DO WING MARKINGS IN FRUIT FLIES (DIPTERA: TEPHRITIDAE) HAVE SEXUAL SIGNIFICANCE?

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ABSTRACT

The patterned wings of tephritid fruit flies often are moved in complex manners during sexual encounters. However, there are few cases of sexual dimorphism, and wing movements also may occur in non-sexual contexts. There was no evidence that enhancing or obliterating the patterns on the wings of male Caribbean fruit flies, *Anastrepha suspensa* (Loew), had any effect on their sexual success. There is convergence in wing patterns with another Dipteran family, the distantly related Bombyliidae. Additional studies of mating systems with this family might illuminate the significance of similar wing patterns in tephritids.

Key Words: sexual selection, mate choice, sexual signal, insect vision, Bombyliidae, courtship, crypsis

RESUMEN

Las alas moteadas de las moscas tefrítidas de fruta a menudo son movidas de una manera compleja durante los encuentros sexuales. Sin embargo, hay pocos casos de dimorfismo sexual, y los movimientos de las alas pueden occurir en un contexto no sexual. No hubo evidencia que el incremento o eliminación de los patrones sobre las alas de los machos de la mosca de la fruta del Caribe, *Anastrepha suspensa* (Loew), tuvo un efecto sobre el exito sexual. Hay una convergencia de los patrones de alas con otra familia en el orden Diptera, la familia Bombyliidae, que esta relacionada lejanamente. Estudios adicionales de los sistemas de apareamiento con esta familia podrian exclarecer el significado de los patrones similares de alas en los tefrítidos.

The wings of tephritid fruit flies, often intricately patterned with spots, stripes, and blotches, are both lovely and mysterious. Within the superfamily Tephritoidea, only the wings of the Lonchaeidae are typically unmarked (Sivinski 2000), and in the Tephritidae, relatively few species, such as some *Bactrocera* spp. and *Neospilota* spp., have largely hyaline wings (e.g., Foote et al. 1993). Yet the significance(s) of these common and complex colorations is obscure.

In many tephritids, specialized wing movements occur in a sexual context (Sivinski et al. 2000). Wings are moved rapidly to create acoustic signals and perhaps to waft pheromones (e.g., Sivinski et al. 1984), but are also more slowly tilted and/or held away from the body in a variety of motions and postures (Headrick & Goeden 1994). These have been described as: (1) arching- the wings are held over the dorsum, slightly spread, and arched from the base to the apex such that the tips nearly touch the substrate; (2) enanation- the extension of both wings away from the body simultaneously; (3) hamation- the movement of the wings together over the dorsum or while they are extended away from the body; (4) lofting- both wings are extended upward 90 degrees above the substrate and supinated up to 90 degrees; and 5) supination- bringing the wing forward perpendicular to the long axis of the body while the ventral surface of the wing is turned to face anterior such that the costal margin of the wing is dorsal (White et al. 2000).

It is tempting to hypothesize that elaborate wing patterns and complex wing movements contribute to visual sexual signals (e.g., Bush 1969), and wing coloration, movements and mating systems frequently are correlated in Californian tephritid genera (Headrick & Goeden 1994). If patterns are sexual signals, it may be no coincidence that clear-winged lonchaeids are the only tephritoid family that appears frequently to mate in aerial swarms where wing patterns are unlikely to serve a communicative function (McAlpine & Munroe 1968; Sivinski 2000). However, there are several inconsistencies in the wing pattern and movement as sexual signal argument. Sexual dimorphisms might be predicted in courtship signals directed by males to females, but differences in visible-light wing patterns are relatively rare, although there are some striking exceptions. For example, *Aciurina idahoensis* Steyskal females have striped wings and males spotted, and in the related *A. semilucida* (Bates), female wings are striped and male wings fully infuscated (Headrick

& Goeden 2000). In some instances, e.g., *Trupanea* spp., dimorphisms are the opposite of expectation with male wings fainter or having fewer markings (Foote et al. 1993). Only the wings of two species, the Caribbean fruit fly, *Anastrepha suspensa* (Loew) and the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) have been examined for ultra-violet reflectance and transmittance (Sivinski et al. 2005). There is little UV transparency in the wings, and there is no sexual dimorphism when placed against a non-UV reflective background such as the leaves from which males are likely to be sexually signaling.

Other objections against patterned wings performing simple sexual signals include the complex wing movements of females, and the wing motions by males and females in apparently nonsexual situations. For example, in the genus *Goedenia* both sexes exhibit hamation throughout the day while grooming, resting, and feeding (e.g., Goeden 2002), although in such species there are often male wing movements unique to courtship (Headrick & Goeden 1994). In addition, markings are occasionally known to serve non-sexual purposes. When seen from behind, the wing patterns of *Zonostemata vittigera* (Coquillett) and *Rhagoletis zephyria* Snow create the illusion of a salticid spider seen face on and the resemblance deters spider attacks (Greene et al. 1987, Mather & Roitberg 1987).

In order to test the hypothesis that wing patterns have been sexually selected and contribute to sexual success, we first quantified the design of wing markings among North American Tephritdae and contrasted these markings to those of a distantly related brachyceran fly family, the Bombyliidae. The latter family was chosen for comparison and contrast because of the large number of species bearing wing patterns and its distant phylogenetic relationship to fruit flies. We then performed an experiment designed to test the importance of wing patterns in male *A. suspensa* sexual success.

MATERIALS AND METHODS

The Nature and Distribution of Wing Patterns

We quantified wing marking patterns in the Tephritidae and Bombyliidae in the following manner. First, illustrations of wings were roughly divided into quadrants: frontal-distal, frontal-proximal, trailing-distal, and trailing-proximal. Then, the markings in each quadrant were characterized as either clear, dark, spotted, striped, or stellate (clear spots on a dark background) and given a numeric value depending on the patterns location on the wing (i.e., a lack of markings in the frontal-distal section would be given the numeric value of 1, in the frontal-proximal the same condition would be characterized as 6, in the trailing-distal it would be 11 and in the trailing-proximal 16). Wings were then categorized by the combined nature of the markings in each quadrant, e.g., dark in frontal proximal and clear in all others or striped in all quadrants but trailing-proximal. Thus a completely hyaline wing would be described by the combined numbers listed above and have the designation 161116.

The samples of wings were obtained from large taxonomic works (Tephritidae; Foote et al. 1993 and Bombyliidae; Hull 1973). The tephritid samples included a species from every North American genus (n = 57 in 3 subfamilies), and multiple species if there was diversity of wing pattern within the genus. Although we attempted to capture pattern diversity at the generic level, this method did not quantify the actual proportions of any particular pattern at the species level. For example, if genus X has 10 species, 9 of which have stripped wings and one spotted, both stripes and spots would be included in the data by a single example. The bombyliid sample contained for the most part single species from each of the 193 genera in 14 subfamilies, but multiple species were included when divergent wing patterns were apparent. However, we did not have access to the wing patterns of every species and as a result we were more likely to have underestimated the diversity in wing pattern in this family than in the Tephritidae. Because of the shortcomings in the samples, the results should be viewed as illustrating possible qualitative examples of convergence and divergence in wing patterns.

Sexual Success Following Wing Pattern Manipulation

The role of wing pattern in male sexual success was investigated by either obliterating or enhancing wing markings. First, virgin female *A. suspensa*, 15-21 d old, were transferred from 20 × 20 × 20-cm screen cages to smaller cylindrical screen cages (6.3 cm × 8.8 cm) prior to the experiment. Temperatures throughout the maturation and experimental periods were 25 ± 1°C and relative humidity 55% ± 5%. Three mature males 15-21 d old that had been treated in the three different manners described below were then added to the cage and their sexual successes noted. The three treatments were: (1) males removed from larger holding cage, chilled and then placed on a plastic sheet that had been stretched over ice; (2) dark wing markings on similarly treated males painted over with a brown India ink artists pen (Faber Castell, Pitt artist pen, medium point, brown, Cleveland, OH 44125); and (3) the hyaline spaces between dark wing markings filled in with the same ink. It was difficult to obtain a marking substance that would adhere to tephritid wings. India ink was the best of several alternatives, but even this coverage deteriorated rapidly over time. Because of this, males were marked the morning prior to sexual exposure in the afternoon (during the last 4 h of the photoperiod). There were 100 replicates and the sexual successes of the various treatments were compared by contingency χ^2 test (Zar 1974).

Male characteristics other than wing pattern, specifically large male size, are known to influence sexual success (e.g., Sivinski et al. 1984). Because of this, we measured the wing lengths of all three males in each cage and they were given a relative rank. The summed ranks of successful males were then compared through a χ^2 test to an expected mean rank *n* replicates (expected product of rank = 2 × 100 = 200) had mating occurred regardless of size. There might also have been an interaction of pattern and size, so that a small male that suffered in competition with a larger rival overcame this disadvantage with a more attractive wing pattern. This possibility was examined with a Mann-Whitney nonparametric *U*-test (Zar 1974) by comparing the rank-sizes of mating males that had their patterns emphasized with ink and those whose patterns had been obliterated. Specifically, we looked to see if a male with one painted treatment was more likely to mate when smaller than was a male with the other treatment.

RESULTS

The Nature and Distribution of Wing Patterns

Keeping in mind the differences in the tephritid and bombyliid samples, there are some suggestive similarities in the types of wing patterns and interesting differences in their purported distribution within their respective families (Fig. 1). Unmarked wings were more common in the Bombyliidae (36%), as were fully infuscated patterns. Pattern diversity appeared to be greater in the bombyliids with 42 patterns other than all hyaline displayed by 126 species (0.33 patterns / species) as opposed to 12 patterns in 61 species of Tephritidae (0.20 patterns / species). The majority of genus-level wing patterns in the Tephritidae were stellate or barred, with a smaller number of spotted and darkened-costal region patterns. Certain patterns were typical of different tephritid subfamilies: 87% of Trypetinae wings patterns could be characterized as barred, while the diversity in the Dacinae and Tephritinae was greater. The Dacinae is relatively species-poor in North America and excluded from further discussion. There were nine different wing patterns found in the Tephritinae, but the most common were stellate (29%) and, again, barred (36%).

Sexual Success Following Wing Pattern Manipulation

There were no significant differences in sexual success among wing treatments: Mated (untreated) = 37; (pattern enhanced) = 32; (pattern obliterated) = 31 ($\chi^2 = 0.62$; $P > 0.50$). There was no evidence that male size by itself played a role in male sexual success (mean size rank of successful males= 1.97; expected value from random mating= 2.0; $\chi^2 = 0.09$; $P > 0.95$). While males who mated and whose patterns had been enhanced tended to be relatively larger than males that mated and had their patterns obliterated (mean rank= 1.69 and 2.11, respectively), the difference was not significant ($U = 252$; $Z = 1.56$, $P = 0.12$).

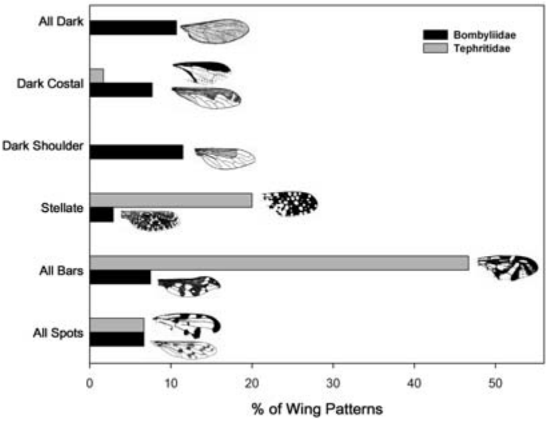

Fig. 1. The more common wing patterns found in Tephritidae (from Foote et al. 1993) and Bombyliidae (Hull 1973) and their proportions of the total number of pattered wings sampled.

DISCUSSION

Given these results, wing markings remain lovely and mysterious; there was no evidence that markings played a role in the abilities of males to mate. However, we do not wish to overstate our results and conclude that markings have no communicative or sexual importance. Negative evidence is often difficult to interpret and, given the limitations of small cage experiments in the laboratory such as restricted movement and atypically high densities, and the likely inexact match of the brown ink to the color of the wing markings, a different experiment may well yield different results. That being said, the present result of finding no diminution of mating success following rather gross manipulation of the markings suggests that alternative explanations for the evolution of wing patterns in the Diptera should at least be considered (see True 2003).

One alternative, spider mimicry, was mentioned in the introduction. Also, the distinctive outline of an animal may be obscured by a disruptive pattern of stripes and spots (Cott 1940) and a resting fly with patterned wings might be thus camouflaged. Beside sexual signaling and adaptive coloration, another hypothesis is that pigments such as melanin are structural components of the wings and that any resulting visual effect is fortuitous and without significance. For example, melanin pigmented surfaces warm up faster and cool down more quickly in a variety of insects, and melanic cuticle can be more resistant to abrasion than unpigmented cuticle (Majerus 1998). The numerous instances of coloration along the leading edge of the wing in the vicinity of the costal vein might be consistent with pigments strengthening a region that receives unusual stress. It may be that all of these factors play a role, and that ". . . wing displays and patterns are part of a dynamic system involving reproductive behavior, crypsis, and thermoregulation" (Headrick & Goeden 1994).

The seeming convergence in wing patterns between the Tephritidae and the Bombyliidae, at least in type if not frequency of design, might offer an opportunity for illuminating comparisons. Little has been published on the mating systems of bee flies. Males in *Comptosia* sp. near *latealis* Newman, perch in clearings and dart at nearby flying insects (Yeates & Dodson 1990). The wings in this genus are typically darkly pattered (Hull 1973), but male-male interactions occur in flight, as do at least some of the matings, which may argue against wing markings having any significance as courtship signals. Males of *Lordotus pulchrissimus* Williston form mating swarms (Toft 1989). The wings of this genus are generally hyaline (Hull 1973) and so are consistent with an aerial lack of signaling opportunity.

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