

Sexual Selection, Ontogenetic Acceleration, and Hypermorphosis Generates Male Trimorphism in Wellington Tree Weta

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Abstract Strong sex-specific selection on traits common to both sexes typically results in sexual dimorphism. Here we find that Wellington tree weta (*Hemideina crassidens*) are sexually dimorphic in both head shape and size due to differential selection pressures on the sexes: males use their heads in male-male combat and feeding whereas females use theirs for feeding only. Remarkably, the sexes share a common ontogenetic trajectory with respect to head growth. Male head shape allometry is an extension of the female's trajectory despite maturing two instars earlier, a feat achieved through ontogenetic acceleration and hypermorphosis. Strong sexual selection also favours the evolution of alternative reproductive strategies in which some males produce morphologically different weapons. Wild-caught male *H. crassidens* are trimorphic with regard to weapon size, a rare phenomenon in nature, and weapon shape is related to each morph's putative mating strategy.

Keywords Morphometrics · Sexual selection · Weaponry · Shape · Allometry · Sexually dimorphism

Introduction

Some of the most impressive examples of sexual dimorphism in nature involve the evolution of weaponry in males (Andersson 1994; Emlen 2008). Male armaments have evolved in a variety of animal clades (Emlen 2008) and

tend to evolve when females—or the resources they require for breeding—are spatially clumped and can be monopolized by males (Emlen and Oring 1977). Males found in resource- or female-defence mating systems benefit by possessing larger or more exaggerated weaponry because this enables them to better control access to females and thus accrue greater reproductive success (Kelly 2008b). Additionally, in such systems it is not uncommon for a subset of males to reduce their investment in weaponry, or forgo its production altogether, and pursue an alternative strategy for securing mates (e.g. sneaking) (Oliveira et al. 2008).

Although increased male armament is generally favored by selection due to their benefit in acquiring mates, like most sexually selected traits, this is counterbalanced by viability selection (Andersson 1994; Oufiero and Garland 2007). Indeed, exaggerated weaponry can increase predation risk via reduced locomotory performance (sensu Oufiero and Garland 2007; but see Allen and Levinton 2007) or by hindering access to refugia during predatory attacks (e.g. Lappin et al. 2006). Sexual selection for increased fighting performance may also compromise other activities, if the same trait is utilized in multiple functions. This is seen, for example, in male mandibles and other mouthparts in beetles and ants, which are used both as weapons and in foraging (Emlen 2008). Interestingly, antagonistic selection pressures on the same structure may also influence the size-shape relationship of these traits, thereby altering patterns of intraspecific allometry exhibited by males and females. However, while sexual dimorphism has been examined in a wide variety of taxa (Fairbairn 1990; Blanckenhorn 2005; Emlen 2008), the intraspecific allometry trajectories that generate sexually-dimorphic traits are less well understood (Fairbairn and Preziosi 1994; Fairbairn 1997).

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The Wellington tree weta, *H. crassidens* (Orthoptera: Tettigonioidae: Anostostomatidae) offers a unique example to examine how selection optimizes a structure experiencing several conflicting demands, namely feeding, fighting and avoiding predators. This large (> 6.5 cm body length), flightless, and nocturnal insect (Gibbs 2001) is sexually dimorphic (Field and Deans 2001), with males displaying highly exaggerated, positively allometric mandibles (Kelly 2005a). These mandibles are used as weapons in contests for access to females residing in tree cavities (hereafter galleries) (Kelly 2006a). By contrast, female tree weta have significantly smaller heads as compared to males, and do not fight. Male weaponry varies considerably in length among individuals (Kelly 2005a) 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 to the other two adult instars (Spencer 1995). Smaller males rarely defend large harems in the wild; in fact, these 8th instar males may represent a sneaker strategy in which they surreptitiously enter a gallery defended by a 10th instar male and copulate with the females therein (Spencer 1995; Kelly 2008a). Moreover, smaller males may be adapted to gain access to galleries with small entrance holes that are off-limits to 10th instar males (Kelly 2006b, 2008a). During contests, males assess each other's combative ability by comparing mandible size in a face-to-face match-up of flared jaws; if an opponent's mandibles are detected on the outside of the jaws, the male concludes the rival is larger and withdraws from the contest (Kelly 2006a). Selection should therefore favour increasing gape width in males, which can be achieved either by widening the head capsule or elongating the jaws. In addition, not only do males enter galleries to extract rivals and acquire mates but, as with females, they also seek diurnal refuge from predators in galleries (Gibbs 2001). Because males must fit through narrow entrance holes to access galleries as well as use their jaws for feeding, sexual selection cannot enlarge the head indiscriminately without facing viability costs.

Here, we test several related hypotheses to explain the evolution of head shape differences between the sexes and among male morphotypes in Wellington tree weta. First, we hypothesize that sexual selection will generate a trimodal distribution in head length in wild-caught animals, because male tree weta mature at one of three instars. Second, because the mandibles are a target of sexual selection in males only, tree weta should exhibit significant sexual dimorphism in head shape. We use the female's morphology as a reference to assess sexual selection's

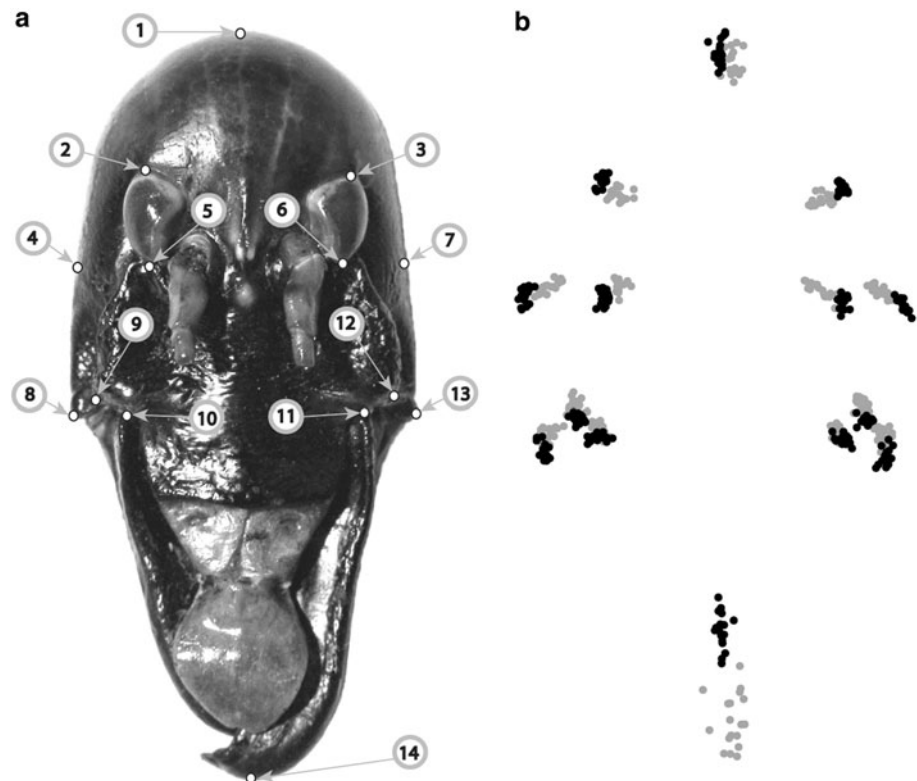
effect on male morphology because female trait values are generally assumed to lie near the optimum set by natural selection (Lande 1980). Third, because male tree weta must fit through gallery entrance-holes while also maximizing their gape width, we hypothesize that selection will generate distinct allometry patterns between males and females, where heads become more elongated and narrower in males as head size increases, but not in females. Finally, if alternative phenotypes vary in their investment in weaponry, then the three male morphs should differ in head shape in addition to length. We therefore predict that 10th instar males will have larger and more elongated heads compared to 8th instar individuals.

Methods

Adult tree weta were opportunistically collected from vegetation in the field at night on Maud Island, NZ (41°02' S, 173°54' E) during April–May in 2001–2004, 2006–2007 and 2009 (see Kelly 2005b for details). Digital calipers (Mitutoyo Digimatic) were used to measure each adult ($n = 854$ males and 480 females) to the nearest 0.05 mm for left and right hind femur length and total head length (top of head capsule to tip of left mandible; see Fig. 1a).

We performed a number of tests to determine whether the distribution of male head sizes in the wild was comprised of three male morphotypes. First, we tested whether head length distributions in male and female tree weta departed from normality using the Shapiro-Wilks test (Zar 1999). If the males comprised multiple morphotypes, it is predicted that their distribution would be non-normally distributed. Next, we used a maximum-likelihood analysis of mixture models, which modeled the distribution of male head size as a function of multiple normal distributions (see McLachlan and Basford 1988 for detailed explanation of likelihood analyses of mixture models). We evaluated several distinct models where males were classified as belonging to one of several morphotypes. Importantly, because laboratory-reared male *H. crassidens* exhibit a trimodal head size distribution as a consequence of maturing at one of three instars (8th, 9th or 10th) and instar number is positively related to head size (Spencer 1995), we predicted that wild-caught individuals would also exhibit a trimodal distribution in head size. To test this prediction, we first generated a bimodal model containing distributions corresponding to two male morphotypes, for which the log likelihood and AIC of this model were determined. Next, we obtained a trimodal model, and again obtained the model log likelihood and AIC. Bimodal and trimodal models were compared using the likelihood ratio

Fig. 1 **a** Positions of the 14 landmarks used to characterize head shape in tree weta. These landmarks include: 1 coronal suture at top of vertex; 2 and 3 top of eye; 4 and 7 top of gena; 5 and 6 bottom of eye; 8 and 13 pleurostoma; 9 and 12 subocular ridge; 10 and 11 anterior mandibular articulation; 14 tip of left mandible. **b** Scatter plot of all 36 landmark configurations after generalized Procrustes superimposition (males grey; females black)



test between the more complex model and the simpler model ($LRT = -2(\ln(L_1/L_2))$); which is asymptotically distributed as χ^2). However, because the two models differed in their component distributions (two vs. three distributions), they were not guaranteed to be nested models. We therefore additionally used AIC to compare the relative support for each model: the lower AIC provided stronger support for its corresponding model. Additionally, we compared the best-fitting model above to both a monomodal model and a model with four modes, to test the robustness of the signal obtained from the biologically-derived multi-modal models. Finally, male morph distributions were analysed for each year separately, and the frequency of morphs among years was statistically compared using as χ^2 . Maximum likelihood analyses and model selection were conducted using ‘mixtools’ (Benaglia et al. 2009) in R 2.9.1 (R Development Core Team 2009).

To examine patterns of head shape variation we used geometric morphometric methods (Bookstein 1991; Rohlf and Marcus 1993; Adams et al. 2004; Zelditch et al. 2004). These approaches quantify the shape of anatomical objects using a set of homologous landmark locations, while mathematically holding the effects of non-shape variation constant. First we digitized fourteen landmarks on the head of a subset of males ($n = 18$) and females ($n = 18$) from the trimorphism analysis (Fig. 1a). This was accomplished by digitizing landmarks from digital images imported

into R 2.9.1 (R Development Core Team 2009). Next, we optimally aligned the landmark configurations for each specimen using a generalized Procrustes superimposition (Rohlf and Slice 1990), and treated the resulting Procrustes tangent coordinates as a set of shape variables for subsequent multivariate statistical analysis (e.g. Bookstein et al. 1999; Mitteroecker et al. 2004; Mitteroecker and Bookstein 2008) (Fig. 1b). The centroid size of each specimen was also retained for further analysis. All morphometric analyses were performed in R 2.9.1 (R Development Core Team 2009) using routines written by Claude (2008) and by the authors.

To test the hypothesis that sexual selection generates sexual dimorphism in head morphology, we used analysis of variance (ANOVA) to compare head sizes (centroid size) between males and females. In addition, we used permutational MANOVA with 1,000 iterations (Anderson 2001) to determine whether significant sexual shape dimorphism was exhibited. Because shape frequently covaries with size, we included size as a covariate in this model. Analyses of shape versus size using permutational MANOVA were also performed for each sex separately. In addition, we performed a permutational MANOVA to test the hypothesis that the three male morphs differed in head shape. In each of these cases, permutational MANOVA was utilized because the number of variables was similar to, or exceeded the number of specimens. Finally,

statistical patterns of head shape variation were visualized in the space of principal components (e.g., Berner et al. 2008; Adams and Collyer 2009; Adams 2010), and the allometric relationship between head size and head shape (PC1) was also visually inspected (e.g., Adams and Nistri 2010). Thin-plate spline deformation grids of the average female and average for each male morph were generated to facilitate biological interpretation of shape differences. All statistical and graphical analyses were performed in R 2.9.1 (R Development Core Team 2009).

Results

Trimorphic Head Size

The distribution of head lengths was significantly non-normal in males ($W = 0.96$, $P < 0.0001$) but not in females ($W = 0.99$, $P = 0.10$; Fig. 2), thus supporting the hypothesis that males displayed a multimodal distribution. In males, a likelihood ratio test revealed that a trimorphic model was a significantly better fit than was a dimorphic model ($\log(L_3) = -2391.694$; $\log(L_2) = -2395.963$; $LRT = 8.538$; $P = 0.0035$), a result confirmed by AIC scores ($AIC_3 = 4797.39$; $AIC_2 = 4801.93$; $\Delta AIC = 4.54$). Further, a trimorphic model provided a significantly better fit than a monomorphic model ($\log(L_1) = -2395.963$; $LRT = 8.538$; $P = 0.0035$), and the four-mode model did not provide a superior fit when compared to the trimorphic model ($\log(L_4) = -2390.712$; $LRT = 1.963$; $P = 0.1612$). Thus, a trimorphic model best explained the distribution of male head sizes. By contrast, a single distribution was better supported in females as compared to a bimodal distribution ($AIC_1 = 1256.00$; $AIC_2 = 1258.74$) (Fig. 3). The mean (\pm SD) head length for each of the three male morphotypes (Fig. 2) were similar to those reported previously (Kelly 2005a). As there is no method available to objectively identify the instar at which a male matures, we follow Spencer (1995) and assume that the smallest head size distribution mode represents 8th instar males, the largest head size mode represents 10th instar males and the intermediate head size mode represents 9th instar males. When examined within years, we found that all three male morphs were produced in each of the study's seven years (Appendix Fig. 6; Table 1). However, while the relative frequency of each male morph differed somewhat among years, this difference was not significant ($\chi^2 = 12.7512$, $df = 12$, $P = 0.3874$), with some years displaying relatively more small morphs and other years displaying relatively more large morphs (Table 1). Therefore, while some variation in the production of male morphs among years is present, there is temporal consistency in the relative proportion of each male morph through time.

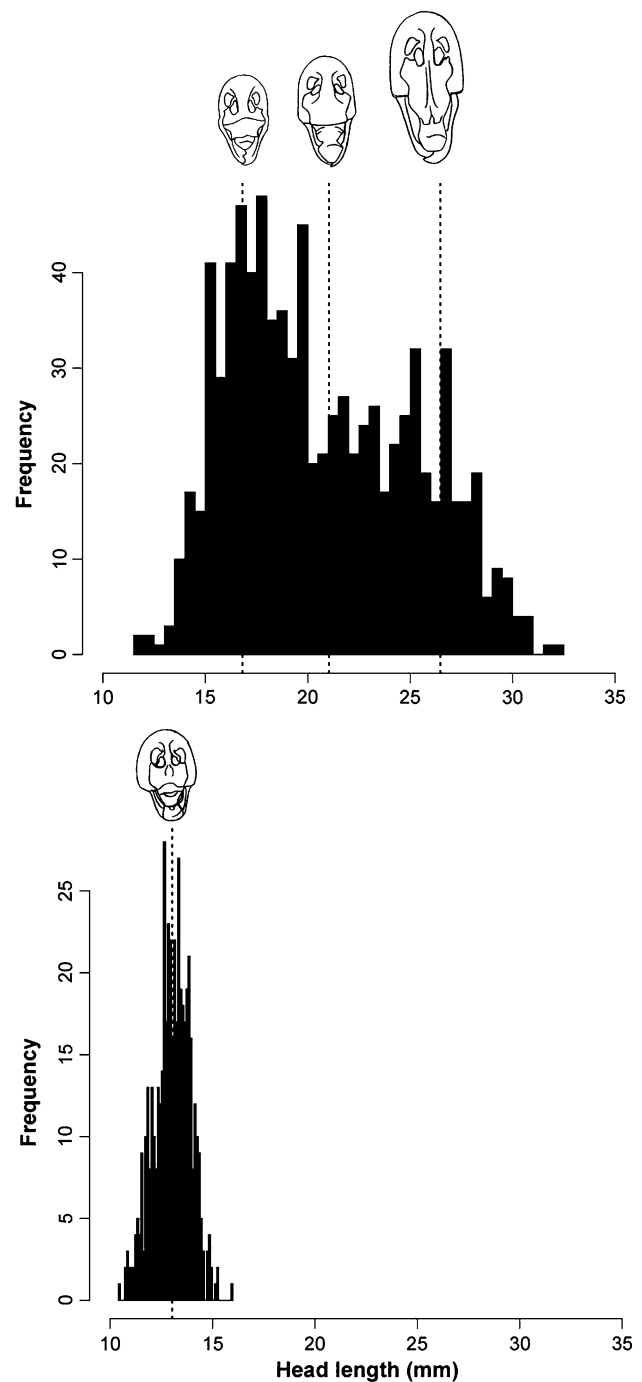


Fig. 2 Head size distribution of adult male (*top panel*) and female (*bottom panel*) *H. crassidens* tree weta. Line drawing of head for representative female and male from each morph shown above mean head size (*dashed line*). Mean values for each male morph are: *small*: 16.81 ± 1.75 mm ($n = 370$), *intermediate*: 21.03 ± 2.72 mm ($n = 264$), *large*: 26.47 ± 2.11 mm ($n = 220$). Line drawings by Jessica Thompson

Head size, Shape, and Allometry

Head size (i.e. centroid size) was significantly larger in males than in females ($F_{1,34} = 47.54$, $P < 0.0001$), and

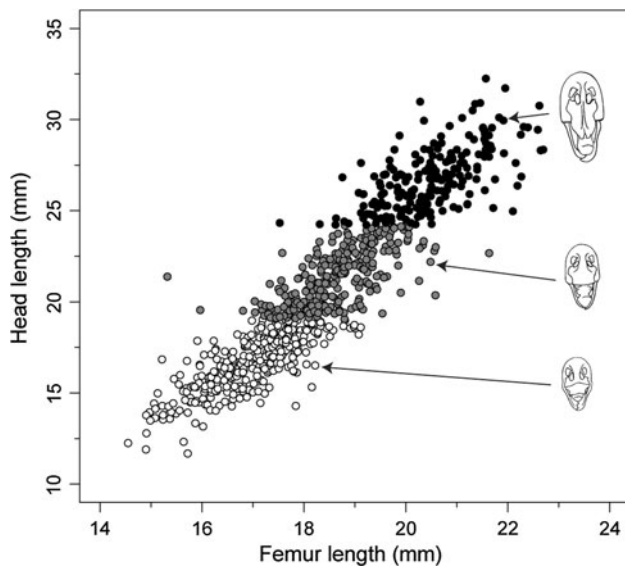


Fig. 3 Scaling relationship for head length and femur length in male tree weta with each of the three morphs denoted by differently coloured circles (*white* 8th instar males; *grey* 9th instar males and *black* 10th instar males). Morph designation based on maximum-likelihood analysis of mixture models, where posterior cut-off values were obtained as: 19.04 mm and 24.20 mm

Table 1 Frequency of male morphs found in each year of the study

Morph	2001	2002	2003	2004	2006	2007	2009
Small (8th instar)	22	67	63	75	59	47	37
Intermediate (9th instar)	9	37	50	71	47	28	22
Large (10th instar)	15	38	45	53	35	18	16

females displayed considerably less variation as compared to males (Fig. 2). We also found that males and females differed significantly in head shape ($F_{1,33} = 103.57$, $P_{\text{rand}} = 0.001$; $R^2 = 0.68$). Taken together, these analyses support our prediction that *H. crassidens* is sexually dimorphic in head size and shape. There was also a significant relationship between head shape and head size ($F_{1,33} = 15.747$, $P_{\text{rand}} = 0.001$; $R^2 = 0.10$). Interestingly, when each sex was examined separately, there was a significant relationship between head shape and head size in males ($F_{1,16} = 16.529$; $P_{\text{rand}} = 0.001$; $R^2 = 0.508$) but not in females ($F_{1,16} = 0.349$; $P_{\text{rand}} = 0.818$; $R^2 = 0.021$). Thus, males displayed an allometric change in head shape as they grew larger, but females did not.

A principal components plot (Fig. 4) revealed distinct separation in morphospace between males and females, largely along the main axis of shape variation (PC1), which

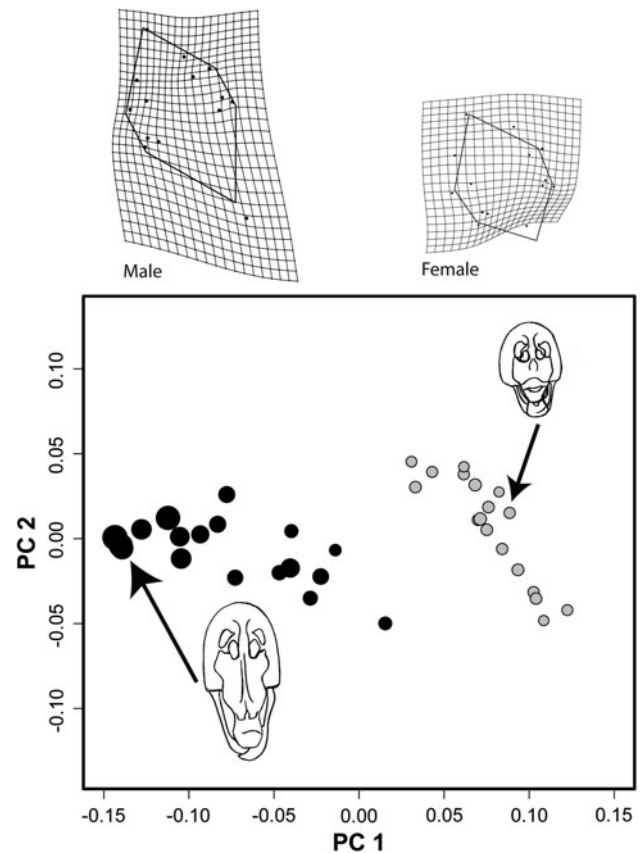
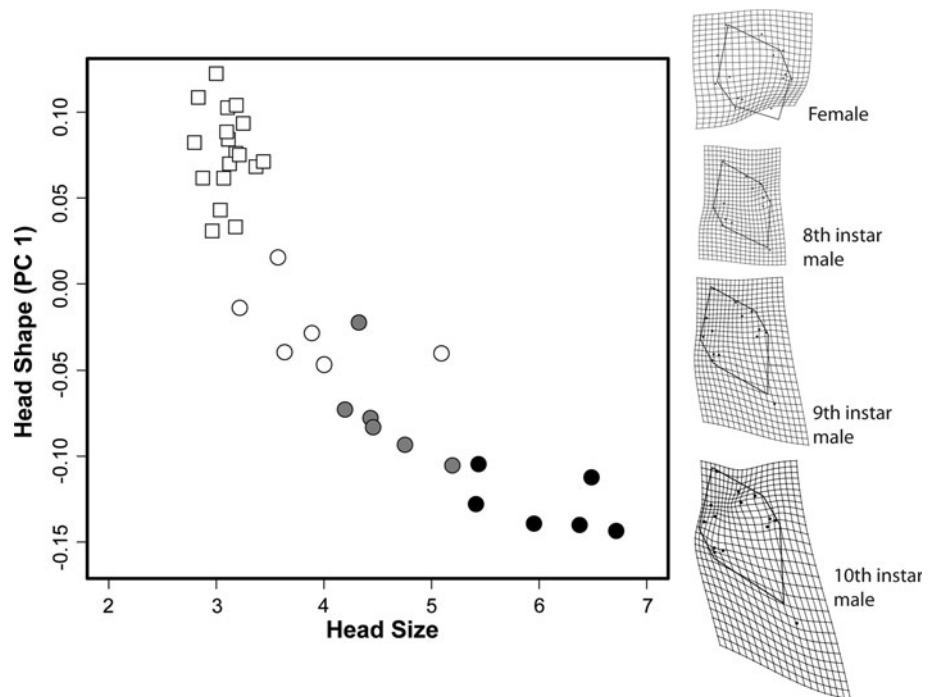


Fig. 4 Principal components plot of shape variation. PC1 explained 83.34% of the variation and PC2 explained 7.57% of the variation. Males are shown in *black* and females in *gray*. Symbol size is proportional to the centroid size of each specimen. Thin-plate spline deformation grids for the average male and average female are also shown

explained 83% of the variation. Examining thin-plate spline deformation grids showed that male head shapes were relatively elongated as compared to females, with a more laterally stretched subocular ridge, expanded vertex and relatively more elongated mandibles (Fig. 4). Strikingly, when head shape (PC1) was plotted against head size (Fig. 5) we found that both males and females shared a common growth trajectory. This was surprising, as males displayed significant head shape allometry but females did not. However, this result was explained by the fact that females were restricted to the lower region of this curve, and displayed little size variation, though there was considerable head shape variation. In stark contrast, the allometric relationship between head size and shape was evident in males, which occupied the remainder of this trajectory. Additionally, male head shape ($F_{2,15} = 9.07$, $P_{\text{rand}} = 0.001$; $R^2 = 0.55$) and size ($F_{2,15} = 25.96$, $P < 0.001$) were significantly different among the male

Fig. 5 Scaling relationship for head shape (PC1) and head size (centroid size) for female (*white squares*) and male (8th instar males *white circles*, 9th instar males *dark grey circles* and 10th instar males *black circles*) tree weta with thin-plate spline shape reconstructions. Reconstructions of typical morph-specific male and female specimens are exaggerated by a factor of 1.5 to facilitate biological interpretation of inter- and intra-sexual shape differences



morphotypes and exhibited continuous change in shape (Fig. 5). Eighth instar males were most similar to females (but significantly different in shape: $F_{1,22} = 24.55$, $P_{\text{rand}} = 0.001$; $R^2 = 0.53$) and had a laterally stretched subocular ridge, expanded vertex and relatively elongated mandibles (Fig. 5). Tenth instar males had the most laterally stretched subocular ridge, expanded vertex and elongated mandibles of the three morphs. Ninth instar head shape was intermediate to 8th and 10th instar morphs.

Discussion

Understanding the mechanisms responsible for the evolution of sexually dimorphic traits has long been of interest to evolutionary biologists. Sex-specific selection on a trait common to both sexes typically produces sexual dimorphism. In this study, we examined patterns of size and shape variation in head traits in the Wellington tree weta to test the hypothesis that antagonistic selection pressures play a role in generating sexual dimorphism. Our findings provide a number of unique insights into the evolution of sexual dimorphism, and how sex-specific patterns of morphological variation arise.

First, we show that tree weta are sexually dimorphic in head shape and size, and that males are comprised of three distinct morphotypes. The differences observed between the sexes are likely due to the distinct selection

pressures on them: males use their heads in male-male combat and feeding whereas females use theirs for feeding only. Indeed, antagonistic selection has resulted in sexual dimorphism of key morphological traits in other organisms, in part because changing a trait's function, or adding an additional function, generally modifies its shape or size (Hens 2005; Kaliontzopoulou et al. 2007; Navarro et al. 2009; Claverie and Smith 2010; Herler et al. 2010). Additionally, differences among the three male morphotypes largely reflect differences in the degree of weaponry exhibited (i.e., mandible length): 10th instar males boast the most elongated jaws and largest vertex, 8th instar males are more female-like head shape and size, and 9th instar males intermediate. Further, these morphological patterns directly associate with the different reproductive strategies they utilize. Specifically, 10th instar males frequently engage in intense combat (requiring exaggerated head weaponry), while 8th and 9th instar males tend to forgo intense combat and instead acquire mates either through sneaking (Spencer 1995) or by mating with females in galleries too small to accommodate large males (Kelly 2006b). Our findings add *H. crassidens* to a short list of animal species in which mature males exhibit irreversible trimorphic phenotypes (Kallman 1984; Shuster 1987; Sinervo and Lively 1996; Correa et al. 2000) and to the even shorter list of cases in which the trimorphic trait is a weapon (Huyghe et al. 2007; Rowland and Emlen 2009).

Second, our study reveals that, within males, antagonistic selection pressures on the same structure can generate distinct morphological patterns that accommodate multiple functional demands. In Wellington tree weta, both natural (i.e. feeding performance and fitting into refugia) and sexual (i.e. fighting performance) selection influence patterns of male head size. We found that head shape is also subject to these same selective pressures. Specifically, because gape width is important to male fitness vis a vis fighting success (Kelly 2006a), particularly in 10th instar males, selection should favour wider gapes. Importantly however, while wider gapes can be achieved by either widening the head or elongating the jaws, head width should be constrained by entrance hole size. In fact, our analyses revealed that male heads became more elongate as they grew larger, supporting the latter prediction. This hypothesis is further strengthened by comparisons with two congeneric species. *H. maori*, a species that defends females under large rocks, have stouter and wider heads than male *H. crassidens* (see Gwynne and Jamieson 1998; Field and Deans 2001; Kelly 2005a). Entrances to cavities defended by male *H. maori* are often much larger than those encountered by male *H. crassidens* (D.T. Gwynne, pers. comm.) and so head width in male *H. maori* is likely not limited by cavity-entrance area. Similarly, *H. femorata* also have wider heads (Field and Deans 2001) and occupy habitats with larger entrance holes to tree galleries compared with *H. crassidens* (Field and Sandlant 2001). In all cases, antagonistic selection pressures have resulted in males that have larger and more-elongate heads.

Finally, our findings show that males and females share a common ontogenetic trajectory with respect to head growth. This result was surprising, as males and females differ dramatically in both head size and head shape, and they exhibit distinct allometries (males displayed head shape allometry, and females did not). Nevertheless, integrating these sex-specific patterns revealed that males and females did not overlap; rather, females displayed little size variation relative to shape variation, and the male allometric trajectory was an extension of the female's trajectory. Thus, despite sex-specific differences in size, shape, and the relationship between the two, a common growth trajectory emerged for both sexes. Interestingly, males do not achieve their increased head size or modified shape through additional instars, as males can mature precociously (8th or 9th instar), or at the same (10th) instar as do females. This pattern clearly indicates that, compared with females, males have evolved a

significantly faster, or accelerated developmental rate, allowing them to 'pass through' the female condition at an earlier developmental stage. In addition, the fact that the male growth trajectory appears to be an extension of the female trajectory suggests that they have derived their exaggerated weaponry through 'ontogenetic hypermorphosis,' (analogous to evolutionary hypermorphosis in descendant species relative to their ancestral state: sensu Alberch et al. 1979). If this is the case, changes in developmental rates and timing through sexual selection may represent an important, but understudied mechanism generating the evolution of such structures. We hypothesize that ontogenetic acceleration and hypermorphosis may be common mechanisms for the evolution of male weaponry; and suggest that examining common male-female ontogenetic trajectories in other species would allow an assessment of the general importance of these mechanisms.

Armaments display amazing diversity in shape across animal species (Emlen 2008). That said, biologists studying weapon evolution, function or mechanics have traditionally relied on linear measures of size to address their hypotheses. Such measures may, however, provide an incomplete picture of weapon evolution if structure shape rather than size is the target of selection. We have shown that head shape is a target of sexual selection in *H. crassidens* to the extent that it has created not only significant sex differences in head shape, but also differences among the three male morphotypes that are related to reproductive strategies. Despite these differences, we found a common ontogenetic trajectory for both species, suggesting sex-specific changes in developmental rates and timing in the development of male weaponry. Much remains to be learned about how conflicting selection pressures balance weapon shape evolution in tree weta and in other animals. Solving this puzzle will require more taxonomically diverse studies that investigate the impact of socioecological factors on armament shape, as well as size.

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Appendix

See Fig. 6.

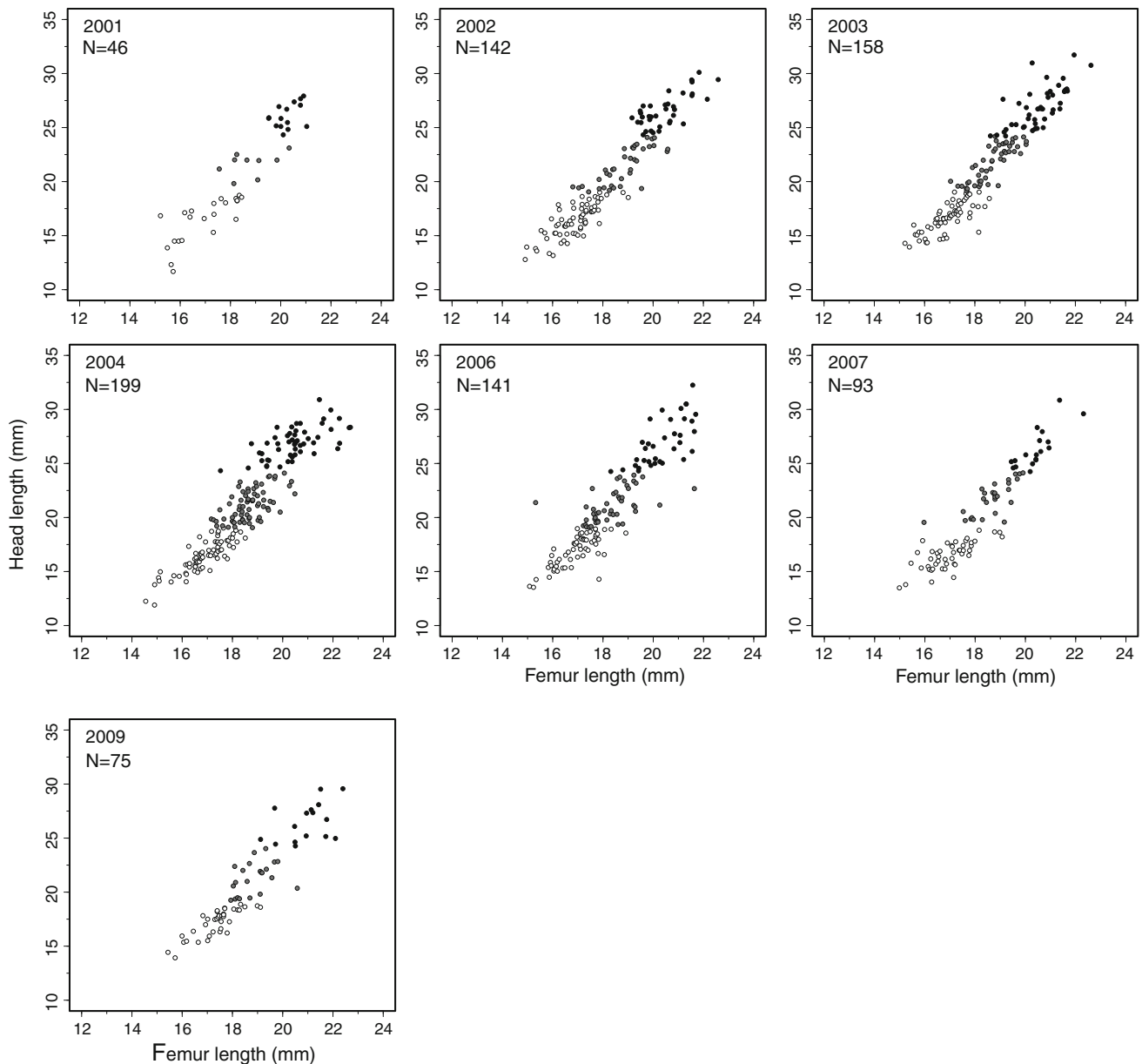


Fig. 6 Scaling relationship for head length (mm) and femur length (mm) in male tree weta for each of the 7 study years. Each morphotype is denoted by differently coloured circles (*white* 8th instar males; *grey* 9th instar males and *black* 10th instar males)

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