Male morphology and dishonest signalling in a fig wasp

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Despite theoretical predictions, dishonest signalling has rarely been observed in aggressive interactions. We present evidence of such signalling in the nonpollinating fig wasp *Philotrypesis* sp. A ex *Ficus rubiginosa*. First, morphometric data indicated that an alternative 'atypical' male morph (17.8% of individuals) exists that tends to be larger in body size and has longer mandibles for a given body size than other 'typical' males. Second, behavioural observations suggested that males use mandible gape width (which depends on mandible length) as a cue to assess opponents before fights and retreat without escalating if they are unlikely to win, and, probably because their greater mandible gape width causes more opponents to retreat without escalating, that atypical males engaged in fewer fights than typical males for a given body size but had higher mating success. Third, atypical males were less likely to win fights than typical males of similar mandible length relative to opponents. In addition, we found that atypical males incur more injuries (greater receiver-dependent signal costs) than typical males of similar body size relative to rivals. We discuss the implications of our findings for future work on dishonest signalling.
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Following theoretical work (Zahavi 1977; Enquist 1985; Grafen 1990), animal signals in aggressive interactions are mostly considered to be honest indicators of the ability and motivation to contest resources (resource-holding potential, or RHP: Maynard Smith & Harper 2003; see also Maynard Smith & Parker 1976). This is because they are thought to be associated with costs that increase with signal effectiveness (size) and fall disproportionately on low RHP individuals. These costs may be incurred in signal production (receiver-independent costs), and/or may be the result of receiver responses, with individuals that produce large signals being attacked more often and/or by high RHP opponents (receiver-dependent costs: Searcy & Nowicki 2005). Less realized though is that signalling systems may not be entirely honest. Theory also indicates receivers need only benefit from responding to the signal for it to evolve, and that often for some individuals the benefits of exaggerating RHP and deceiving receivers will exceed any increase in associated costs (Adams & Mesterton-Gibbons 1995; Számadó 2000, 2003, 2008). Such dishonesty is predicted to be particularly likely when (some of) the costs associated with signalling are only incurred if a fight takes place (i.e. are receiver dependent), as, for example, in species where individuals signal then retreat without escalating if their opponents' signal suggests they are unlikely to win. The frequency of honest and dishonest signallers in a population (and indeed whether signalling evolves at all) will depend on resource value, fight costs and the probability of being able to flee without cost if attacked (the proximity risk: Számadó 2008).

The main reason why the potential for dishonest signalling in aggressive interactions is less recognized is that it has rarely been found in nature (but see Popp 1987; Adams & Caldwell 1990; Backwell et al. 2000; Hughes 2000). Backwell et al. (2000) argued that this paucity is due to difficulties in distinguishing dishonest signals from natural variation in signal size. Here we report on a group in which distinctions may be possible, the nonpollinating fig wasps. Females of these species oviposit in fig inflorescences (*Ficus* spp.), their larvae mature in galls, and then the males eclose and compete for females, often fighting injuriously with their mandibles. Male RHP in fights increases with body size and/or mandible length (which are allometrically related: Moore et al. 2008). Importantly, there is evidence that this relationship is used to assess opponent RHP before fights. Pereira & Prado (2005) described a display in *Idarnes* species in which males face each other, mandibles open and almost touching, with antennae aligned

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along their mandibles. After this, fighting may occur, but often one male instead retreats. Mandible gape width depends on mandible length, so the authors argued that males use gape width to assess opponents and retreat without escalating if they are unlikely to win (see Enquist & Leimar 1983 for theory).

We studied *Philotrypesis* sp. A ex *Ficus rubiginosa*, a species with similar behaviour to that described above. In this species, the posited assessment phase frequently occurs before fighting or after a first strike by one of the males (J.C. Moore personal observation). In our initial studies, we collected morphometric data indicating that an alternative 'atypical' morph exists that has longer mandibles/greater gape width for a given body size than 'typical' males, and made behavioural observations suggesting that atypical males fight less often than typical males of similar body size, but have higher mating success. An explanation for this given the posited assessment strategy is that more opponents retreat without escalating from atypical males because they have wider mandible gapes, and therefore they can spend more time locating mates and are more successful contesting for them once found. Hence, we then tested whether assessment occurs, and also whether during it atypical morphology functions as a dishonest signal of RHP. First, we compared mandible length differences between pairs of fighting males to those between randomly chosen pairs, predicting that with assessment fighting males will differ less. Second, we studied fight outcome, investigating: (1) whether gape width predicts RHP, that is, whether males with longer mandibles win; (2) whether atypical mandibles exaggerate RHP, that is, whether atypical males are less likely to win for a given mandible length relative to opponents; and (3) proximal fight resolution, by quantifying the determinants of fight duration and the injuries incurred (see Discussion for theory). Third, we quantified the receiver-dependent costs of signalling. Morphology is fixed for (adult) life, so we estimated these as the injuries males incur in their lifetimes. We discuss our findings with reference to our understanding of signal stability and the occurrence of dishonest signalling.

METHODS

Study Species

We made observations on wasps from *Ficus rubiginosa* figs collected in and around the city of Brisbane, Queensland, Australia (27°24′S, 153°09′E) during January–May 2004 and November 2005–March 2006. *Ficus rubiginosa* also hosts another *Philotrypesis* species, *Philotrypesis* sp. B. *Philotrypesis* sp. A females are black-bodied and *Philotrypesis* sp. B females brown-bodied, but we did not find morphological characteristics allowing us to distinguish males, so we used molecular techniques to type them using their DNA (see Moore et al. 2008 for details). We note this meant that the species involved in an observation was not known until the male was typed.

Male Morphology

We found two morphs visually distinguishable by mandible morphology, and investigated body size and mandible length differences between them. We estimated body size by head width. We did not use another (more independent of mandible length) measure such as tibia length because limbs were often lost. However, in species in which both traits have been measured they are highly correlated (e.g. Bean & Cook 2001), and in *Philotrypesis* sp. ex *Ficus septica*, in which similar dimorphism occurs, morphs differ in both traits (Cook & Bean 2006; J.M. Cook & D. Bean, unpublished data). We measured head width (across the eyes: see Fig. 1 for head and mandible morphology) at ×10 under
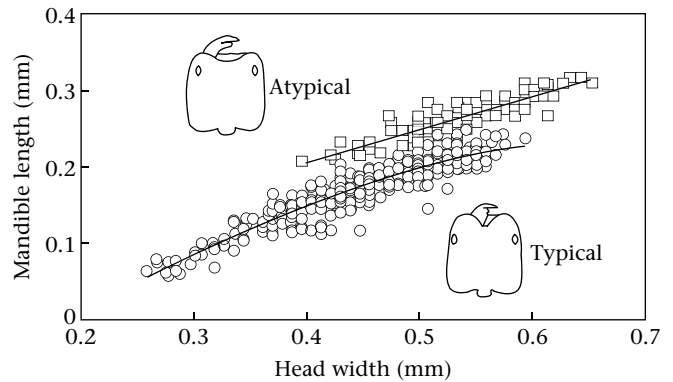

Figure 1. Relationships between male head width (body size) and mandible length in *Philotrypesis* sp. A. Circles indicate typical males, squares atypical males. The lines indicate the allometric relationships between traits in each morph (see text for explanation). The line drawings show male head and mandible morphology (for clarity only the left mandible is included; the right mandible is of similar size and structure).

a microscope and mandible length (from the tip to where the outer edge articulated with the head) at ×40, collecting data on 625 males.

Data analysis

We analysed between-morph differences in head width using an ANOVA, and differences in head width–mandible length allometry using an ANCOVA with mandible length as the response variable and head width and male morph as explanatory variables. We note here that unlike in the related *Philotrypesis* sp. B ex *rubiginosa* (J. C. Moore, D. J. Obbard, J. M. Cook & S. A. West, unpublished data) there was no evidence of further polymorphism: in both morphs the nonlinear regression methods of Eberhard & Guiterrez (1991) failed to indicate discontinuity in the allometric relationship between head width and mandible length (unpublished data). Instead, there was slight negative allometry in typical males (quadratic allometry model: quadratic term: $\beta \pm SE = -0.72 \pm 0.01$, $F_{1,511} = 51.85$, $P < 0.001$), and a linear relationship in atypical males (quadratic allometry model: quadratic term: $F_{1,111} = 0.14$, NS; see Fig. 1). These analyses, as with the others in this paper, were carried out using S-Plus 8.0.2 (Insightful Corp., Seattle, WA, U.S.A.).

Focal Male Observations

We cut open figs in the early stages of wasp eclosure from stalk to ostiole (the pore by which pollinating wasps enter) so that the larger section was around two-thirds of the fig. We then observed the behaviour of randomly chosen focal males in these larger sections at ×10 under a microscope. Males spent time either in the lumen or among the galls, but rarely left the opened fig. We recorded the number of fights each focal male engaged in (physical interactions >2 s duration) until they left the fig, or for a maximum of 45 min. We also recorded any matings they obtained, their length and whether the female was fought over and/or multiply mated, and counted any females eclosing. After an observation (one was made per fig), we noted the focal male morph and measured and typed it as before, and placed the fig sections in a mesh-lidded pot. Ninety-six hours later we counted any females in the pot, and noted the morphs and measured and typed any males in the pot or among the galls. After we excluded observations where the focal male was the only one of its species in the fig (one cannot fight without rivals), the data set contained >10 h of observations on 15 males (10 typical and five atypical). We also note here that only two focal males disappeared from view among the fig galls for more than 60 s during observations,