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# Combat in a cave-dwelling wētā (Orthoptera: Rhaphidophoridae) with exaggerated weaponry

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A R T I C L E I N F O

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Animals sometimes possess extraordinarily enlarged or specialized structures used as weaponry for intrasexual combat. The way in which an animal's mating system leads to the diversity of exaggerated armaments we see in nature is a matter of current and ongoing research. Central to this enquiry is the question of how animal weapons are involved in assessment: how, when and why is the decision made to retreat from a contest by combatants fighting over their future fertilization success? We investigated the agonistic role of highly elongated male hindlegs in an Orthopteran insect found in dense aggregations in New Zealand caves: the cave wētā, *Pachyrhamma waitomoensis* (Rhaphidophoridae). We found a large degree of sexual dimorphism in the hindlegs. In contests among males in the field, males with longer hindlegs were more likely to win contests, while body size did not influence contest outcome. We also assessed the influence of winner, loser and relative hindleg length on contest escalation, finding that fights among males with greater differences in leg length were resolved by less-escalated contests. In addition, the level of contest escalation was positively correlated with the loser's, but not the winner's, leg length, matching the predictions of self-only models of animal assessment.

The exaggeration of male morphology driven by competition and combat has interested evolutionary biologists since Darwin (1871). Sexual selection is recognized as a key driver of morphological trait exaggeration (Lavine, Gotoh, Brent, Dworkin, & Emlen, 2015), and this selection can be driven by female mate choice, in the case of ornaments, or direct male competition, in the case of weapons. However, most research has focused on the drivers behind ornamentation rather than weaponry (Emlen, 2008; McCullough, Miller, & Emlen, 2016). Weapons can be modifications of almost every type of appendage or completely new structures adapted specifically to fighting (Emlen, 2008). For example, *Cyrtodiopsis* sp. stalk-eyed flies defend aggregation sites from other males in fights with their elongated eye stalks (Wilkinson & Dodson, 1997) and European earwig, *Forficula auricularia*, males fight using forceps formed from extremely enlarged cerci (Kamimura, 2014). Pseudoscorpions wield pincers adapted from pedipalps (Zeh, 1987) and narwhals, *Monodon monoceros*, fight with tusks developed from an elongated canine tooth (Kelley, Stewart, Yurkowski, Ryan, & Ferguson, 2015). Ungulate mammals bear enormous horns and antlers (Emlen, 2008), various decapod crustaceans have huge claws developed from oversized chelipeds (e.g. fiddler crabs, Sneddon, Huntingford, & Taylor, 1997), and some salmonid fish (e.g. sockeye salmon, *Oncorhynchus nerka*) have elongated jaws used in intermale combat (Quinn & Foote, 1994). In addition, some insects such as frog-legged leaf beetles, *Sagra femorata*, and leaf-footed bugs, *Mictis longicornis*, use exaggerated hindlegs in male–male combat (Emberts, Miller, Li, Hwang, & Mary, 2017; O'Brien, Katsuki, & Emlen, 2017).

Many of the animal weapons that have been investigated in detail display positive allometry in the scaling relationship between their magnitude and the size of their bearers (Berns, 2013; Emlen & Nijhout, 2000; Gould, 1966; Kodric-Brown, Sibly, & Brown, 2006; but see; Bonduriansky, 2007). Departures from a 1:1 relationship (isometry) are thought to commonly result from selection on reaction norms between condition of the animal and the development of the trait, which often means that larger individuals end up carrying far larger weaponry than their smaller rivals (Cassidy, Bath, Chenoweth, & Bonduriansky, 2014; Emlen & Nijhout, 2000; O'Brien et al., 2017). However, the importance of allometry in indicating the action of sexual selection on exaggerated traits and the mechanisms of their development are matters of ongoing debate (Berns, 2013; Bonduriansky, 2001, 2007; Bonduriansky & Day, 2003; Cassidy et al., 2014).

Understanding the evolution of animal weaponry is intrinsically linked to our understanding of animal contests. Animals engaging

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in fights must make decisions about how long to persist, how much damage to endure, how much energy to expend, and when to initiate, escalate or retreat from combat (Kokko, 2013). Since the 1970s the decisions made by fighting animals have been best understood in terms of game theory: the rules governing optimal choices in the presence of other decision makers or ‘optimizing agents’ (Maynard Smith, 1976, 1982; Maynard Smith & Price, 1973;). The application of models derived from game theory helped to resolve the long-standing evolutionary question of why animals should show restraint in contests: through negative frequency-dependent selection (Huxley, 1966; Maynard Smith & Parker, 1976).

Elwood and Arnott (2012) outlined four main game-theoretical models which describe different ways that simple agents may make the apparently complex decisions involved in animal contests: the hawk/dove game, the pure self-assessment model, the cumulative assessment model and the sequential assessment model. Central to the latter three of these models is the concept of assessment: the gathering and use of information that is required to make decisions (Kokko, 2013). Under the pure self-assessment and cumulative assessment models, the source of this information is considered to be entirely endogenous (Elwood & Arnott, 2013). More complexity is added by the possibility that animals can assess their opponents (simple mutual assessment and sequential assessment), and more still if we predict that they combine this with information about themselves (‘complex mutual assessment’) to reach a conclusion about which has greater fighting ability or resource-holding potential (RHP). The latter mutual assessment models ascribe more information-processing ability to the animals involved and thus it has been proposed that we should begin by invoking the simpler, self-only assessment models unless evidence mounts to suggest otherwise (Briffa & Elwood, 2009; Elwood & Arnott, 2013; Taylor & Elwood, 2003). In addition, measures of correlation between RHP difference and contest cost (e.g. escalation, intensity or duration) alone cannot be taken as evidence of mutual assessment. This is because apparent effects of RHP difference may appear when the weaker rival's decision to retreat is based entirely on assessment of its own RHP or accrued damage (Briffa et al., 2013; Taylor & Elwood, 2003).

The need to test carefully for mutual assessment rather than assume that it occurs has been reiterated in recent years by studies demonstrating more and more examples of animals appearing to rely on pure self-assessment (Brandt & Swallow, 2009; Bridge, Elwood, & Dick, 2000; Copeland, Levay, Sivaraman, Beebe-Fugloni, & Earley, 2011; Elias, Kasumovic, Punzalan, Andrade, & Mason, 2008; Elwood & Prenter, 2013; Jennings, Gammell, Carlin, & Hayden, 2004; Kasumovic, Mason, Andrade, & Elias, 2010; Kelly, 2006; McGinley, Prenter, & Taylor, 2015; Moore, Obbard, Reuter, West, & Cook, 2008; Morrell, Backwell, & Metcalfe, 2005; Prenter, Elwood, & Taylor, 2006; Stuart-Fox, 2006; Taylor, Hasson, & Clark, 2001; Tsai, Barrows, & Weiss, 2014). Nevertheless, the extent to which animals gather and use information about themselves and/or their opponents is a matter of ongoing inquiry, with individuals of some species matching the predictions of each major assessment model (Stuart-Fox, 2006; Taylor & Elwood, 2003). For example *Diastatops obscura* dragonfly males appear to use mutual assessment (Junior & Peixoto, 2013), *Gryllus bimaculatus* crickets show evidence for cumulative assessment (Rillich, Schildberger, & Stevenson, 2007), *Calopteryx maculata* damselflies conform to an energetic war of attrition (Marden & Waage, 1990) and *Lasiorhynchus barbicornis* giraffe weevils use sequential assessment (Painting & Holwell, 2014). Others are found not to match the predictions of any common model formulation (e.g. Jennings, Gammell, Payne, & Hayden, 2005; Reichert & Gerhardt, 2011; Stuart-Fox, 2006).

Among the Orthoptera (crickets, grasshoppers, locusts, katydids and wētā), males exhibit diverse weaponry: enlarged mandibles (Kelly, 2006), heads (Judge & Bonanno, 2008), horns (Kim, Jang, & Choe, 2011) and, in some species, hindlegs (Conroy & Gray, 2015). Members of the order, especially grylline crickets, have also been used as model systems for studying combat. Here, we report on the fighting behaviour and weaponry displayed by a species not previously known to possess either: the large New Zealand cave wētā, *Pachyrhamma waitomoensis* (Rhaphidophoridae). We set out to test the predictions that: (1) the hindlegs of males will show a positively allometric scaling relationship with body size; (2) the extremely long legs of males function as weaponry in combat; and (3) leg length will correlate with measures of contest outcome and escalation. We also set out to compare the relationships between contest winner's and loser's weaponry and contest escalation with the predictions of differing assessment models, to determine which forms of assessment *P. waitomoensis* males are most likely to be using.

## METHODS

### *Study Organism*

*Pachyrhamma waitomoensis* are omnivorous, nocturnal insects which forage in forests at night and retreat during daylight into dense aggregations within limestone karst caves in the Waitomo district of New Zealand. They possess enormously long legs and antennae, summing to a total length from hind tarsus to antenna tip of over 350 mm in males, despite having actual body lengths of only 30–35 mm (M. Fea & G. Holwell, personal observation, see Fig. 1). The extreme development of the antennae is no mystery considering the dark caves they inhabit, leading them to rely on touch and chemoreception to navigate, but why the hindlegs should be similarly elongated is not as obvious. Long legs are a common feature of cavernicolous animals (Lavoie, Helf, & Poulson, 2007), but in the case of *P. waitomoensis*, they are also sexually dimorphic (Fig. 2), suggesting that sexual selection may have driven the extreme leg length of males.

*Pachyrhamma waitomoensis* appear to have a convenience polyandry mating system, with pairs forming and reforming continually throughout the daylight hours which they spend in caves (M. Fea & G. Holwell, personal observation). While paired, the wētā mate many times, with the length of association seeming to dictate the number of copulations a male can achieve with any one female. In the field, we found that males often disrupt the mating of others, resulting in fights between them in many cases. Unpaired

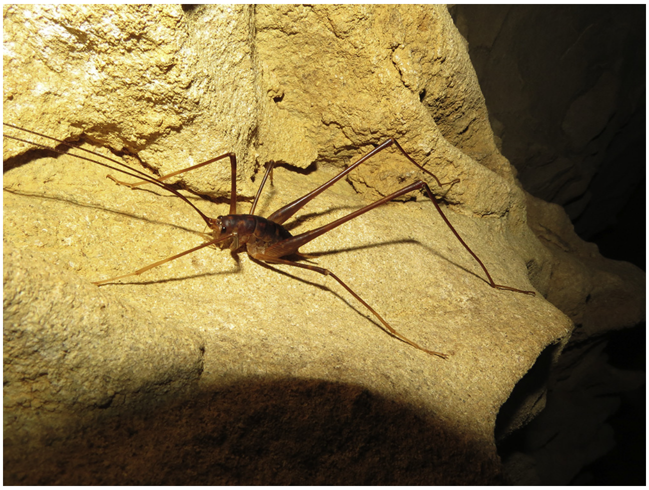

**Figure 1.** Adult male *P. waitomoensis* on a cave wall.