



Effect of an immune challenge on the functional performance of male weaponry



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ABSTRACT

Theories of parasite-mediated sexual selection predict a positive association between immune function and the expression of sexually selected ornaments. Few studies, however, have investigated how an immune challenge affects the performance of sexually selected weaponry. Male Wellington tree weta (*Hemideina crassidens*) (Orthoptera: Anostomatidae) possess enlarged mandibles that are used as weapons in fights for access to females residing in tree galleries. Intense sexual competition appears to have favoured the evolution of alternative male mating strategies in this species as males have a trimorphic phenotype in which weapon size varies across morphotype: 8th instar males have the smallest jaws, 10th instar males have the largest and 9th instar males being intermediate to the other two. After injecting males and females with either lipopolysaccharide (LPS; immune challenge) or saline (control) I measured over a 24 h period each weta's body mass to assess whether they responded immunologically to the LPS and their bite force to assess the functional performance of their jaws. Both sexes responded immunologically to the immune-challenge as LPS-injected individuals lost significantly more body mass than saline-injected controls with females losing more mass than males. Female bite force was significantly reduced 8 h after LPS-injection whereas male bite force did not significantly decline. Both sexes regained pre-injection functional performance of their jaws 24 h after the immune challenge. My results suggest that females trade-off bite force for immune function whereas males do not.

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1. Introduction

Mounting an immune response imposes a significant drain on an individual's pool of resources and energy. Optimal allocation of resources to immunity thus requires individuals to trade off the costs of immune function with those of other critical fitness components (Schmid-Hempel, 2011; Sheldon and Verhulst, 1996; Sorci et al., 2009). The predicted pattern of association between fitness-related traits among individuals, however, is less straightforward as associations can be either negative or positive (Jacobs and Zuk, 2011). Negative associations (i.e. trade-offs) arise when individuals vary more in how they allocate resources to various functions than in their ability to acquire resources (Reznick et al., 2000; van Noordwijk and de Jong, 1986). Immune system activation negatively affects a variety of fitness-related traits including fecundity

(Ahmed et al., 2002; Fevrier et al., 2009; Kelly, 2011; Rolff, 1999), male ejaculates (spermatophore size Kerr et al., 2010; sperm viability Simmons, 2012), and parental care (Bonneau et al., 2003; Raberg et al., 2000). Conversely, positive associations arise between fitness-related traits when individuals vary more in their ability to acquire resources than in how they allocate those resources (Reznick et al., 2000; van Noordwijk and de Jong, 1986). This scenario underlies theories of parasite-mediated sexual selection, which predict that only males with sufficient resources (i.e. in good condition) can invest in costly sexually selected traits while maintaining an effective immune system. Indeed, several empirical studies have shown that male sexual signals positively covary with some aspect of the immune system (e.g. Ahtiainen et al., 2004; Gilman et al., 2007; Griggio et al., 2010; Jacot et al., 2004; Kurtz and Sauer, 1999; Mougeot and Redpath, 2004; Munoz et al., 2010; Peters et al., 2004; Rantala et al., 2002, 2000; Rantala and Kortet, 2003; Ryder and Siva-Jothy, 2000; Simmons et al., 2005; Siva-Jothy, 2000).

Considerably more attention has been paid to the effects of immune challenges on sexually-selected traits involved in female mate choice versus those involved in male-male competition.

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Consequently, we have poorer knowledge of whether theories of parasite-mediated sexual selection apply to traits used in male-male combat compared with traits used in female mate choice. A handful of studies suggest that they do given that some immune parameters function better in dominant males than in subordinates (Ahtiainen et al., 2006; Rantala and Kortet, 2004; Steiger et al., 2012; Vaananen et al., 2006) and that immune challenges can prevent males from becoming behaviourally dominant (Freeland, 1981).

Males in many animal species compete against rival males for access to females by using weaponry (Emlen, 2008; Kelly, 2008a). Weapons can be costly to produce – as their development trades-off with other fitness-related traits (Emlen, 2001; Simmons and Emlen, 2006) such as immunity (Demuth et al., 2012) – and costly to transport (Allen and Levinton, 2007; Lailvaux et al., 2005). Such costs suggest that only high-condition males can obtain sufficient resources during development to permit investment in weaponry while maintaining an effective immune response. Therefore, a positive relationship is expected between weapon size and immune function and indeed this prediction is supported in the horned beetle *Euoniticellus intermedius* (Pomfret and Knell, 2006; see also Kelly and Jennions, 2009). Rantala et al. (2007), however, found that immune function is not correlated with the length of male forceps, a putative weapon, in the earwig *Forficula auricularia* but the role that forceps play in male fitness is unclear (Forslund, 2000).

Weaponry can also impose costs in addition to those associated with building and carrying the structure. For example, males in many animal species use mandibles, claws or forceps to grasp and exert pressure (i.e. bite force) on the opposing structures of their rivals. Operating such structures requires energy and resources, which should be costly to other fitness-related traits, such as immunity. Moreover, because larger weaponry exert greater bite forces (Husak et al., 2009; Huyghe et al., 2009a; Taylor, 2001) they likely require more resources. Again, theories of parasite-mediated sexual selection predict that males with larger weaponry (i.e. high-condition males) should better maintain the performance of their weapons in the face of an immune challenge than males with smaller weaponry.

We know very little about how an immune challenge affects the functional performance of male weaponry (Irschick et al., 2007; Lappin et al., 2006). Here, I perform a functional test of the hypothesis that males able to invest in larger weaponry also maintain weapon performance after an immune challenge because they are able to allocate more resources to immune function than males with smaller weaponry. I test this hypothesis using the Wellington tree weta, *Hemideina crassidens* (Orthoptera: Anostostomatidae), an orthopteran insect that is endemic to New Zealand. This large (approx. 70 mm body length), flightless, and nocturnal insect (Gibbs, 2001) is sexually dimorphic (Field and Deans, 2001; Kelly, 2005a; Kelly and Adams, 2010), with males displaying highly exaggerated, positively allometric mandibles (Kelly, 2005a; Kelly and Adams, 2010). Males use their mandibles as weapons in contests for access to females residing in tree cavities (hereafter galleries) (Kelly, 2006a). By contrast, female tree weta have significantly smaller jaws and do not fight. Male weaponry varies considerably in size among individuals (Kelly, 2005a; Kelly and Adams, 2010) apparently due to precocial male maturation: males can mature at either the 8th, 9th, or 10th instar, whereas females mature at the 10th instar only (Spencer, 1995). Male jaw length is positively correlated with ultimate instar number with 8th instar males having the smallest heads, 10th instar males having the largest heads and 9th instar males being intermediate in size to the other two adult instars (Kelly and Adams, 2010; Spencer, 1995).

The fitness of 10th instar males is tied to their ability to control access to groups of females, which depends on their ability to defeat rivals in contests (Kelly, 2008b, 2006b, 2005a). During escalated male-male contests over access to females, rivals face each other,

interlock their jaws, and wrestle until one combatant is thrown from the tree. Males with larger jaws are typically the winners (Kelly, 2006a). On the other hand, 8th instar males rarely engage in escalated fights or defend large harems in the wild (Kelly, 2008b, 2005a) and may thus represent a sneaker strategy in which they surreptitiously enter a gallery defended by a 10th instar male and copulate with the females therein (Kelly, 2008b; Spencer, 1995). Moreover, smaller males might be adapted to gain access to galleries with small entrance holes that are off-limits to 10th instar males (Kelly, 2008b, 2006c; Kelly and Adams, 2010). Ninth instar males appear to represent a mating strategy that is intermediate to the other morphs whereby they will engage in fights with rivals for access to females but might also sneak into harems guarded by 10th instar males.

I hypothesize that in *H. crassidens* the ability to acquire resources for fitness-related traits is positively related to instar number (i.e. weapon size). This hypothesis predicts that 10th instar males will have more resources to allocate to immunity and to the functional performance of their jaws than either 9th or 8th instar males. Thus, the loss of bite force after an immune challenge should be inversely related to male morphotype; that is, 8th instar males should suffer a greater reduction in their bite force compared with 9th instar males which, in turn, should suffer a greater reduction than 10th instar males. I also predict that because female fitness is likely not dependent on the performance of their jaws (at least in the short term), they should allocate resources to immunity rather than mandible performance and thus exhibit a significant decline in bite force after an immune challenge.

2. Methods

Adult male and female *H. crassidens* were field-collected from a single population (Maud Island) and placed in individual cages (100 × 40 × 50 cm³) provisioned with apple slices ad libitum. Apple slices provide *H. crassidens* with water, as these insects do not ‘drink’ from the cotton-plugged water vials typically used in studies on orthopterans. Apple slices comprise mostly carbohydrate and very little lipid and protein. Care was taken to collect tree weta of overall excellent general health, free of ectoparasites (Kelly, 2005b), and without missing body parts (Kelly, 2006c). Tree weta were kept in their cages for three days to standardized recent experience, diet, oviposition behaviour, and mating history.

Males and females were randomly assigned to either a control (saline-injected) or an experimental (lipopolysaccharide, LPS) treatment. LPS is a non-pathogenic and non-living elicitor that stimulates several pathways in the immune system of insects (Ahmed et al., 2002; Moret and Schmid-Hempel, 2000), including orthopterans (e.g. Adamo, 1999; Fedorka and Mousseau, 2007; Jacot et al., 2004; Kelly, 2011; Kelly et al., 2014; Leman et al., 2009; Shoemaker and Adamo, 2007), without infecting the subject. LPS manipulates immunocompetence in contrast to assays that measure its function (e.g. lysozyme-like assay, phenoloxidase assay, etc.) and is known to affect the expression and function of sexually-selected traits in a variety of animal taxa (e.g. Fedorka and Mousseau, 2007; Jacot et al., 2005a; Leman et al., 2009; López et al., 2009; Munoz et al., 2010).

Fighting an immune challenge generally causes a loss of body mass in animals (e.g. Bize et al., 2010; Bonneaud et al., 2003; Hanssen, 2006; Jacot et al., 2004; Lifjeld et al., 2002; Moreno-Rueda, 2011; Ots et al., 2001). Therefore, I measured each weta’s fresh body mass to the nearest 0.001 g (Fisher Scientific SLF103 field balance) before (time = 0 h) and after (time = 24 h) injection of either lipopolysaccharide (LPS) or saline to confirm that my experimental

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