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SHORT COMMUNICATION

Metabolic incentives for dishonest signals of strength in the fiddler crab *Uca vomeris*

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ABSTRACT

To reduce the potential costs of combat, animals may rely upon signals to resolve territorial disputes. Signals also provide a means for individuals to appear better than they actually are, deceiving opponents and gaining access to resources that would otherwise be unattainable. However, other than resource gains, incentives for dishonest signalling remain unexplored. In this study, we tested the idea that unreliable signallers pay lower metabolic costs for their signals, and that energetic savings could represent an incentive for cheating. We focused on two-toned fiddler crabs (*Uca vomeris*), a species that frequently uses its enlarged claws as signals of dominance to opponents. Previously, we found that regenerated *U. vomeris* claws are often large but weak (i.e. unreliable). Here, we found that the original claws of male *U. vomeris* consumed 43% more oxygen than weaker, regenerated claws, suggesting that muscle quantity drives variation in metabolic costs. Therefore, it seems that metabolic savings could provide a powerful incentive for dishonesty within fiddler crabs.

KEY WORDS: Signal reliability, Strength, Performance, Metabolic rate

INTRODUCTION

Intra-specific combat is energetically expensive and can increase the risk of injury and death (Briffa and Sneddon, 2007). To reduce these potential costs animals often seek to resolve disputes without fighting by signalling intent, and using assessments of weapon size, body mass and/or aggressive displays (Bywater et al., 2008; Smith and Harper, 1995). Visual signals, and the intrinsic quality they represent, are used by receivers to assess the likelihood of combat success should physical confrontation ensue (Bradbury and Vehrencamp, 2011; Hughes, 2000). Reliance upon these signals provides an opportunity for individuals to deceive stronger opponents and elicit a submissive response by producing signals that do not accurately reflect their actual ability (Lailvaux et al., 2009). This enables poor quality or weaker individuals to gain access to resources that would not be otherwise obtainable, highlighting the benefit for producing unreliable signals. Still, there are likely to be other incentives encouraging animals to use deceptive strategies. Using the fiddler crab *Uca vomeris* McNeill 1920, we explored the possibility that producing unreliable signals of strength can also provide metabolic savings.

Many crustaceans, the fiddler crab included, use their greatly enlarged front claws as weapons to intimidate opponents during displays, and as a means of inflicting injuries during physical contests (Emlen, 2008). When individuals display their claws they are signalling their potential to inflict costly injuries upon their opponents (Arnott and Elwood, 2010). While most disputes are settled during the signalling stage, when contests escalate to physical contact the stronger animal generally prevails (Bywater et al., 2008; Walter et al., 2011; Wilson et al., 2007). Because the claw muscles of crustaceans – which underpin their fighting capacity – are cryptically concealed beneath an exoskeleton, it is difficult for competitors to accurately assess the strength of their opponents without physical contact. This allows for the potential decoupling of weapon size and underlying ability, enabling individuals to display large weaponry without necessarily having the strength to match their signals (Bywater and Wilson, 2012; Lailvaux et al., 2009). As such, unreliable signallers could gain access to resources by deceiving opponents, and may also save substantial energy by developing less muscle and by reducing the cost of its ongoing maintenance.

In this study, we compared the metabolic costs of reliable and unreliable signals of strength in the two-toned fiddler crab (*U. vomeris*), a species that is known to produce unreliable signals. When male *U. vomeris* lose their original (brachychelous) claw, they regenerate a replacement (leptochelous) claw that is an unreliable indicator of strength – the new claw is less robust, weaker, contains less muscle, and is less effective in combat (Lailvaux et al., 2009; McLain et al., 2010). Despite the disadvantages of a regenerated claw, male fiddler crabs are not able to visually distinguish between claw morphs and some leptochelous males are able to induce retreat from some stronger brachychelous males (Backwell et al., 2000; Lailvaux et al., 2009). We compared the metabolic costs of claw muscles for reliable and unreliable signallers in the fiddler crab (brachychelous versus leptochelous claw types).

RESULTS AND DISCUSSION

Our study found that investing in reliable high quality signals, which act as effective weapons during combat, is metabolically costly. Original brachychelous claws of male *U. vomeris* contained over 50% more muscle and consumed 43% more oxygen than the weaker leptochelous claws. Total claw size did not differ between original and regenerated claw types of *U. vomeris* (t=–0.65, d.f.=105, P=0.52; Fig. 1A,B); however, the relative muscle mass of regenerated claws was lower than that of original claws (t=–9.11, d.f.=105, P<0.0001). Whole-animal oxygen consumption did not differ between individuals bearing each claw type (t=0.20, d.f.=105, P=0.84). The rate of oxygen consumption per gram of claw muscle tissue was not significantly different between claw types (t=–0.44, d.f.=105, P=0.66; Fig. 1C); however, whole-claw oxygen consumption was significantly higher for males with original claws (t=–3.09, d.f.=105, P<0.01; Fig. 1D). As the maintenance of the muscle within the claw can represent a considerable metabolic cost, any reduction in muscle mass within the regenerated claws provides a substantial metabolic saving.

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Received 11 November 2013; Accepted 30 May 2014

The Journal of Experimental Biology

The Journal of Experimental Biology (2014) doi:10.1242/jeb.099390

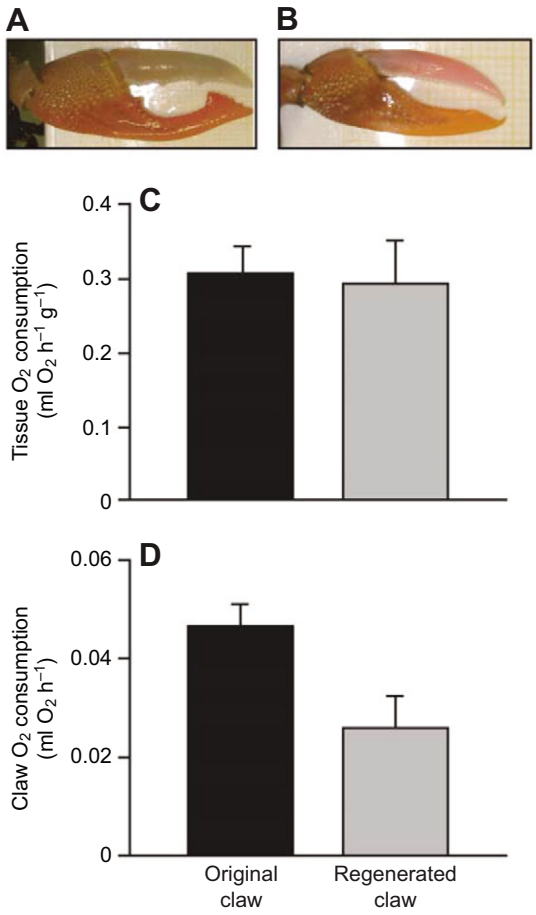

Fig. 1. Metabolic costs of claw muscle for male *Uca vomeris* with either an original or a regenerated claw. (A) Original and (B) regenerated major claw of male fiddler crab, *Uca vomeris*. (C) The average rate of oxygen consumption (ml O_2 h^{-1} g^{-1}) for claw muscle tissue was not significantly different between original (black) and regenerated claws (grey) (t=–0.44, d.f.=105, P=0.66). (D) The average rate of oxygen consumption (ml O_2 h^{-1}) for the whole claw was significantly higher in original (black) than regenerated claws (grey) (t=–3.09, d.f.=105, P<0.01).

The development of exaggerated reliable signals is governed, in part, by the costs incurred by the signaller (Smith and Harper, 2003), and our findings support one of the main assumptions of the handicap principle, which predicts that reliable signalling is costly. However, merely demonstrating that a signal is costly does not necessarily guarantee that a handicap is acting upon the signal (Lachmann et al., 2001; Számadó, 2011). One must separate the costs involved in ensuring the signal remains reliable (strategic costs) from those required to unambiguously communicate a message to a receiver (efficacy costs) (Grose, 2011; Számadó, 2011). For example, in the common nightingale, *Luscinia megarhynchos*, loud calling to females causes large reductions in body mass for males (Thomas, 2002). This was considered an efficacy cost, as males must call loudly in order to be heard above any background noise. However, the intricacy of the male nightingale's song and the patterns sung vary greatly among males and affect male fitness (Hughes et al., 2002). Whether the cost of learning songs should be considered strategic, or merely an additional efficacy cost, is dependent on the extent to which females respond to variation in song quality. Although it is these strategic costs that are expected to maintain reliability rather than efficacy costs, empirical studies rarely, if ever, attempt to separate their relative roles (Bergstrom and Lachmann, 1997; Grose, 2011; Lachmann et al., 2001; Smith and Harper, 2003; Számadó, 2011). In our study, we were able to quantify a strategic cost for signals of strength in the fiddler crab. As the reliability of the male signal (claw size) is governed by its correlation to the actual underlying strength of the weapon, the cost of maintaining claw muscle represents a strategic investment. To our knowledge, our study represents the first to quantify the metabolic strategic costs of reliable and unreliable signals of strength.

For the fiddler crab it seems that receivers cannot distinguish between reliable and unreliable signallers without actively engaging in physical contact (Backwell et al., 2000). Without escalation of contests, individuals with large but weak claws can drive some competitors to incorrectly withdraw from the dispute (Lailvaux et al., 2009). This means that individuals that employ this deceptive strategy (by producing large but weak claws) can successfully intimidate rivals into retreating on some occasions. Given the additional metabolic incentives for producing an unreliable signal of strength as quantified in our study, it is then intriguing that receivers do not ignore the signals completely and actively engage in combat. It is likely that the maintenance of this crustacean signalling system is driven by the costs imposed on individuals testing an opponent's strength.

We have demonstrated that investing in a reliable high quality signal, which in these species can also be an effective weapon during combat, is metabolically costly. As the metabolic expense is greatly reduced in individuals that produce unreliable signals, these represent clear strategic costs for reliably signalling fighting capacity to opponents. The prevalence of unreliable signals of strength within natural populations of fiddler crabs is thus unsurprising, given the substantial incentives for individuals to reduce investment in a metabolically expensive claw.

MATERIALS AND METHODS

We collected 125 male *Uca vomeris* (original claws: 85; regenerated claws: 40) from southeast Queensland. Individuals were housed at the University of Queensland in 40 l plastic containers with gravel and shelters, and maintained at 23±1°C (mean ± s.e.) in groups of 10 individuals. For each individual, we measured the aquatic rate of oxygen consumption as a proxy for whole-animal metabolic rate using closed-system respirometry (Lighton, 2008). We also measured tissue respiration rates of isolated muscle taken from the major claw.

Seven morphological measurements were recorded for the major claw as per Bywater and Wilson (Bywater and Wilson, 2012) and we conducted a principal components analysis to derive a single measurement of claw size. Body mass and carapace width, length and depth, and claw muscle mass were also measured for each individual. The claw type (original or regenerated) for each *U. vomeris* was identified using morphological and physiological features, as per Lailvaux et al. (Lailvaux et al., 2009).

Aquatic respiration was measured using a two-channel closed system, a dissolved oxygen electrode and associated oxygen meter and software. Individuals were placed in cylindrical glass chambers (147 ml) submerged in water baths at 24±1°C with a salinity of 27‰. Continuous mixing within the chambers was achieved by circulating water through the chambers in a closed loop at a constant flow rate using 5 mm Tygon tubing and a Masterflex peristaltic pump (model 77202-50, Cole-Parmer, USA). Dissolved oxygen content was measured using fibre-optic sensors (Ocean-Optics, FOXY-OR125-G, Lastek, Australia) connected to an oxygen meter (ThauTheta MFPF100-2, Lastek). Oxygen levels and temperature were simultaneously sampled every 2 s for 1 h. Respiratory control measurements of the water were taken regularly.

Whole major claws of each individual were removed and weighed (±0.002 g) before muscle tissue was extracted. Claw muscle tissue was dissected from the dactyl tendon and placed in an aerated marine crustacean Ringer's solution [525 mmol l^{-1} NaCl, 13.27 mmol l^{-1} KCl, 12.39 mmol l^{-1} $CaCl_2$, 24.78 mmol l^{-1} $MgCl_2$, H_2O, $NaHCO_3$ to pH 7 (Pantin, 1934)].

Measurements of muscle tissue oxygen consumption were made using optical-fluorescence-based oxygen respirometry at 25±1°C. Tissues were placed in 5 ml glass vials containing oxygen sensor spots (SP-PSt5-NAU-D5-YOP, PreSens). Vials were filled with aerated Ringer's solution and samples were suspended in a nylon mesh net within each vial to prevent the formation of a hypoxic boundary layer. Vials were then placed in a 24-channel Sensor Dish Reader 207 (PreSens SDR2 AS1, New Zealand) and oxygen levels were recorded every 2 min for at least 45 min. Control vials were added to each experimental run and all vials were stirred continuously using a platform shaker (Ratek, Australia).

The rate of oxygen consumption ($\dot{V}_{O_2}$; ml h^{-1}) for whole crabs and claw muscle tissues was calculated as per Alton et al. (Alton et al., 2007):

$$\dot{V}_{O_2} = -1 \times \left[\frac{(m_f - m_c)}{100} \right] \times V \beta_{O_2}, \quad (1)$$

where m_f is the slope derived from the whole animal or tissue (% air saturation h^{-1}), m_c is the slope derived from controls (% air saturation h^{-1}), V is the chamber volume (l) and β_{O_2} is the oxygen capacitance of the medium (ml l^{-1}). β_{O_2} for air-saturated seawater used in whole-animal calculations (27‰, 24°C) was 5.03 ml l^{-1}. β_{O_2} for air-saturated Ringer's solution for tissue calculations (35‰, 25°C) was 4.62 ml l^{-1}. The total rate of oxygen consumption for each whole claw was estimated from the product of total claw muscle mass and its oxygen consumption per gram.

All statistical analyses were performed using R (Version 2.12.2) or JMP (Version 8). Statistical significance was taken at the level of $P<0.05$. ANCOVAs and ANOVAs were used to compare the differences between claw types for rates of oxygen consumption.

Acknowledgements
We thank J. Heiniger, L. Alton, S. Cameron, G. David, A. Findsen and J. Andersen for field assistance and data collection, and C. Condon for statistical advice. We also thank three anonymous reviewers for their constructive feedback.

Competing interests
The authors declare no competing financial interests.

Author contributions
C.L.B., R.S.W. and C.R.W. conceived and designed the experiments, C.L.B. collected and analysed the data, and C.L.B., R.S.W. and C.R.W. wrote the manuscript.

Funding
This research received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

References

Alton, L. A., White, C. R. and Seymour, R. S. (2007). Effect of aerial O_2 partial pressure on bimodal gas exchange and air-breathing behaviour in *Trichogaster leeri*. *J. Exp. Biol.* **210**, 2311-2319.
Arnott, G. and Elwood, R. W. (2010). Signal residuals and hermit crab displays: flaunt it if you have it! *Anim. Behav.* **79**, 137-143.
Backwell, P. R. Y., Christy, J. H., Telford, S. R., Jennions, M. D. and Passmore, N. I. (2000). Dishonest signalling in a fiddler crab. *Proc. Biol. Sci.* **267**, 719-724.
Bergstrom, C. T. and Lachmann, M. (1997). Signalling among relatives. I. Is costly signalling too costly? *Philos. Trans. R. Soc. B* **352**, 609-617.
Bradbury, J. W. and Vehrencamp, S. L. (2011). *Principles of Animal Communication*. Sunderland, MA: Sinauer Associates, Inc.
Briffa, M. and Sneddon, L. U. (2007). Physiological constraints on contest behaviour. *Funct. Ecol.* **21**, 627-637.
Bywater, C. L. and Wilson, R. S. (2012). Is honesty the best policy? Testing signal reliability in fiddler crabs when receiver-dependent costs are high. *Funct. Ecol.* **26**, 804-811.
Bywater, C. L., Angilletta, M. J. and Wilson, R. S. (2008). Weapon size is a reliable indicator of strength and social dominance in female slender crayfish (*Cherax dispar*). *Funct. Ecol.* **22**, 311-316.
Emlen, D. J. (2008). The evolution of animal weapons. *Annu. Rev. Ecol. Evol. Syst.* **39**, 387-413.
Grose, J. (2011). Modelling and the fall and rise of the handicap principle. *Biol. Philos.* **26**, 677-696.
Hughes, M. (2000). Deception with honest signals: signal residuals and signal function in snapping shrimp. *Behav. Ecol.* **11**, 614-623.
Hughes, M., Hultsch, H. and Todt, D. (2002). Imitation and invention in song learning in nightingales (*Luscinia megarhynchos* B., Turdidae). *Ethology* **108**, 97-113.
Lachmann, M., Számadó, S. and Bergstrom, C. T. (2001). Cost and conflict in animal signals and human language. *Proc. Natl. Acad. Sci. USA* **98**, 13189-13194.
Lailvaux, S. P., Reaney, L. T. and Backwell, P. R. Y. (2009). Dishonest signalling of fighting ability and multiple performance traits in the fiddler crab *Uca mjoebergi*. *Funct. Ecol.* **23**, 359-366.
Lighton, J. R. B. (2008). *Measuring Metabolic Rates: A Manual for Scientists*. Oxford: Oxford University Press.
McLain, D. K., McBrayer, L. D., Pratt, A. E. and Moore, S. (2010). Performance capacity of fiddler crab males with regenerated versus original claws and success by claw type in territorial contests. *Ethol. Ecol. Evol.* **22**, 37-49.
Pantin, C. F. A. (1934). On the excitation of crustacean muscle. I. *J. Exp. Biol.* **11**, 11-27.
Smith, M. J. and Harper, D. G. C. (1995). Animal signals: models and terminology. *J. Theor. Biol.* **177**, 305-311.
Smith, M. J. and Harper, D. G. C. (2003). *Animal Signals*. New York, NY: Oxford University Press.
Számadó, S. (2011). The cost of honesty and the fallacy of the handicap principle. *Anim. Behav.* **81**, 3-10.
Thomas, R. J. (2002). The costs of singing in nightingales. *Anim. Behav.* **63**, 959-966.
Walter, G. M., van Uitregt, V. O. and Wilson, R. S. (2011). Social control of unreliable signals of strength in male but not female crayfish, *Cherax destructor*. *J. Exp. Biol.* **214**, 3294-3299.
Wilson, R. S., Angilletta, M. J., Jr, James, R. S., Navas, C. and Seebacher, F. (2007). Dishonest signals of strength in male slender crayfish (*Cherax dispar*) during agonistic encounters. *Am. Nat.* **170**, 284-291.