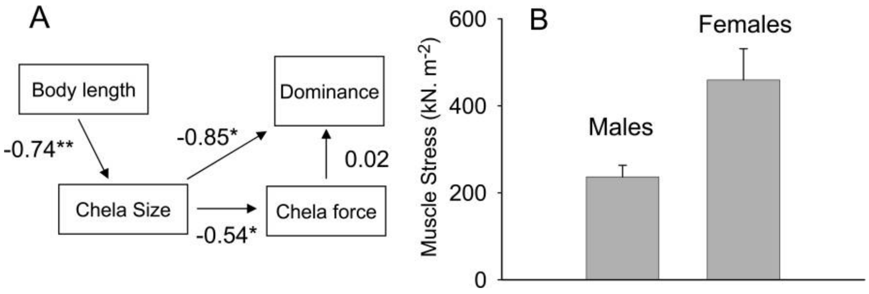

Figure 3: *A*, Best path model relating morphological and physiological traits to dominance; it showed that dominance is determined largely by chela size ($P < .001$) rather than chela force ($P = .84$). Path coefficients were standardized. Chela size was estimated as the mean of principal component scores for the left and right chelae. Because all chela dimensions loaded negatively onto these principal components, smaller scores reflect larger chelae; hence, the negative path coefficient between chela size and dominance. *B*, Chela muscle from male crayfish produced only half of the stress (force per cross-sectional area of muscle) that was produced by chela muscle from female crayfish ($t = 2.9$, $P < .01$).

the signal can occur only via physical contact. Few studies have directly assessed the performance of weaponry, but nearly all reported cases of dishonest signals of strength involve species of crustaceans. Additional studies across a wide variety of taxa are required to determine the frequency of dishonest signals of strength.

Given that signals of strength among male slender crayfish appear misleading, we expected males to have invested more in developing larger chelae than they did in producing high-quality chela muscle. We evaluated this idea by comparing the force production of muscles taken from male and female chelae. Consistent with our prediction, we found that chela muscle from male crayfish produced only half the force that chela muscle from female crayfish produced (236.6 ± 26.4 vs. 459.5 ± 71.6 kN m^{-2}; fig. 3*B*). To our knowledge, this finding is the first demonstration of sexual dimorphism in muscle quality related to intraspecific signaling. Sexual dimorphism in muscle size has been described for a number of amphibians, with males of many anurans possessing enlarged forelimb muscles for use during male-male combat and in clasping females during amplexus (Wells 1977; Peters and Aulner 2000). For male crayfish, production of high-quality muscle could correlate negatively with either the size of chelae or the strength of their exoskeletons because of an energetic trade-off. If so, only the highest-quality males can possess chelae that are both large and proportionally strong. Male crayfish often lose their chelae during territorial bouts that escalate to physical contact and may preferentially invest more energy in the rapid regrowth of the exoskeleton before the development of muscle. Because female crayfish also commonly fight over resources, the higher-quality muscle of the chelae of females indicates that their displays of weaponry are honest signals of strength.

In summary, slender crayfish use their chelae to signal dominance, but these displays are often poor reflections of strength. Dishonest signals of strength are designed to go unnoticed, thus making their detection difficult for both researchers and conspecific competitors. From our studies of crayfish, we believe dishonest signaling could play a greater role in territorial disputes than previously imagined.

Acknowledgments

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APPENDIX

Calculation of Dominance Scores

Dominance results in all three bouts for each individual were used to rank all individuals. The two crayfish from each group with the highest scores proceeded to the next round of the competition. The two crayfish with the lowest scores from each group proceeded to the next round of a “losers” competition. Two further rounds were conducted for each crayfish (fig. A1). In the second round, crayfish ranked first in their group were matched against those ranked second (round 2A), while crayfish ranked third were matched against those ranked fourth (round 2B). Winners and losers of the second round (2A and 2B) were then matched against each other in a third and final round (3A–3D; see fig.

A1 for details). Because wins in the different divisions of the second and third rounds were not equivalent, points were awarded to each crayfish to reflect their qualification for certain rounds (20, 20, 10, and 5 points for qualifying for groups 2A, 3A, 3B, and 3C, respectively). By summing points for all bouts, we produced a score for each individual that enabled us to rank the dominance of all crayfish on a continuous scale (mean = 17.4, SD = 11.2).

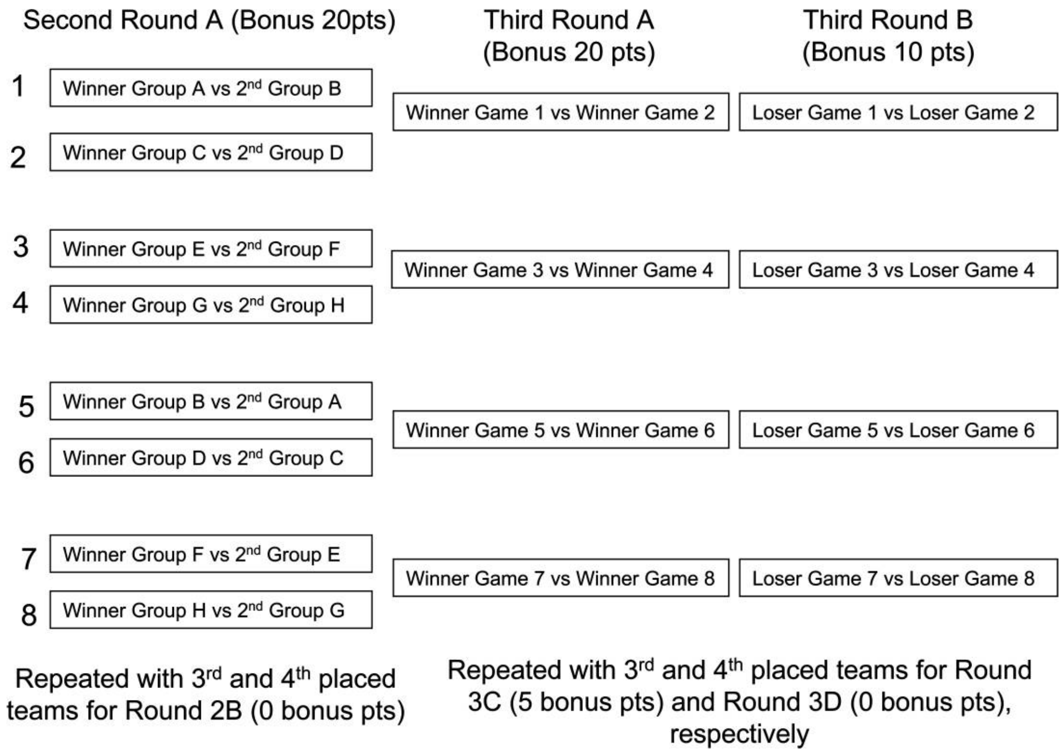

Figure A1: Experimental design used to rank the dominance of all crayfish. Crayfish were initially randomly separated into eight groups of four individuals each. In the first round, each crayfish competed against all others in the same group (six bouts per group). After the first round, the top two crayfish proceeded to the second round, while the bottom two crayfish also proceeded to a "losers" round. This diagram depicts the pairing of males from the second round through the final round of the competition.

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