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

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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.

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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’ ability to assess themselves (simple mutual assessment and sequential assessment), and more still if we predict that they combine this with information about others of their species matching the predictions of each major assessment model (Kokko, 2013). Nevertheless, it is still if we predict that they combine this with information about other agents of the population 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, & Poulsom, 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.

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, & Poulsom, 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.

Data collection

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 weta 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.](image-url)
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