

Exaggerated displays do not improve mounting success in male seaweed flies *Fucellia tergina* (Diptera: Anthomyiidae).

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Abstract

Signals of individual quality are assumed to be difficult to exaggerate, either because they are directly linked to underlying traits (indices) or because they are costly to perform (handicaps). In practise advertisement displays may consist of conventional and costly components, for instance where a morphological structure related to body size is used in visual displays. In this case, there is the potential for dishonest displays, due to the population level variance around the relationship between body size and display structures. We examine the use of wing flicking displays that we observed *in situ* in a strandline dwelling seaweed fly *Fucellia tergina*, using overall body size and the size of their eyes as underlying indicators of condition. Males displayed far more frequently than females, and were also observed to frequently mount other flies, a behaviour that was rare in females. The rate of display was greater for males that had positive residual values from relationships between wing length and body length. In other words those males with larger than expected wings for their underlying quality displayed more frequently, indicating that these displays are open to exaggeration. Males with larger than expected wings (for the size of their body or eyes), however, mounted less frequently. We suggest that small bodied males are less successful in terms of mounting, but that those small males with relatively large wings may attempt to compensate for this through increased display effort.

Keywords: signal, display, handicap, honesty, seaweed-fly, diptera

Introduction

Advertisement displays are used by animals when senders try to impart some information about their quality to a single receiver or, in the case of communication networks (McGregor and Peake 2000) to a wider audience of receivers. Such displays typically occur in an intraspecific context, such as contests over the ownership of a resource or during courtship. Advertisement displays can often be decomposed into conventional (Guilford and Dawkins 1995) and costly components, also described respectively as index and handicap signals (Bradbury and Vehrencamp 2011). Both components entail costs and in the case of the conventional component these costs accrue during the development and maintenance of a body structure that is used to perform a display. In contrast, the costly component entails performance costs such as the energy expended in performing the display, time lost to other activities, and increased visibility to predators. The benefit from these displays comes from an increased chance that a rival will decide to relinquish a resource in the case of contests, or from enhanced mating opportunities in the case of courtship.

For certain conventional signal components the expression of the morphological structure, typically its size, is expected to correlate strongly with an underlying aspect of sender quality such as body size (Guilford and Dawkins 1995). Nevertheless, we should still expect a degree of variation around population level relationships between signals and

underlying aspects of quality. Thus, some individuals should have larger conventional signalling components than expected. A common theme that unites several versions of the handicap principle (Zahavi 1975; Zahavi 1977; Grafen 1990) is that the use of such exaggerated signals should be selected against because poor quality individuals should not be able to bear the costs of signals that indicate high quality. However, empirical data (Nakagawa et al. 2008) and theoretical studies (Számadó 2000) suggest that low levels of ‘cheating’ – expressing signals that exaggerate an individual’s underlying quality – might be maintained (at the population level) in otherwise honest signalling systems (although see Helgesen et al. 2013). Hughes (2000) described an approach for detecting the potential use of exaggerated signals based upon analysis of residuals from the population level relationship between conventional signal components and underlying markers of quality. Evidence of exaggeration is present if individuals with positive residuals (e.g. larger than expected conventional signalling components for their body size) perform displays more frequently than those with negative residuals (Wilson and Angilletta 2015). Furthermore, if such exaggeration benefits the sender, this should lead to positive outcomes. For example, individuals with positive residuals should win more contests or gain more mating opportunities than individuals with negative residuals. Thus, in several crustacean species including snapping shrimp *Alpheus heterochaelis*, (Hughes 2000), mantis shrimp *Gonodactylus oerstedii* (Adams and Caldwell 1990) and fiddler crabs *Uca spp.* (Backwell et al. 2000; Bywater and Wilson 2012) there is evidence of exaggerated chelar displays. However, there do appear to be limits on the ability to exaggerate. While hermit crabs, *Pagurus bernhardus*, can bluff during pre-fight cheliped displays (Elwood et al. 2006; Arnott and Elwood 2010), exaggeration does not seem possible during the vigorous shell rapping signals used during the later escalated stage of fighting (Briffa 2006). Thus, it is relatively low intensity visual displays that appear to be the most susceptible to exaggeration.

Thus far, analysis of signal residuals has been focussed on examples of pairwise agonistic encounters, where senders advertise their fighting ability to a single rival. There are, however, other contexts where signals of individual quality might be susceptible to exaggeration. First, signals that have evolved under direct sexual selection advertise the sender’s quality to potential mates might be susceptible to bluffing. Indeed, both agonistic behaviour and courtship are characterised by processes where the sender attempts to convince a receiver of its quality and therefore we might expect substantial similarities between these types of display (Payne and Pagel 1997; Mowles and Ord 2012). In both cases, signal receivers make a decision in respect of the sender; either to relinquish a resource in the case of fights or to accept a mate in the case of courtship. Second, as well as occurring in pairwise encounters, advertisement signals are also used in situations where multiple individuals within aggregations display simultaneously. For example, the burrows of male fiddler crabs such as *Uca annulipes* are densely aggregated on intertidal mudflats. Males display their enlarged major claws during intraspecific agonistic encounters and also wave this claw to court females. Males with weaker but visually similar regenerated claws perform displays identical to males that bear the stronger original claws (Backwell et al. 2000). This indicates the potential for bluff in the case of displays that are observed by several individuals. However, signal residuals have yet to be analysed in this type of situation. Here we

investigate the use of wing flicking displays in the seaweed fly *Fucellia tergina*. As in other seaweed flies *F. tergina* form dense aggregations on the strandline of seashores. Within these aggregations we observed individual flies rapidly moving either a single wing, both wings together or each wing alternately. These behaviours were often followed by the individual mounting another fly. Our observations indicated that *F. tergina* are unselective in this regard, mounting individuals of either sex. In many dipterans males show similarly unselective mounting behaviour, presumably because they cannot readily distinguish between males and females prior to mounting. Notwithstanding the possibility that some effort is wasted in mounting other individuals of the same sex, mounting is a pre-cursor of copulation across the diptera.

In the heavily studied kelp fly *Coelopa frigida*, males and females form similarly dense aggregations on the strandline. Sexual displays are absent and males simply mount other flies and then attempt to copulate with females (Day et al. 1990). Females, however, are more amenable to copulation (struggling less) when they are mounted by large males (quantified by measuring wing size) (Shuker and Day 2002) and when females carry a specific chromosomal inversion that confers large size (Gilburn and Day 1994; Gilburn and Day 1999), which also confers a preference for large males (Butlin et al. 1982). Although wing displays have yet to be documented in any seaweed flies, other dipterans have been shown to use their wings in display behaviour (Alonso-Pimentel et al. 2000; Briceno and Eberhard 2000; Lasbleiz et al. 2006). In the dung fly *Scathophaga stercoraria*, females move towards large males, such that displays benefit males by increasing the likelihood of encountering receptive females (Borgia 1980). We hypothesised that the wing movements we observed in *F. tergina* were displays used by males to either attract females or as a form of competition against other males over access to females. Our initial aim was to determine whether these wing movements are indeed displays that have arisen from either direct (to attract females) or indirect (to compete with males) sexual selection on males. In both cases males should perform the wing movements more frequently than females and high rates of wing movement should be associated with a greater number of mountings. Our secondary aim was to determine whether these wing movements might advertise individual quality, in which case better quality males should perform the behaviour more frequently than poorer quality males. Typically, underlying traits related to the size of conventional signal components are assumed to provide indices of an individual's condition (e.g. Hughes 2000). Typically overall body size is used as an underlying marker of individual quality, which has been used previously in dipterans (e.g. Zimmer et al 2001). However, other aspects that vary across individuals might also be pertinent in this respect. In insects, eyes are costly structures to grow and maintain and there is significant among individual variation in eye size, independent of overall body size (Niven and Laughlin 2008). Therefore, we used both traits as markers of underlying quality. Finally, by analysing residuals on conventional signal components (wing length) and these underlying traits, we addressed the potential for exaggeration in *F. tergina* wing displays. If males with larger than expected wings (for the size of their body or eyes) exploit the opportunity for exaggeration we would expect individuals with positive residuals to perform more wing displays than those with negative

residuals. And if exaggeration is beneficial for males, those with positive residuals should achieve more mountings than those with negative residuals.

Materials and methods

Field observations

Video films of wing movements in stationary flies and mounting behaviour were recorded using a tripod mounted Canon 60D digital SLR camera (Canon EFS 17-85mm lens) between 1000h and 1705h, when flies were observed to be active, *in-situ* on randomly selected sections of the strandline at Wembury beach, South Devon, UK (SX 51687 48513) between April and August 2013. Focal individuals within aggregations (see below for analysis of the effect of aggregations size) were recorded for observation periods of up to 240s (mean = 119s \pm SE = 6.2s), following which they were immediately trapped using either an aspirator or hand-held net. Additional flies were trapped at random for estimation of the sex-ratio within these aggregations. Captured flies were placed into individually marked bags and returned to the laboratory and stored in a freezer (-20°C) for later morphometric analysis and identification of sex (it was not possible to identify the sex of flies at during observations). Species confirmation of *Fucellia tergina* was obtained from the Angela Marmont Centre for UK Biodiversity, The Natural History Museum, London, UK.

Morphometric analysis

Flies were photographed using a Canon macro MP-E 65mm lens attached to the Canon 60D digital SLR, with a Canon MT-24EX macro twin lite flash system. This was placed onto a Shoot Photographic fine focusing rack on a tripod. Flies were photographed on each lateral side, as well as dorsally and ventrally. The following measurements were then taken using Image J photographic analysis software: *Wing length* (mean of both wings, from the base of the subcosta to the wing tip), *eye height* (mean of both eyes measured from upper to lower margin), *body length* (anterior margin of head to posterior margin of posterior abdominal tergite). Any flies revealed to have obvious external parasites (mites) during this procedure were excluded from further analysis.

Behavioural scoring

The video recordings obtained in the field were scored on a PC configured as a time-event recorder using the Observer XT 7.0 (Noldus IT, Wageningen, The Netherlands) behavioural observation software. Observable footage duration varied between recordings (due to factors such as sudden movement leading to blurred images and individuals shifting position so as to obscure the focal individual of interest). Prior to scoring, an initial review of the recordings was used to define three distinct wing display behaviours of interest, as follows: *Single wing display*, one wing only is raised then immediately lowered; *double wing display*, both wings raised simultaneously then immediately lowered; *alternate wing display*, a single wing is raised then lowered followed immediately by the same movement of the alternate wing. The frequencies (number of occurrences during the observable portion of video footage) of each

of these individual wing movements and the number of mountings performed during the observation period were scored for each focal male. The duration of time spent preening and in locomotion were also scored, but these are not included in the analyses presented here. The videos were also used to estimate the number of conspecifics in the immediate vicinity of the focal individual at the start of the observation period, which was defined as the number of flies within a 10 body-length radius centred on the middle of the focal individual's body.

Statistical methods

To determine the effects of sex, size and the density of conspecifics on the occurrence of wing displays we used a series of generalised linear models with a Poisson error distribution, which we ran using the lme4 (Bates et al. 2013) package for R. The dependent variable was either the number of wing displays performed during the observation period or the number of mountings observed. Since observable periods varied in duration we used the offset function within lme4 to adjust for observations of differing duration. *A priori* we might expect the display rate to vary with body length and density, so we initially included the 'sex x body length' and 'sex x density' interaction effects as predictors in the models. We used similar models to assess the effects of morphology and display behaviour on the number of times males mounted other flies, and we used linear models with a normal error distribution to investigate the relationships between wing-length and body and eye length. Residuals extracted from these linear relationships were then used as predictors of display rate and mounting success.

Results

General observations of seaweed flies

Initial analyses of temperature, wind speed and humidity indicated that these variables did not influence wing displays, so these were not included in subsequent analyses. In the three aggregations sampled to estimate sex ratio we found 41 males and 16 females, (proportion of males = 0.72) such that the sex-ratio in these aggregations was significantly male-biased ($\chi^2_1 = 10.97$, $P < 0.001$). Body lengths ranged from 4.01 to 6.5mm (males; mean = $5.39 \pm \text{SE} = 0.11$, females; mean = $5.54 \pm \text{SE} = 0.23$) and were normally distributed (Figure 1).

Display behaviour in males and females

Males performed single wing flicks more frequently than females ($\chi^2_1 = 259$, $P < 0.0001$). The rate of single wing flicks increased with body size ($\chi^2_1 = 5.0$, $P < 0.05$) (Figure 2) and with the number of individuals in proximity to the focal individual ($\chi^2_1 = 59$, $P < 0.0001$) (Figure 3a). Significant interaction effects between sex and size ($\chi^2_1 = 17.0$, $P < 0.0001$) and sex and density ($\chi^2_1 = 9.7$, $P < 0.002$) indicated that the effects of body size and density were present in males but absent in females (see figures 2 and 3a). In the case of double wing flicks there was no interaction between sex and density ($\chi^2_1 = 0.6$, *NS*) so this was removed and the model

recalculated. Males performed more double wing flicks than did females ($\chi^2_1 = 997$, $P < 0.0001$) and the number of double flicks increased with the number of surrounding individuals ($\chi^2_1 = 851$, $P < 0.0001$) (Figure 3b) but there was no overall effect of body size on double flick rate ($\chi^2_1 = 0.4$, *NS*). However, a significant interaction between sex and body length indicated that the double flick display rate increased with body size for males but did not vary with body size for females ($\chi^2_1 = 4.5$, $P < 0.05$) (see figure 3b). For alternate wing flicks there were no significant interaction effects between sex and density ($\chi^2_1 \approx 0$, *NS*) or sex and body length ($\chi^2_1 \approx 0$, *NS*) so these were removed and the model recalculated. Males performed more alternate wing flicks than did females ($\chi^2_1 = 320$, $P < 0.0001$) but the number of alternate wing flicks by focal individuals decreased with the number of surrounding individuals ($\chi^2_1 = 43$, $P < 0.0001$) (Figure 3c). The number of alternate wing flicks did not show significant variation with body length ($\chi^2_1 = 3.5$, $P = 0.06$).

Analysis of single wing flicks in males only

We conducted the following analyses on data for males only. Since the clearest pattern of display use emerged for single wing-flicks we focussed on this behaviour here, and in the following analyses. For ready comparison the parameter estimates from the following analyses of wing flicking and mounting behaviour are given in Table 1. The rate of single wing flicks by males increased with body length ($\chi^2_1 = 7.86$, $P = 0.005$) and wing length ($\chi^2_1 = 16.69$, $P < 0.0001$) but not with eye length ($\chi^2_1 = 2.5$, *NS*). In each model there was a significant effect of density ($P < 0.0001$, $\beta = 0.06 - 0.07 \pm \text{SE} = 0.009$).

Single wing flicks by males with smaller and larger than expected wings

For males only we first used linear models, with a normal error distribution, to obtain relationships between wing length and body length and wing length and eye height. In both cases there was a significant linear relationship, with males with larger bodies ($F_{1,25} = 33.7$, $P < 0.0001$, (Figure 4a) and larger eyes ($F_{1,21} = 8.95$, $P < 0.007$, (Figure 4b) having longer wings. Wings had a hypoallometric ($\beta = 0.58 \pm \text{SE} = 0.1$) relationship with body length and a hyperallometric ($\beta = 3.4 \pm \text{SE} = 1.14$) relationship with eye height. To further explore the relationships between these different organs we also regressed eye height against body length and found a hypoallometric relationship indicating that eyes grow slowly in relation to overall body size ($F_{1,21} = 9.1$, $P < 0.007$, $\beta = 0.07 \pm \text{SE} = 0.02$). Analysis of allometric relationships is often performed on log-transformed data, so that linear relationships may be obtained in cases where the growth of one structure in relation to another reaches an asymptote (Huxley 1972). However, visual examination of the data indicates that there is no evidence of this here. Moreover, as in previous studies of signal residuals, use of raw data allows the extraction of meaningful values for the analyses that follow.

We then used linear models (with a Poisson error structure, weighted for observation duration as above) to determine the effect of residual wing length on the rate of wing flicking.

As above, we again included density as a covariate. Males that had larger than expected wings in terms of body length (positive residuals) tended to perform more displays than those with shorter than expected wings (negative residuals) ($\chi^2_1 = 7.42$, $P = 0.0006$) (Figure 4c) but there was no effect of wing length relative to eye height on the number of displays ($\chi^2_1 = 1.8$, *NS*) (Figure 4d). In both models display rate increased with density ($P < 0.0001$, $\beta = 0.07 \pm \text{SE} = 0.008$, in each case). Since eye height increases as a function of body length, to aid our interpretation of the effect of residuals from the relationship between wing-length and eye-height, we repeated this analysis based upon the residuals from wing length regressed on eye height corrected for body length (eye length / body length). This provides a measure of eye height independent of body length. There was no significant variation in wing length as a function of eye height corrected for body length ($F_{1,21} = 1.1$, *NS*) (Figure 4e). Nevertheless, the number of displays increased with eye height corrected for body length ($\chi^2_1 = 4.3$, $P = 0.03$) and individuals with positive residuals from the relatively flat relationship (between wing size and eye size / body size) also performed more displays compared to those with negative residuals ($\chi^2_1 = 4.5$, $P = 0.03$) (Figure 4f). Again, there was a significant effect of density on display rate in this model ($\chi^2_1 = 53.1$, $P < 0.0001$; $\beta = 0.06 \pm \text{SE} = 0.009$).

Mounting

The number of mountings was not influenced by male body-length ($\chi^2_1 = 0.34$, *NS*) but there was a near-significant trend for the number of mountings to decrease with male wing-length ($\chi^2_1 = 3.8$, $P = 0.052$) and the number of mountings increased with male eye height ($\chi^2_1 = 13.6$, $P = 0.0002$), an effect that remains when eye height is corrected for body size ($\chi^2_1 = 14.98$, $P = 0.0001$) (Figure 5). In previous studies of the effect of signal residuals and outcomes (e.g. Hughes 2000; Briffa 2006), the outcomes were binary categories (e.g. win or lose) but here we observed males mounting several individuals during the observation period, so our response variable is continuous count data. Therefore, as above, we used a linear model with Poisson errors (again offset by observation duration, and including density as a covariate) to determine whether the number of times that focal males mounted another fly varied with morphology and display performance. The number of mountings decreased with wing length residuals on body-length ($\chi^2_1 = 13.7$, $P < 0.0005$) and eye height ($\chi^2_1 = 30.2$, $P < 0.0001$) (Figure 6). This effect remained when wing length residuals are calculated against eye height adjusted for body length ($\chi^2_1 = 3.8$, $P = 0.049$). In each of these models, density again had a significant effect on the number of mountings ($P < 0.0001$ in each case, raw measures: $\beta = 0.12 - 0.13 \pm \text{SE} = 0.17 - 0.19$, residual measures: $\beta = 0.10 - 0.12 \pm \text{SE} = 0.17 - 0.18$). In other words, males with large wings and eyes mounted more frequently, but males with larger than expected wings for the size of their body or the size of their eyes mounted less frequently. Overall, however, the number of times that males mounted other flies increased with the frequency of their displays ($\chi^2_1 = 9.1$, $P < 0.003$, $\beta = 0.015$) (Figure 7).

Discussion

Our analyses of wing displays, morphology and male mounting behaviour can be summarised as follows. Males performed more wing displays than females, females being very unlikely to perform these displays at all, and males performed more displays when conspecifics were in close proximity. Analysis of the sex-ratio indicates that the vast majority of these surrounding individuals are other males. Thus, wing-flicking appears to be a sexually selected trait in *F. tergina* that either facilitates inter-male competition or allows direct assessment of male quality by females. Indeed, single wing flick rate had a positive effect on the frequency of mounting, a pre-cursor of copulation in seaweed flies, so that males that displayed more had more opportunities for mating. In contrast to *C. frigida*, there was no evidence of a binomial distribution of male body sizes. The display rate was greatest in males with long wings and large eyes (adjusted for body length) but males that had larger wings than expected for their body length and eye length (adjusted for body length) also displayed more frequently. However, this increased display effort did not appear to benefit small bodied males (or those with small eyes) in terms of mounting. Rather, when males had larger than expected wings, there was a reduced chance of mounting. The only morphological character that had a positive influence on the frequency of mounting was eye size, an effect that remained when eye length was standardised against body length. Although mounting could be directed at males and females, it is required before copulation and therefore a higher mounting rate should correspond to a higher rate of copulation.

In *F. tergina*, then, the size of a conventional signal component (wing size) influences the rate of display, but wing-size itself does not influence the outcome (mounting). Rather, mounting success increases with an underlying trait related to wing size, investment in large eyes. In other examples where residuals from the relationship between the size of a conventional signalling structure and underlying traits have been analysed with respect of display frequency, the structure of interest (e.g. claws in crustaceans) does not function only as a signal. In fiddler crabs, hermit crabs, snapping shrimp and mantis shrimp the claw also serves as a weapon. Therefore, there is the possibility that receivers are assessing the displayed structure itself, rather than using it as an indicator of underlying quality. Indeed, in the shore crab, *Carcinus maenas*, which use their claws both for giving agonistic displays and as weapons during fights, claw strength (and hence fighting ability) correlates with several aspects of claw morphology (Sneddon et al. 2000). In the case of seaweed flies, large wings in males might similarly be of direct interest to receivers, rather than being indicative of another underlying trait. Large wings might increase the potential for dispersal and if wing size is heritable this could enhance offspring fitness. In this case we might expect wing size to have a positive effect on the chance of copulation, especially if wing displays are assessed by females (direct sexual selection). However, we found no evidence that large wings improve the chances of mounting, which is required prior to copulation, and in fact the frequency of mounting had a marginally negative association with wing size (table 1). Thus, since wing size correlates with body size and eye size, it might allow receivers to assess other underlying traits from a distance. Perhaps then, wing displays provide an initial source of information, but more accurate information (such as eye size) is gathered when individuals

are in closer proximity. It is curious that male body size did not influence mounting success, while eye length had a clear effect. In another seaweed fly *Coelopa ursina*, the importance of male body size derives from intersexual conflict, rather than female choice, whereby large males are difficult for mounted females to dislodge during a pre-copula struggle (Crean and Gilburn 1998). Perhaps then, this form of sexual conflict is absent (or less important) in *F. tergida*. Furthermore, investment in eyes might be more indicative of individual quality than overall body size. Eyes are costly sensory structures to maintain (in insects and other animals, Niven and Laughlin 2008) but investment in acute vision is of obvious benefit, and if heritable could enhance the fitness of offspring. It is also possible that large eyes confer a direct advantage on displaying males, facilitating the identification of flies to mount and the mounting process itself. Since male *F. tergida* mount both males and females there may be an element of scramble competition in the strategy of males for securing mountings, as seen in other flies such as *Rutilla micans* (Alcock and Smith 1995). If this is the case then males would presumably benefit from optimising the proportion of females that they mount, so as to avoid wasting time by mounting other males. Larger eyes therefore might also assist males in identifying the sex of other flies prior to mounting them. However, these two explanations for the positive effect of large eyes on mounting success (female preference and enhanced vision in males) are not mutually exclusive.

An alternative explanation for the association between high rates of wing flicking and mounting frequency is direct inter-male competition for access to females. Although the present study cannot rule out this possibility, this explanation seems the less likely than either female preferences of males with large eyes or enhanced visual acuity in males with large eyes. We observed large numbers of males, of varying body, wing and eye sizes, displaying simultaneously in dense aggregations. Yet we did not see any direct interactions among males, such as one individual retreating from another or any of the physical interactions typical of escalated fighting in dipterans (e.g. Benelli 2014). If these displays are indeed aimed at females rather than other males, these aggregations would share features associated with lekking behaviour, as in other species of insect including dipterans (Shelly and Kaneshiro 1991; Jones et al. 1998). Note, however, that seaweed flies also use the strandline as a food source. Furthermore, in *C. frigida* there is no evidence that females sample from the population of displaying males (Shuker and Day 2002) and it is yet to be established whether sampling is present in *F. tergida* females. It should also be noted that female choice based on male displays and the use of such displays in direct inter-male competition are not mutually exclusive hypotheses. In fiddler crabs for example, claw waving displays by males are used both to attract females and in male-male contests (Zeil et al. 2006). There is also the possibility that greater wing flicking and mounting do not reflect courtship activity, but simply greater activity rates in general. However, the behaviours observed are cosimilar to courtship behaviour in other diptera (e.g. Zimmer et al. 2001), and it thus seems unlikely that males (but not females) would perform wing flicks and mounting if these activities did not lead to opportunities for copulation.

Previous studies on flies have found that animals observed in artificial environments might demonstrate a reduced or different suite of behaviours compared to those in the wild

(Suzuki and Koyama 1980). Thus, our field based observations reported here are a necessary first step in elucidating the behavioural repertoire and functions of wing displays in *F. tergina*. It is clear that having established this basic information on male displays, manipulative laboratory experiments are now warranted. In particular, experiments will be required to elucidate the causes of the mounting advantage for males with large eyes, to explore the relative contribution of direct and indirect sexual selection to these displays, and to investigate the relationship between mating opportunities (mounting of females) and eventual copulation. It appears clear, however, that in common with many other dipterans, *F. tergina* males do engage in a display behaviour that appears to be directly related to their success in acquiring mating opportunities. Moreover, there is evidence of exaggerated displays on the part of low quality males with large wings but relatively small bodies and eyes. However, this high display rate did not translate into greater mounting success. Although these males with larger than expected wings put more effort into displays, the most successful males (in terms of mounting) are those with large eyes, that wing flick at a high rate using wings that are proportionate to their body size and eye size. Conversely, males with small bodies and eyes for the size of their wings achieve fewer mountings but may attempt to compensate for this by performing wing displays more frequently. Although we did not detect any benefits from this (i.e. enhanced mounting) there might be marginal gains, for example during periods when there are few competitors in close proximity.

We observed exaggerated displays within aggregations of males. In the case of simultaneously displaying male fiddler crabs exaggeration is possible due to rapidly regenerated appendages (Backwell et al. 2000) but here we show that it may also occur as a result of normal variation around the relationship between the size of conventional signal components and measures of underlying quality. Male displays have not previously been documented in seaweed flies, and are absent in the heavily studied species *C. frigida* (Day et al. 1990). Nevertheless, our findings seem relevant to this species as well. In previous studies of *C. frigida*, male size is typically quantified as wing length (Shuker and Day 2002). Although highly correlated with body length (as in the case of *F. tergina*) the variance around this body size – wing size relationship has yet to be examined with respect of mating success in this species or in any other species of dipteran, a group which has proved extremely useful in the study of sexual selection. Our study shows that although wing displays can be exaggerated in *F. tergina*, males appear to receive little benefit from their efforts.

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Table 1: Parameter estimates for the effect of raw morphological measures and wing-length residual measures on the rate of single wing flicking and the rate of mounting by male flies. Significant effects are shown in bold (see text for test statistics and P-values).

Parameter	Single wing flicks		Mounting	
	Estimate	SE	Estimate	SE
Body length	0.26	0.08	0.21	0.27
Wing length	0.66	0.13	-0.21	0.26
Eye length	1.16	0.82	8.18	0.21
Eye length / body length	0.40	0.14	22.8	0.20
Residuals (Wing v body length)	0.78	0.19	-1.19	0.40
Residuals (Wing v eye length)	0.49	0.18	-1.20	0.30
Residuals (Wing v eye / body length)	0.43	0.14	-0.28	0.31

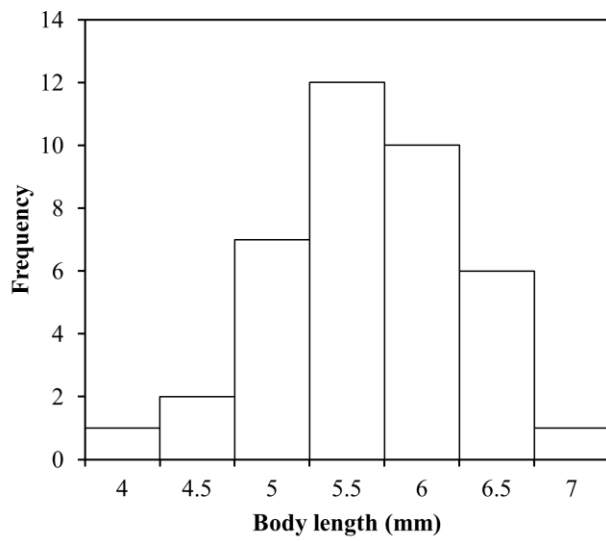


Figure 1: Frequency distribution of *F. tergina* body lengths (males and females combined).

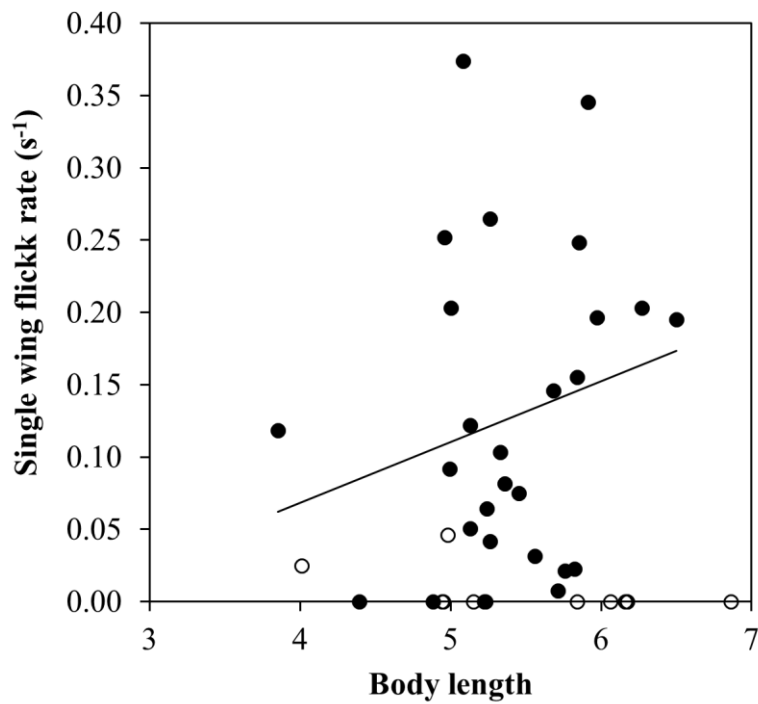


Figure 2: The positive correlation between body size and number of single wing flicks for males (filled circles) and females (open circles). Regression line fitted to male data only for illustration.

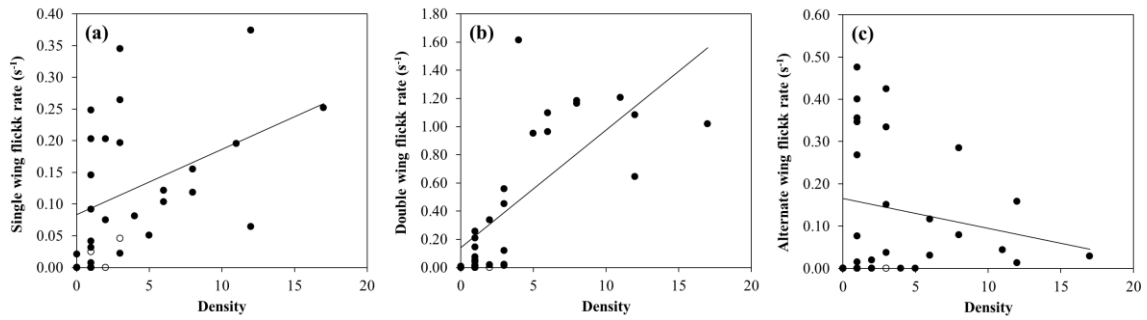


Figure 3: The positive correlation between density and single wing flicks (a) and double wing flicks (b), and the negative correlation between density and alternate wing flicks (c). Filled circles represent males and open circles represent females. Note that few points for females are visible because their display rates converge on or close to zero. Regression line fitted to male data only, for illustration.

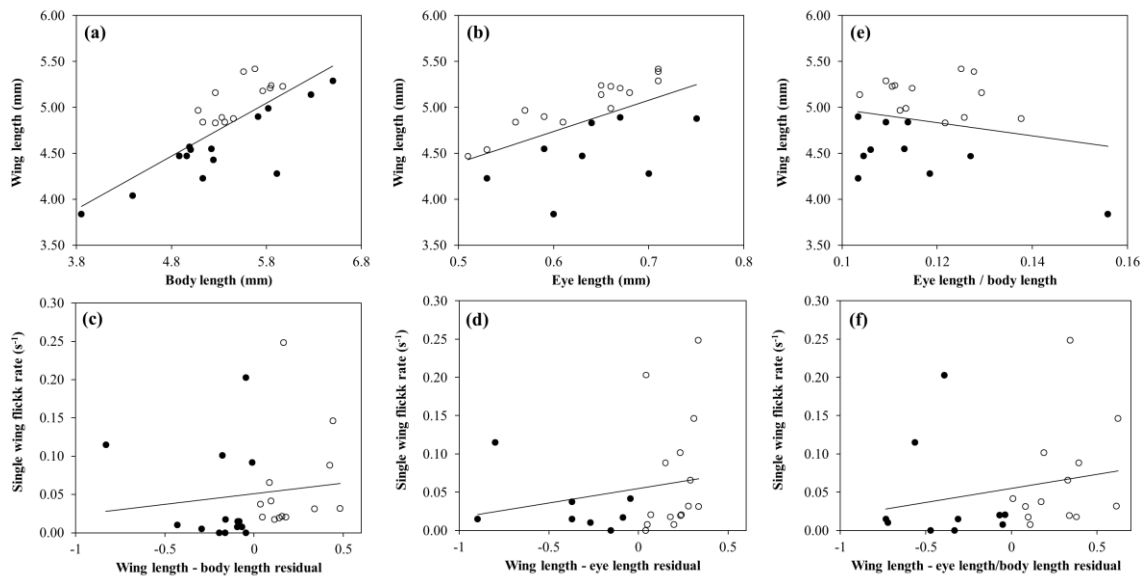


Figure 4: Analysis of residuals from wing-body size and wing-eye size relationships. The upper panels show the correlations between body length (a), eye length (b) and eye length corrected for body length (e) and wing length. Open circles show individuals with positive residual wing length values and closed circles show individuals with negative residuals. The lower panels (c), (d) and (f) show the correlations between residuals and display rate. Note that since display rate is highly dependent on density, the single wing flick rates displayed here have been adjusted for density. Regression lines fitted for illustration.

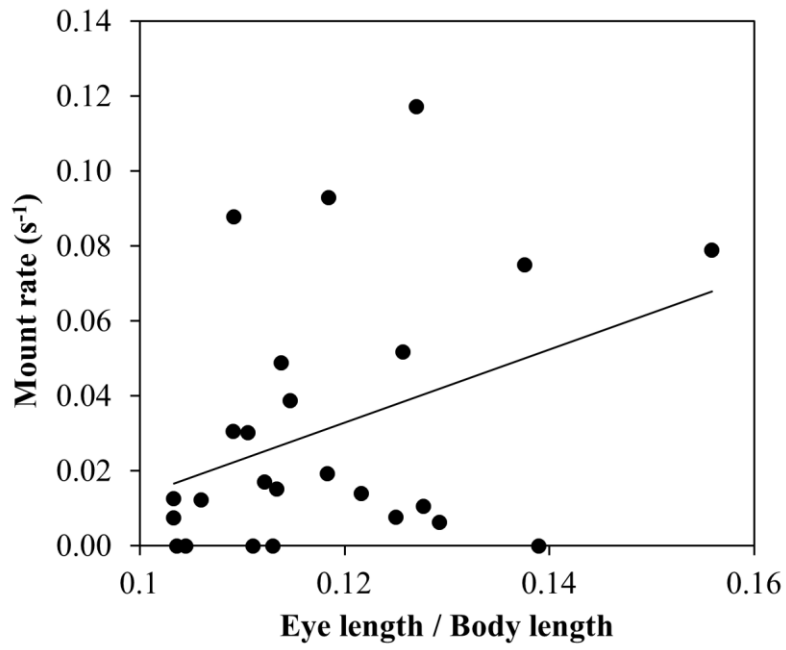


Figure 5: The positive correlation between male eye length standardised for body length and the number of mountings that they achieved during the observation period. Regression line added for illustration.

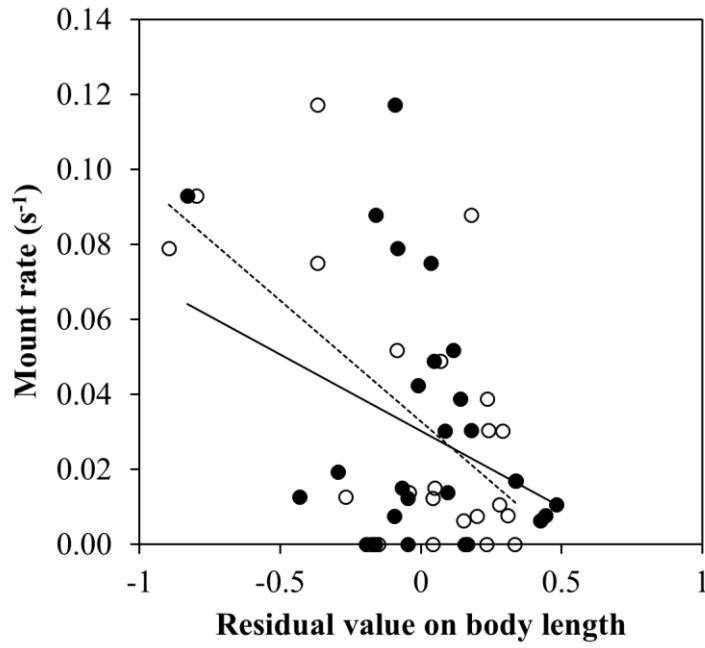


Figure 6: The negative correlations between residuals of wing-length on body-length (filled circles, solid line) and eye length on body length (open circles, dashed line), and mounting rate in males. Regression lines fitted for illustration.

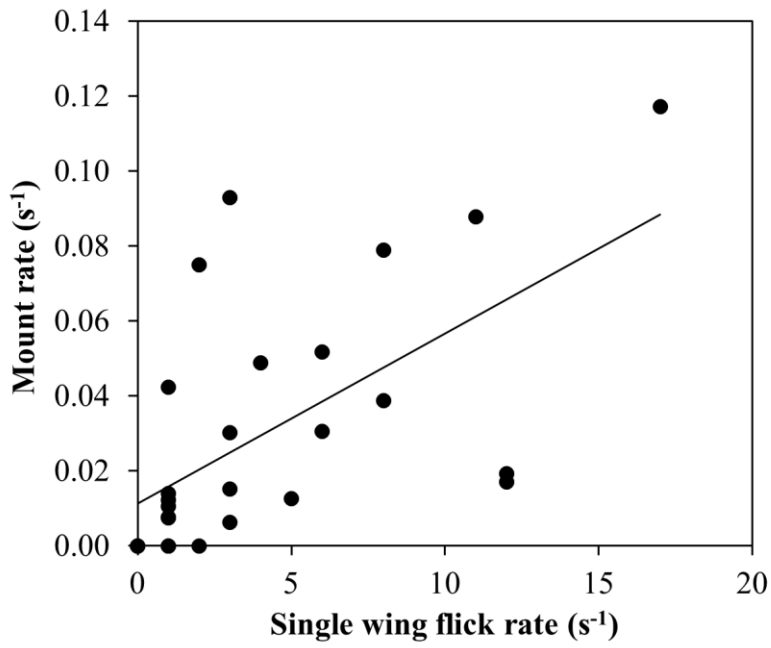


Figure 7: The positive correlation between number of single wing flicks performed by focal males and the number of mountings that they achieved during the observation period. Regression line fitted for illustration.