



Male morphology and dishonest signalling in a fig wasp

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ARTICLE INFO

Article history:

Received 23 August 2008

Initial acceptance 4 November 2008

Final acceptance 9 April 2009

Published online 24 May 2009

MS. number: 08-00552R

Keywords:

alternative behaviour

dishonest signalling

Ficus

fighting behaviour

fig wasp

morphology

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 $\times 10$ under

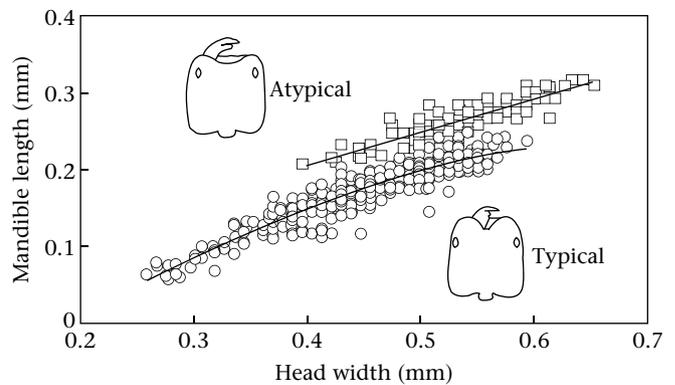


Figure 1. Relationships between male head width (body size) and mandible length in *Philotrypesis* sp. A. Circles indicate typical males, squares atypical males. The lines indicate the allometric relationships between traits in each morph (see text for explanation). The line drawings show male head and 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 $\times 40$, 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 & Guterrez (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 eclosion 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 $\times 10$ 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,

one of each morph. This implies that neither morph uses the alternative nonfighter mating strategy (mating unnoticed by others among the galls) found in the related *Philotrypesis* sp. B ex *F. rubiginosa* (J. C. Moore, D. J. Obbard, J. M. Cook & S. A. West, unpublished data).

Data analysis

We analysed factors affecting the number of fights males engaged in with generalized linear models (GLMs) with Poisson errors. We took into account observation length, with which fight number increased, by fitting it as a covariate. Plots suggested a dome-shaped relationship between focal male head width or mandible length, either on its own or relative to rivals in the fig (focal male trait value/average trait value of rivals) and fight number, and an increase at a decreasing rate with competitor number. However, it was difficult to determine which of these highly correlated trait variables best predicted fight number by conventional statistical tests: the data set was too small. Therefore, we took a more exploratory approach. We fitted four models, one for each trait variable. In a model, we fitted the variable, its quadratic, log competitor number and male morph as explanatory terms. Then, in each case we found the minimum adequate model (MAM), containing only significant terms, by stepwise deletion, comparing changes in model deviance to the chi-square distribution (we report term significance when deleted from/added to the MAM). From this, we made inferences about the predictors of fight number by calculating Akaike information criterion (AIC) values for each MAM. The AIC is a penalized log likelihood measure of model fit, with a lower value indicating a better fit. Specifically, we calculated AIC_c, AIC corrected for sample size and the number of model parameters, which is recommended for small data sets (Burnham & Anderson 2002).

We had planned to analyse mating behaviour as we had fighting behaviour, but only observed 10 matings. Hence, to provide a mainly qualitative description of behaviour we combined these records with those of eight matings by nonfocal males collected during our observations. These latter records differed only in that the male was not removed, measured and typed. Instead, its morph was identified while it mated, and its species from the female it mated with (males do not mate with heterospecifics: J.C. Moore, unpublished data). To test whether mating success differed between morphs, we also used a *G* test (Sokal & Rohlf 1995) to compare the number of matings obtained by each morph to that expected given their population frequency.

Focal Fight Observations

We collected figs, cut them open, observed males and counted eclosing females as before. If a fight occurred between previously uninjured males, we recorded whether it was over a mating opportunity (had a male been excavating or mating a female?), who attacked, who won (defined by the loser becoming moribund or retreating), fight duration and the injuries incurred. We scored injuries using Murray's (1987) index, in which a damaged or lost antenna scores 0.5 points, a damaged or lost tarsus 1 point, a damaged or lost tibia 2 points, a damaged or lost femur 3 points, a damaged or lost coxa 4 points, up to half a severed abdomen or head 4 points, and more than half a severed abdomen or head 8 points. Points are then summed to give a total score, with a score ≥ 8 considered a serious injury. Afterwards, we noted male morphs and measured and typed them, and placed the fig in a mesh-lidded pot (we made only one observation per fig). Ninety-six hours later we counted any females in the pot, noted the morphs, and measured and typed any males in the pot or among the galls. We observed 35 fights, 16 between typical males, 13

between males of different morphs, and six between atypical males. Five (14.2%) were over a mating opportunity.

Data Analysis

We addressed several questions with these data. First, we investigated whether fights were between closely matched males. We used paired *t* tests to compare mandible length and head width differences between fighting male pairs to differences between randomly chosen pairs from the population, estimating the latter value as the average difference between all possible pairings in the fig (see also Cook & Bean 2006) and restricting our analysis to the 25 fights in figs with other conspecific males.

Second, we investigated who won fights. Following Hardy & Field (1998), we randomly assigned one male in each fighting pair as the focal male, and used whether it lost (0) or won (1) as the response variable in a binary logistic GLM. We fitted as explanatory terms focal male morph, mandible length relative to its opponent (focal male trait value/opponent trait value), relative head width and whether it attacked first, then found the MAM by stepwise deletion, evaluating term significance with chi-square tests. Fitting correlated terms such as relative head width and mandible length means there is potential for collinearity, where an underlying relationship is missed because terms cancel each other out (Crawley 2002). This was also a problem in the analyses described below. In all of these analyses, if such terms were nonsignificant when both were in the model we also evaluated significance with the other term omitted. We note below when such collinearity occurred.

Third, we investigated factors affecting fight duration. We fitted a linear model (LM) to the data (which were log transformed so model residuals approximated the normal distribution) with loser mandible length and head width, winner mandible length and head width, whether the fight was over a mating opportunity, loser morph (winner morph did not affect duration: unpublished data), and female number and competitor number in the fig as explanatory terms. We then found the MAM as in the probability of winning analysis, evaluating term significance with *F* tests.

Fourth, we investigated factors affecting the injuries incurred in fights. Injury score was an ordinal variable, so we used a proportional odds model (POM: Proc LRM in library 'Design' from Harrell 2000 imported into S-Plus), a multinomial logistic GLM that models the probability of an event occurring given its position on an ordinal scale (see also Harrell et al. 1998; Guisan & Harrell 2000). We used losing male injury score as the response variable (too few winning males were injured to analyse: see Results), and fitted the same explanatory terms as in the fight duration analysis. We then found the MAM as in the probability of winning analysis, evaluating term significance with Wald (χ^2) tests.

Lifetime Injury Costs

We quantified lifetime injuries by placing nearly mature figs separately in mesh-lidded pots. Ninety-six hours after enclosure began we counted the females in the pots, and then split the fig open and counted the males. We then scored male injuries as before, noted their morphs, and measured and typed them. We collected data on males from 71 figs in total, 41 of which contained two or more males (193 males).

Data analysis

We also analysed the lifetime injury data using a POM. Plots suggested a dome-shaped relationship with male head width or mandible length relative to rivals in the fig (male trait value/average trait value of rivals). Hence, as explanatory terms we fitted

these variables and their quadratic terms, male morph, head width and mandible length (with which nonlinearity was not indicated), and female number and competitor number in the fig. We then found the MAM as before (again checking for collinearity), evaluating term significance with Wald (χ^2) tests.

RESULTS

Population Characteristics

Mean \pm SE *Philotrypesis* sp. A brood size (total wasps) in figs (quantified using all the figs collected for the male lifetime injury analysis) was 7.07 ± 0.70 wasps (range 1–29), mean female number was 4.14 ± 0.42 wasps (range 0–15), and mean male number was 2.93 ± 0.37 wasps (range 0–15). The mean brood sex ratio (males/brood size) in figs was 0.40 ± 0.04 (range 0–1).

Male Morphology

Males are dimorphic, with morphs distinguishable by mandible structure. 'Typical' males constituted 82.2% of individuals, and 'atypical' males, which have more falcate mandibles with a narrower area of articulation with the head, 17.8% of individuals (Fig. 1). Although there was considerable overlap, atypical male head widths (estimated body sizes) were larger than those of typical males (ANOVA: $\beta \pm SE = 0.05 \pm 0.01$, $F_{1,623} = 127.73$, $P < 0.001$), and they also had longer mandibles for a given head width (ANCOVA: head width: $\beta \pm SE = 0.49 \pm 0.01$, $F_{1,622} = 3310.85$, $P < 0.001$; morph term: $\beta = 0.04 \pm 0.01$, $F_{1,622} = 1153.37$, $P < 0.001$).

Focal Male Observations

Focal males fought between 0 and 0.29 (mean \pm SD = 0.07 ± 0.08) times per min. Plots suggested fight number increased then decreased (a dome-shaped relationship) with focal male head width or mandible length either on its own or relative to rivals in the fig, and increased logarithmically with competitor number (see Methods). Table 1 gives details of the statistical models fitted to the data to test which trait variable best predicted fight number, along with their MAM AIC_c values (a lower value indicates a better fitting model) and the amount of deviance in the data they explained. The best fitting model included relative mandible length (and its quadratic) and log competitor number, with no male morph effect (deviance explained = 90%; Fig. 2a). The second best model, including mandible length and log competitor number and again with no morph effect, fitted nearly as well (deviance explained = 89%). The third best model is also notable, although it fitted slightly less well. For a given head width, atypical males fought less often than typical males, with competitor number having no effect (deviance explained = 86%; Fig. 2b). The lack of a similar morph effect in the (relative) mandible length model implies that this difference arose because atypical males have longer mandibles for a given body size than typical males. The fourth model, containing relative head width, a competitor number effect but no morph effect, fitted less well than the other models (deviance explained = 74%).

Mating occurred after the female eclosed from the gall through a hole excavated by a male. Mean \pm SD mating length was 37 ± 23 s (range 5–90 s). No females were multiply mated, and only one excavating male was challenged by and fought with another male (the challenger won and mated with the female). Ten of the matings observed were by typical males, fewer than expected given the population frequency (expected = 14.74), and eight were by atypical males, more than expected given the population frequency

Table 1

Results of statistical models fitted to test how focal male physical trait variables predict fight number per min (observation length was fitted as a covariate)

Trait variable	Statistical model details		
	Variable	Statistic	$\beta \pm 95\%$ CI
Relative mandible length	Observation length	17.74***	0.04 \pm 0.01
	Trait variable quadratic term	12.40***	L: 59.46 \pm 22.52 Q: -25.91 \pm 10.09
	Log (competitors)	18.86**	0.99 \pm 0.24
	Morph	0.91	-0.38 \pm 0.50
	MAM AIC _c	15.67	
	Deviance explained	90%	
Mandible length	Observation length	23.94***	0.05 \pm 0.01
	Trait variable quadratic term	14.40***	L: 114.56 \pm 31.71 Q: -270.55 \pm 78.29
	Log (competitors)	5.94*	0.53 \pm 0.23
	Morph	1.24	-0.77 \pm 0.74
	MAM AIC _c	16.17	
	Deviance explained	89%	
Head width	Observation length	4.36*	0.01 \pm 0.007
	Trait variable quadratic term	8.52**	L: 192.94 \pm 81.50 Q: -189.27 \pm 85.13
	Log (competitors)	0.58	0.16 \pm 0.25
	Morph	11.92***	-1.19 \pm 0.37
	MAM AIC _c	18.52	
	Deviance explained	86%	
Relative head width	Observation length	2.64†	0.01 \pm 0.007
	Trait variable quadratic term	6.64**	L: 114.01 \pm 70.46 Q: -51.59 \pm 32.33
	Log (competitors)	16.05***	-1.19 \pm 0.37
	Morph	0.13	-0.12 \pm 0.45
	MAM AIC _c	24.67	
	Deviance explained	74%	

Test statistics represent changes in model deviance following variable removal from/ addition to the MAM (see text), compared to the chi-square distribution with 1 *df*. Only trait variable quadratic term (Q) significance is given because in such situations linear term (L) significance is irrelevant. For each MAM we also give AIC_c, a measure of model fit (see text), and the percentage deviance explained. Models are ordered from best fitting to worst, based on their AIC_c values.

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

(expected = 3.26; G test with Williams' correction: $G_1 = 6.10$, $P < 0.01$), implying that atypical males have higher mating success.

Size Differences Between Fighting Males

Fights tended to be between evenly matched males: both mandible length (mean difference_{fighters} - difference_{males} = -0.013 mm, 95% confidence interval, CI = -0.025 to -0.001 mm; paired *t* test: $t_{24} = -2.30$, $P < 0.05$) and head width (mean difference_{fighters} - difference_{males} = -0.025 mm, 95% CI = -0.039 to -0.01 mm; $t_{24} = -3.50$, $P < 0.01$) differences between fighters were less than average differences between males in figs.

Fight Outcome

The male with the longer mandibles won 65% of fights, and the male with the wider head won 58%. Atypical males had a lower probability of winning fights than typical males (GLM: $\beta \pm SE = -3.49 \pm 1.49$, $\chi^2_1 = 8.57$, $P < 0.01$) for a given mandible length relative to opponents ($\beta = 6.59 \pm 3.06$, $\chi^2_1 = 8.48$, $P < 0.01$; Fig. 3), with which the probability of winning increased. The probability of the focal male winning also increased if it attacked first ($\beta = 2.41 \pm 1.19$, $\chi^2_1 = 5.40$, $P < 0.05$). Atypical males were also less likely to win fights for a given relative head width: a model with the term replacing relative mandible length (the two terms were collinear when fitted together) gave similar results (GLM: morph: $\beta \pm SE = -3.22 \pm 1.47$, $\chi^2_1 = 7.24$, $P < 0.01$; relative head

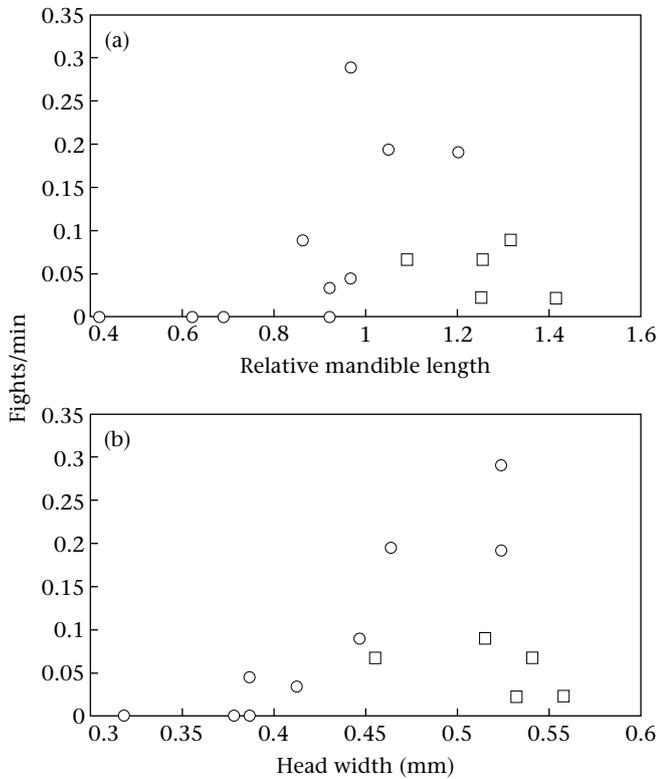


Figure 2. Relationships between (a) mandible length relative to rivals, and (b) head width, and the number of fights engaged in per min by focal males. Circles indicate typical males, squares atypical males.

width: $\beta = 15.56 \pm 6.94$, $\chi^2_1 = 8.12$, $P < 0.01$; attacking first: $\beta = 2.26 \pm 1.07$, $\chi^2_1 = 5.66$, $P < 0.05$). The two models both explained 38% of the deviance in the data.

Fight Duration and Injuries Incurred

Mean \pm SD fight duration was 75.50 ± 68.70 s (range 3–216 s). Fight losers were more frequently and seriously (score ≥ 8) injured (18 injured, 12 seriously, mean score = 3.76, range 0–12) than winners (three injured, none seriously, mean score = 0.26, range 0–4). For a given loser mandible length, with which duration increased, fights were shorter if the loser was an atypical rather than

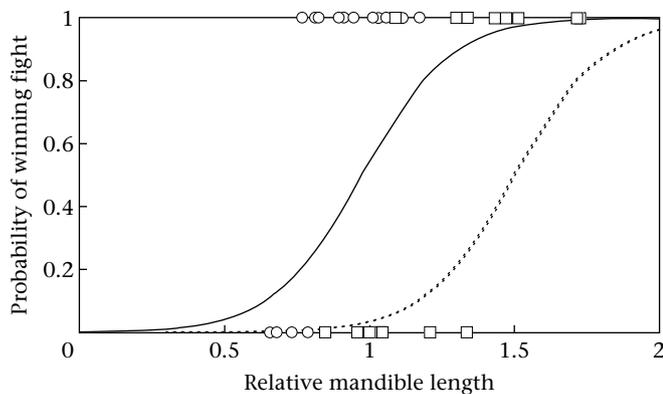


Figure 3. Relationships between mandible length relative to the opponent and the probability of focal males winning fights. Circles indicate typical males (predicted relationship indicated by solid line), squares atypical males (predicted relationship indicated by dotted line).

typical male (Table 2, Fig. 4a). Fight duration also increased if it was over a mating opportunity and decreased with competitor number in the fig. It was unaffected by loser head width, winner head width or mandible length, winner or loser injury score, or female number in the fig. When loser mandible length was omitted from the model, duration increased instead with loser head width (LM: $\beta \pm SE = 21.05 \pm 4.88$, $F_{1,29} = 18.63$, $P < 0.001$), with fights again shorter when the loser was an atypical male ($\beta = -1.35 \pm 0.42$, $F_{1,29} = 18.63$, $P < 0.001$). This model, though, explained less variance (adjusted $R^2 = 0.48$) than the one containing loser mandible length (adjusted $R^2 = 0.55$). Loser injuries were correlated with fight duration. For a given mandible length, with which injuries increased, atypical males incurred fewer injuries than typical males (Table 2, Fig. 4b). Injuries were unaffected by loser head width, winner head width or mandible length, competitor or female number in the fig, or whether the fight was over a mating opportunity. When loser mandible length was omitted from the model, injuries increased instead with loser head width ($\beta = 42.39 \pm 13.40$, $\chi^2_1 = 10.01$, $P < 0.01$) but were unaffected by loser morph ($\chi^2_1 = 0.53$, NS). The latter model explained slightly less deviance (39%) than the one containing loser mandible length (42%).

Lifetime Injury Costs

Seventy-two per cent of males were injured. Mean injury score was 6.59 (range 0–32). For a given head width relative to rivals in the fig, with which a dome-shaped relationship occurred, atypical males incurred more injuries than typical males (Table 3). Injuries also increased with competitor number, but were unaffected by relative mandible length, male head width or mandible length, or female number in the fig.

DISCUSSION

Our results suggest atypical male morphology in the dimorphic *Philotrypesis* sp. *A ex F. rubiginosa* functions as a dishonest signal of RHP. We have shown that atypical males (17.8% of individuals) tend to be larger in body size than typical males (82.2%), and have longer mandibles for a given body size. Then, supporting qualitative observations (see Introduction), we have presented data consistent with males using mandible gape width as a cue to assess opponent RHP before fighting and retreating without escalation if they are unlikely to win (see Enquist & Leimar 1983 for theory). We have shown that: (1) 65% of fights are won by the male with the longer mandibles, indicating (as it is depends on mandible length) that gape width predicts RHP; (2) the number of fights males engage in

Table 2
The determinants of fight duration and loser injury scores during the focal fight observations

Explanatory term	Fight duration		Loser injuries	
	Test statistic	$\beta \pm SE$	χ^2_1	$\beta \pm 95\% CI$
Loser morph	$F_{1,29} = 32.72^{***}$	-3.90 ± 0.68	8.72**	-5.26 ± 1.78
Loser mandible length	$F_{1,29} = 28.32^{***}$	50.66 ± 9.52	12.23***	94.72 ± 27.08
Loser head width	$F_{1,28} = 1.53$	8.01 ± 6.47	2.34	27.83 ± 19.82
Loser injuries	$F_{1,28} = 0.50$	0.04 ± 0.13		
Winner mandible length	$F_{1,28} = 0.01$	-0.52 ± 4.60	0.41	7.11 ± 11.11
Winner head width	$F_{1,28} = 0.22$	2.28 ± 4.89	0.36	7.40 ± 12.29
Winner injuries	$F_{1,28} = 0.01$	0.01 ± 0.22		
Over a mating	$F_{1,29} = 11.44^{**}$	1.65 ± 0.49	0.01	-0.12 ± 1.05
Competitor number	$F_{1,29} = 4.16^*$	-0.07 ± 0.03	2.35	-0.15 ± 0.11
Female number	$F_{1,28} = 1.05$	0.06 ± 0.05	2.64	-0.21 ± 0.14

Fight duration results are from a linear model with term significance evaluated with *F* tests; the loser injury score results are from a proportional odds model with term significance evaluated with Wald (χ^2) tests.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

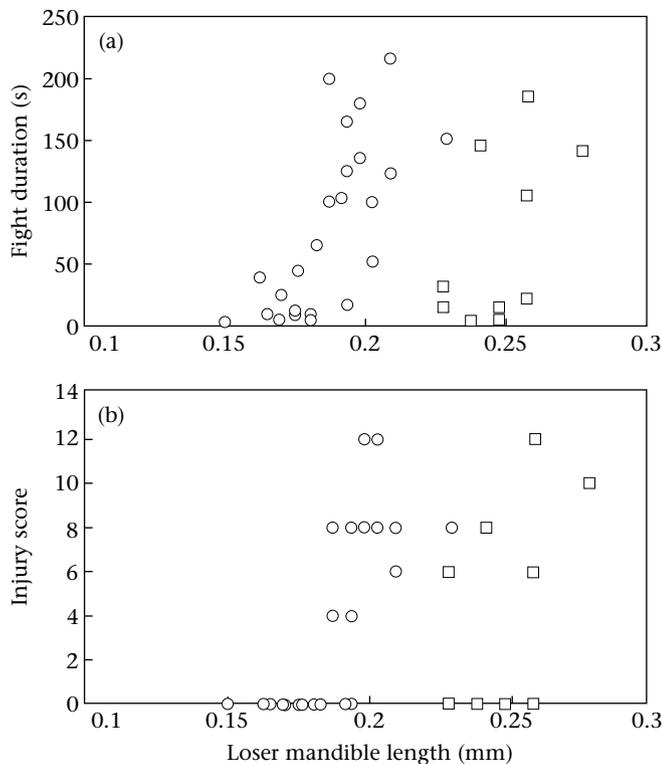


Figure 4. Relationships between loser mandible length and: (a) fight duration, and (b) the injuries incurred in fights in *Philotrypesis* sp. A. Circles indicate typical males, squares atypical males.

is best predicted by a dome-shaped relationship with mandible length relative to rivals in the fig, indicating that they fight most often when there are a number of rivals with similar gape widths; and (3) mandible length differences between fighting male pairs are smaller than those between randomly chosen pairs, indicating that fights tend to be between similarly equipped rivals. We have also shown here that atypical males fight less often than typical males for a given body size, and that they have higher mating success. A parsimonious explanation for this given the posited assessment phase is that more opponents retreat without escalating from atypical males because they have wider mandible gapes for a given body size, and that therefore they can spend more time locating females and challenge for them more successfully once found. Further investigation of these arguments is now needed. An additional indirect test of whether mandible gape width is used to assess opponents (small male size makes manipulative experiments difficult) would be to quantify rates of retreat from different-sized males: more opponents should retreat from atypical males for

Table 3
The determinants of the lifetime injuries incurred by males

Explanatory term	Test statistic	$\beta \pm 95\%$ CI
Morph	$\chi^2_1 = 5.02^*$	0.96 ± 0.43
Head width relative to rivals	Q: $\chi^2_1 = 7.90^{**}$	L: 32.80 ± 11.80 Q: -17.27 ± 6.14
Competitor number	$\chi^2_1 = 10.44^{***}$	0.11 ± 0.03
Head width	$\chi^2_1 = 1.99$	3.62 ± 2.57
Mandible length	$\chi^2_1 = 0.34$	2.81 ± 4.97
Mandible length relative to rivals	L: $\chi^2_1 = 0.19$ Q: $\chi^2_1 = 0.03$	L: -0.74 ± 1.71 Q: 0.48 ± 2.86
Female number	$\chi^2_1 = 0.32$	0.02 ± 0.04

Results are from a proportional odds model, with term significance evaluated with Wald (χ^2) tests. L: linear term; Q: quadratic term.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

a given body size, but the best predictor should be male mandible length, with which an increase should occur.

We have also shown that atypical morphology will exaggerate RHP during this assessment phase. Atypical males are less likely to win fights than typical males for a given mandible length relative to opponents. This suggests the extra rivals posited to retreat from atypical males (see above) may often be able to win fights, that is, that the morphology dishonestly signals RHP. Given limited overlap in mandible length between morphs (see Fig. 1), it is perhaps surprising that such a strategy persists: deception could be avoided by ignoring gape widths over a certain size. Possibly, its persistence indicates that gape width assessment is constrained. The dark fig interior means that visual cues are unlikely to be used for this, but antennae alignment along the mandibles during this phase suggests chemical cues are involved. Intuitively, with the latter detecting more than whether a rival is smaller (inside one's own gape) or larger (outside it) than oneself will be difficult. Regarding proximal fight resolution, we found that 34% ended in severe injury. Fight duration increased with loser mandible length and decreased if the loser was an atypical male, but was not affected by injuries incurred or winner traits. Few fight winners were injured, but loser injuries increased with duration. Fight severity probably reflects low female number in figs (mean = 4.14) and so the large contribution each mating makes to male lifetime fitness (see Enquist & Leimar 1990 for theory, and also West et al. 2001). However, its relationship with loser mandible length (owing to the correlation between duration and loser injuries) suggests fights were not to the death. Instead, as we have argued in another fig wasp species (Moore et al. 2008), the relationship between loser mandible length and fight duration is consistent with fights continuing until the loser reaches a size (and hence RHP)-dependent cost threshold and retreats. Apparently, only the energetic cost of fighting is included in this threshold, as duration did not decrease with loser injuries. Given this, the observed morph effect on duration suggests atypical males retreat more quickly and lose more fights because they are of lower RHP for a given mandible length. We return to this subject below.

In addition, we quantified the receiver-dependent costs (those arising from receiver responses) of the two morphologies/signalling strategies. Morphology is fixed for (adult) life, so we estimated these as the injuries males incurred over their lifetimes. We found that atypical males incurred more lifetime injuries than typical males for a given body size relative to rivals in the fig, with which there was a dome shaped relationship. The latter relationship probably reflects the number of fights males engage in. That it was not with body size itself is likely to be because of correlated variation in male size in figs (unpublished data): this will mean that large males will often only be average sized in their natal fig, with the result that they still fight frequently. That atypical males incurred more lifetime injuries than typical males must have been a consequence of losing more of the fights they did engage in, as they fought less often and incurred similar injuries per lost fight. In the context of theory, the greater costs incurred by atypical males is predicted in a signalling system stabilized by the cost of being attacked by high RHP opponents (Számádó 2000, 2008). That atypical males exist also leads to the (testable) prediction that they have a chance of fleeing without cost if attacked: the high value of matings and cost of (losing) fights (see above) make dishonest signalling unlikely to evolve unless there is some probability of escaping opponents that do not retreat (Számádó 2008). A caveat to the arguments about signal stability, though, is that they concern differences in costs for a given signaller RHP. We found that atypical males retreated more quickly and were more likely to lose fights than typical males for a given (relative) body size as well as mandible length.

One interpretation of this is that morphs differ beyond mandible morphology, and atypical males are of lower RHP for a given body size. If so, body size metrics are at best an inaccurate way to compare RHP across morphs. However, other explanations are possible: for example, atypical males may reduce the threshold beyond which they retreat in fights because they are of lower RHP than most opponents that do escalate against them. Therefore, further investigation is required to confirm such inferences.

Our findings suggest that atypical male mandible morphology in *Philotrypesis* sp. A functions as a dishonest signal of fighting ability. Dishonest signalling is predicted by theory (Adams & Mesterton-Gibbons 1995; Számadó 2000, 2003, 2008), but other empirical examples are rare (Popp 1987; Adams & Caldwell 1990; Backwell et al. 2000; Hughes 2000). Atypical morphology occurs in several other fig wasps (Cook & Bean 2006; J. C. Moore, D. J. Obbard, J. M. Cook & S. A. West, unpublished data; R.A.S. Pereira, unpublished data), implying that the group could be used as a model system to study such signalling. However, we also note that dishonest atypical males are similar-sized to or larger than honest typical males. It is unclear how accurate body size-based metrics are in estimating morph differences in RHP (see earlier), but so far theory only considers situations where dishonest signallers are of lower RHP (Adams & Mesterton-Gibbons 1995; Számadó 2000, 2008). Hence, further theoretical models of dishonest signalling are also likely to be required.

Acknowledgments

We are grateful to Paul Cunningham, Mike Furlong and Myron Zalucki for assistance in Australia, and to Rodrigo Santinelo Pereira for allowing us to quote unpublished data. We also thank Jaco Greeff, Jason Peinaar, Szabolcs Számadó and an anonymous referee for comments on the manuscript. This research was supported by the BBSRC, NERC and The Royal Society.

References

- Adams, E. S. & Caldwell, R. L. 1990. Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. *Animal Behaviour*, **39**, 706–716.
- Adams, E. S. & Mesterton-Gibbons, M. 1995. The cost of threat displays and the stability of deceptive communication. *Journal of Theoretical Biology*, **175**, 405–421.
- Backwell, P. R. Y., Christy, J. H., Telford, S. R., Jennions, M. D. & Passmore, N. I. 2000. Dishonest signalling in a fiddler crab. *Proceedings of the Royal Society of London, Series B*, **267**, 719–724.
- Bean, D. & Cook, J. M. 2001. Male mating tactics and lethal combat in the non-pollinating fig wasp *Sycoscapter australis*. *Animal Behaviour*, **62**, 535–542.
- Burnham, K. P. & Anderson, D. R. 2002. *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*, 2nd edn. New York: Springer-Verlag.
- Cook, J. M. & Bean, D. 2006. Cryptic male dimorphism and fighting in a fig wasp. *Animal Behaviour*, **71**, 1095–1101.
- Crawley, M. J. 2002. *Statistical Computing: an Introduction to Data Analysis using S-Plus*. Chichester: J. Wiley.
- Eberhard, W. G. & Guitierrez, E. E. 1991. Male dimorphisms in beetles and earwigs and the question of developmental constraints. *Evolution*, **45**, 18–28.
- Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour*, **33**, 1152–1161.
- Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, **102**, 387–410.
- Enquist, M. & Leimar, O. 1990. The evolution of fatal fighting. *Animal Behaviour*, **39**, 1–9.
- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.
- Guisan, A. & Harrell, F. E. 2000. Ordinal response regression models in ecology. *Journal of Vegetation Science*, **11**, 617–626.
- Hardy, I. C. W. & Field, S. A. 1998. Logistic analysis of animal contests. *Animal Behaviour*, **56**, 787–792.
- Harrell, F. E. 2000. *Design: S-Plus Functions for Biostatistical/epidemiologic Modelling, Testing, Validation, Graphics, Prediction, and Typesetting by Storing Enhanced Model Design Attributes in the Fit*. <http://biostat.mc.vanderbilt.edu/twiki/bin/view/Main/FrankHarrell>.
- Harrell, F. E., Margolis, P. A., Gove, S., Mason, K. E., Mulholland, E. K., Lehmann, D., Muhe, L., Gatchalian, S. & Eichenwald, H. F. 1998. Development of a clinical prediction model for an ordinal outcome. *Statistics in Medicine*, **17**, 909–944.
- Hughes, M. 2000. Deception with honest signals: signal residuals and signal function in snapping shrimps. *Behavioral Ecology*, **11**, 614–623.
- Maynard Smith, J. & Harper, D. 2003. *Animal Signals*. Oxford: Oxford University Press.
- Maynard Smith, J. & Parker, G. A. 1976. The logic of asymmetric contests. *Animal Behaviour*, **24**, 159–175.
- Moore, J. C., Reuter, C., West, S. A. & Cook, J. M. 2008. Fighting strategies in two species of fig wasp. *Animal Behaviour*, **78**, 315–322.
- Murray, M. G. 1987. The closed environment of the fig receptacle and its influence on male conflict in the Old World fig wasp, *Philotrypesis pilosa*. *Animal Behaviour*, **35**, 488–506.
- Pereira, R. A. S. & Prado, A. P. D. 2005. Recognition of competitive asymmetries reduces the severity of fighting in male *Idarnes* fig wasps. *Animal Behaviour*, **70**, 249–256.
- Popp, J. W. 1987. Risk and effectiveness in agonistic displays by American goldfinches. *Behaviour*, **103**, 141–168.
- Searcy, W. A. & Nowicki, S. 2005. *The Evolution of Animal Communication: Reliability and Deception in Signalling Systems*. Princeton, New Jersey: Princeton University Press.
- Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*, 3rd edn. New York: W.H. Freeman.
- Számadó, S. 2000. Cheating as a mixed strategy in a simple model of aggressive communication. *Animal Behaviour*, **59**, 221–230.
- Számadó, S. 2003. Threat displays are not handicaps. *Journal of Theoretical Biology*, **211**, 327–348.
- Számadó, S. 2008. How threat displays work: species-specific fighting techniques, weaponry and proximity risk. *Animal Behaviour*, **76**, 1455–1463.
- West, S. A., Murray, M. G., Machado, C. A., Griffin, A. S. & Herre, E. A. 2001. Testing Hamilton's rule with competition between relatives. *Nature*, **409**, 510–513.
- Zahavi, A. 1977. The cost of honest signalling (further remarks on the handicap principle). *Journal of Theoretical Biology*, **67**, 603–605.