

Cryptic asymmetry: unreliable signals mask asymmetric performance of crayfish weapons

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Animals commonly use their limbs as signals and weapons during territorial aggression. Asymmetries of limb performance that do not relate to asymmetries of limb size (cryptic asymmetry) could substantially affect disputes, but this phenomenon has not been considered beyond primates. We investigated cryptic asymmetry in male crayfish (*Cherax dispar*), which commonly use unreliable signals of strength during aggression. Although the strength of a chela can vary by an order of magnitude for a given size, we found repeatable asymmetries of strength that were only weakly related to asymmetries of size. Size-adjusted strength of chelae and the asymmetry of strength between chelae were highly repeatable between environmental conditions, suggesting that asymmetries of strength stemmed from variation in capacity rather than motivation. Cryptic asymmetry adds another dimension of uncertainty during conflict between animals, which could influence the evolution of unreliable signals and morphological asymmetry.

Keywords: asymmetry; performance; signalling; weaponry; crustaceans

1. INTRODUCTION

The asymmetry of limb use or function, commonly referred to as handedness, represents one type of lateralized performance. Handedness has influenced the evolution of tool use and manual gestures in humans and other primates [1,2]. In fact, more than 90 per cent of the human population, regardless of ethnic or cultural background, has a bias towards the use of the right hand [3]. Studies of non-primates have predominantly focused on the behavioural or morphological aspects of limb asymmetry [4–6]. The consequences of limb asymmetries for performance are virtually unknown. This oversight is surprising given the importance of limb performance during combat [7], escape [8], foraging [9] and mating [10].

In particular, asymmetries of performance have implications for signalling during aggressive interactions. Males often display their limbs to opponents as signals of their potential to defend resources [11]. This behaviour enables individuals to assess their chances of winning disputes before a costly escalation into physical combat. When signals reflect strength,

asymmetry of limb size should also cause asymmetry of performance. However, when signals fail to reflect strength, asymmetry of limb size does not necessarily indicate an asymmetry of strength (and vice versa). Thus, unreliable signalling can mask asymmetry of performance, which we refer to as cryptic asymmetry. In its most extreme form, cryptic asymmetry implies that the largest limb may not represent the greatest threat to an opponent.

Crustaceans offer an opportunity to investigate cryptic asymmetry of performance. Males possess pairs of chelae used during aggressive signalling [12–14]. For example, Wilson *et al.* [15] observed that males of the slender crayfish (*Cherax dispar*) assessed each other's chelae by rubbing and tapping. This ritual either escalated into physical combat or ended with one individual fleeing. The male with larger chelae usually won a dispute without combat. When combat occurred, the stronger male usually prevailed. Surprisingly, the size of a chela provided poor information about its strength. In fact, the strength of this weapon varied by as much as an order of magnitude for a given size. Moreover, males produced a poorer quality of muscle in chelae than did females, indicating that males exaggerated the sizes of their chelae by investing less energy in muscle. Consequently, a large number of disputes between slender crayfish were settled through unreliable signalling, such that weak males with large chelae dominated stronger males. Here, we show that unreliable signalling hides the majority of asymmetry in performance between pairs of chelae.

2. MATERIAL AND METHODS

We collected crayfish from North Stradbroke Island (27°29' S, 153°24' E) and transported them to Moreton Bay Research Station. Crayfish were housed individually in 21 containers containing creek water at 24°C. Commercial food pellets were provided daily, and water was changed between feedings.

We determined the size and strength of chelae for 97 adult males. Size was determined from images captured by a digital camera and analysed using morphometric software (SIGMA SCAN v. 5.0). Seven measurements were made for each chela: chela length to the dactyl joint, chela heights at the carpus and dactyl joints, dactylus length and height, and propodus length and height. Because these variables were highly correlated, we used principal component (PC) analyses to derive a single measurement of size, which described more than 88 per cent of the variation in the original variables. Because all variables loaded negatively onto the first PC, we multiplied the scores for this PC by –1 to simplify the interpretation of subsequent analyses.

Maximal strength of each chela was estimated as the force produced by the dactylus closing on the fixed propodus [15]. The position of closure was standardized to maximize the repeatability of force. Force was recorded by a sensor that consisted of two metal plates (25 × 5 × 1 mm) separated by a third metal plate (4 mm thick), which acted as a pivot. Each strain gauge was connected to a Wheatstone bridge linked to a bridge amplifier (AD Instruments, Australia). Outputs were monitored by a data-recording system (PowerLab, AD Instruments). Strain gauges were calibrated such that the voltage output could be converted to force. Crayfish readily closed their chelae on the two plates, enabling us to measure the greatest force produced by three to five pinches by each chela.

Because asymmetry of strength could reflect differential motivation more than differential capacity, we assessed the repeatability of strength (and its asymmetry) by measuring maximal force at two temperatures: 14°C and 24°C. Measurements were conducted on consecutive days, with the order of the temperatures being randomly determined for each crayfish. For measurements at 14°C, crayfish were cooled at a rate that did not exceed 4°C h⁻¹. Measurements began at least 10 min after the water reached 14°C.

To compare the repeatability of chela strength between temperatures, we statistically controlled for potential effects of temperature on force. To do so, we calculated the relative strength of each crayfish as the residual of maximal force regressed onto chela size (–1 PC score). Separate regressions were carried out for left and right chelae. We used a power function as the error term of our model [16], because

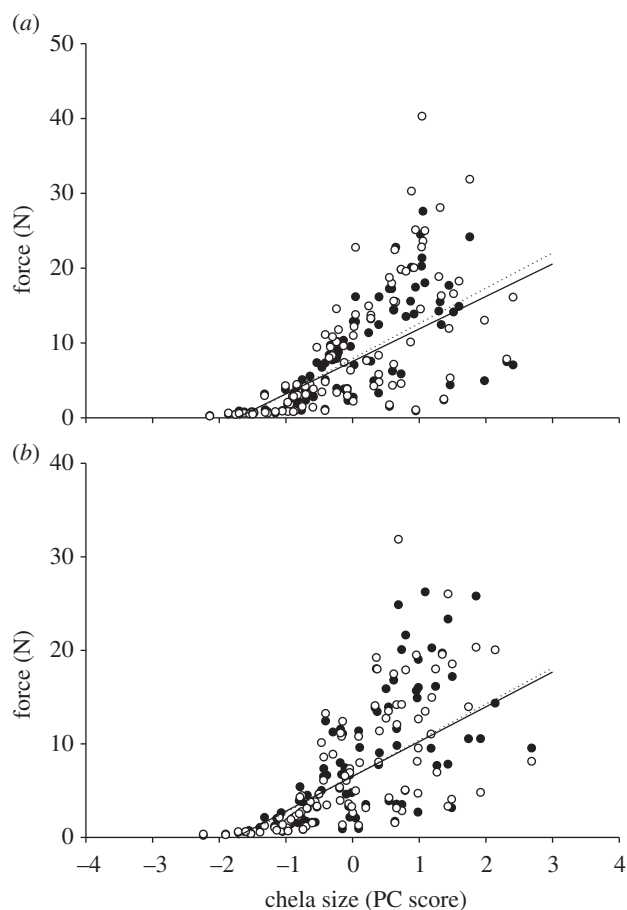


Figure 1. The mean and variance of chela strength increased with chela size. Size was characterized by a principal component (PC) derived from seven linear measurements. Filled and unfilled circles are data for 14° and 24°C, respectively. (a) Left chela and (b) right chela.

the variance of chela force increased with chela size (figure 1). We then examined the correlation between relative strengths at 14°C and 24°C. Finally, we calculated the asymmetries of size and strength for each crayfish by subtracting the PC and force values for the left chela from those for the right chela. Correlation was used to assess whether the asymmetry of strength was repeatable and whether this asymmetry reflected an asymmetry of size. Analyses were conducted in the R statistical software package [17].

3. RESULTS

The strength of a crayfish's chela depended on its size, however, the unexplained variation in strength increased exponentially with chela size (figure 1). Consequently, size did not necessarily reflect strength. The weak relationship between the size and strength of a chela effectively masked pronounced asymmetry of performance. Crayfish that exhibited extreme asymmetry in chela size (figure 2a) did not necessarily exhibit a corresponding asymmetry in chela strength (figure 2b). Two observations indicate that asymmetries of performance between paired chelae stemmed from asymmetries in ability, rather than motivation or error. First, the residual forces generated by chela at 14°C and 24°C were highly correlated (left chela: $r^2 = 0.569$, $n = 97$, $p < 0.001$; right chela: $r^2 = 0.701$, $n = 97$, $p < 0.001$), indicating that performances of chelae were repeatable between environmental conditions. Second, the asymmetry of chela strength was also correlated between thermal conditions (figure 2c; $r^2 = 0.416$, $n = 97$, $p < 0.001$).

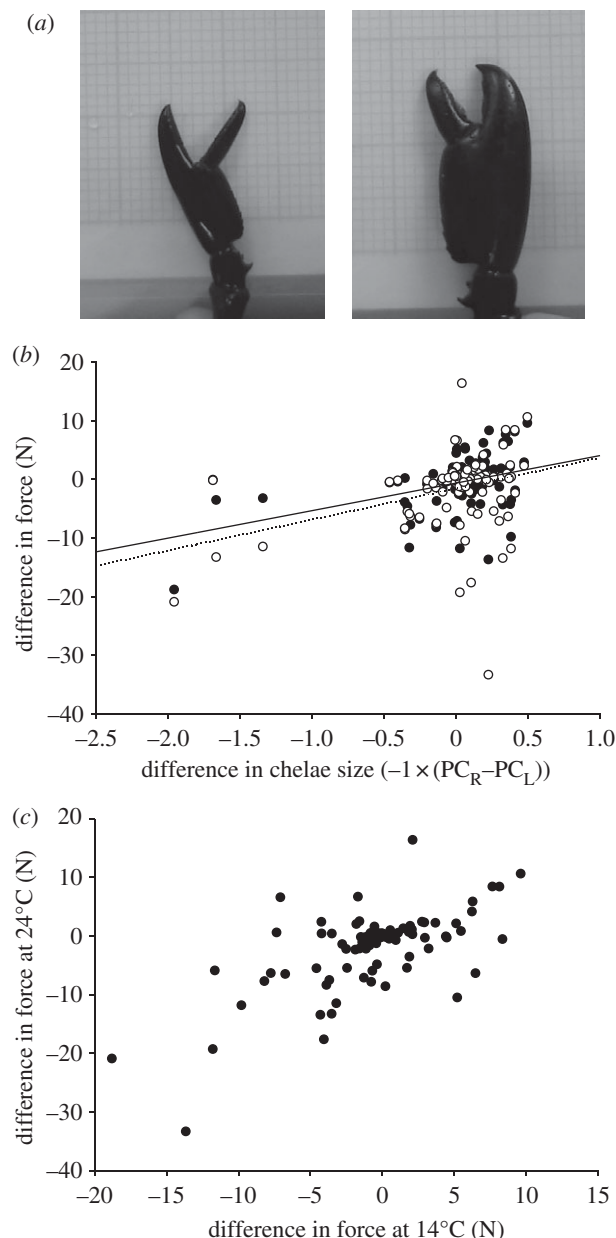


Figure 2. (a) Chelae of a male crayfish, illustrating extreme morphological asymmetry; the difference between principal component scores for this individual was 1.52. (b) The asymmetry of chela strength was weakly related to the asymmetry of chela size (14°C: d.f. = 1,95; $F = 14.60$, $p = 0.0002$, $r^2 = 0.16$; 24°C: d.f. = 1,95; $F = 8.10$, $p = 0.0054$, $r^2 = 0.11$). Asymmetry of size was the difference between the PC scores for the right and left chelae (PC_R and PC_L , respectively). Asymmetry of strength was the difference between the maximal forces generated by the right and left chelae. Filled and unfilled circles are data for 14° and 24°C, respectively. (c) The asymmetries of strength at 14°C and 24°C were positively correlated ($r^2 = 0.42$, $n = 97$, $p < 0.000001$).

4. DISCUSSION

Our analyses conclusively demonstrate unreliable signals in crayfish, a phenomenon previously suggested by Wilson *et al.* [15]. The tremendous variation in strength among chelae of similar size was highly repeatable between body temperatures. The widespread occurrence of unreliable signals in crayfish suggests one of two conditions: either crayfish receive great benefits by making deceptive chelae or crayfish incur great costs to identify deceitful opponents. Such conditions could occur when

individuals must regenerate a chela after injury, as documented in fiddler crabs (*Uca annulipes*) [18]. In this case, we should expect only the regenerated chela in a pair to be an unreliable signal of strength. Alternatively, unreliable signals could reflect a constraint imposed by the moulting process. Newly moulted individuals might be unable to generate a force proportional to the size of their appendages, as often occurs in species of stomatopods [19]. In which case, every crayfish would periodically possess a pair of relatively weak chelae. This latter mechanism could explain why a modest proportion of males within a population possess relatively weak chelae.

The existence of unreliable signals in a population enables, but does not guarantee cryptic asymmetry of performance. When the sizes of chelae poorly reflect their strength, asymmetry of performance cannot be accurately detected by asymmetry of size. Accordingly, crayfish exhibited large asymmetries of strength between chelae that were weakly related to asymmetries of size (figure 2). Asymmetries of strength were repeatable between two temperatures, suggesting that the pattern reflects a real difference in the capacity for performance between appendages. Given the asymmetric performance of chelae, moulting of the exoskeleton seems an unlikely origin for unreliable signalling in slender crayfish. Rather, processes during either juvenile or regenerative development could generate the poor relationship between the size and strength of chelae.

Cryptic asymmetry raises important questions about the ecology and evolution of aggression. Previous analyses have focused on either the properties of individual chelae or the average properties of paired chelae [15,20,21,22], ignoring the role of asymmetry in dominance. These analyses indicated that stronger individuals were more likely to win disputes that escalated into fighting. But what factor most determines dominance? Could a crayfish defeat an opponent with a single strong chela, such as fiddler crabs do, or does dominance require two chelae stronger than those of an opponent? How does asymmetry of strength affect tactics during combat? Cryptic asymmetry adds another dimension of uncertainty to aggressive encounters, because a crayfish cannot predict which chela poses the greater threat. At least initially, a crayfish facing an asymmetric opponent will be vulnerable to attack from a relatively strong chela. Such a chela can inflict serious injuries during fighting by tearing off an opponent's antenna, rostrum, or chela (R. S. Wilson 2012, personal observation). Because the majority of animals possess an exoskeleton, which effectively masks internal structures, cryptic asymmetry of performance could be a fairly common phenomenon. Future studies that focus on the benefits of cryptic asymmetry could shed new light on the evolution of unreliable signalling.

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