

Ultra violet reflectance on the heads and wings of *Anastrepha suspensa* (LOEW) and *Ceratitis capitata* (WIEDEMANN) (Diptera: Tephritidae)

[Reflexion ultravioletten Lichts an den Köpfen und an den Flügeln von
Anastrepha suspensa (LOEW) und *Ceratitis capitata* (WIEDEMANN) (Diptera: Tephritidae)]

by

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Abstract

Tephritid fruit flies have a number of behaviors and structures suggestive of visual sexual and agonistic displays. These include elaborate and stylized movements of patterned wings in both the Caribbean fruit fly [*Anastrepha suspensa* (LOEW, 1862)] and the Mediterranean fruit fly [*Ceratitis capitata* (WIEDEMANN, 1824)] and the white, sexually dimorphic, face of male *C. capitata*. Ultraviolet (= UV) reflections may play a previously undescribed role in these displays, particularly since nearly all tephritid species so far examined exhibit a peak of spectral sensitivity at the UV wavelength of 365 nm. The faces and wings of both male and female *A. suspensa* and *C. capitata* were compared for reflectance at 365 nm. Male *C. capitata* faces reflected more UV than those of females, but the faces of *A. suspensa* were monomorphic. UV reflectance of the wings depended on the reflectance of the background, presumably because portions of the wing are translucent. There were significant sexual differences in UV reflectance / translucency in both species when observed against a highly reflective background. Male *C. capitata* and female *A. suspensa* wings were UV- brighter than those of their opposite sexes. However, this dimorphism was limited to UV- bright backgrounds, and relatively little UV was reflected from the leaves of important host plants and mating sites, *Psidium guajava* L. (for *A. suspensa*) and *Coffea canephora* var. *robusta* L. (for *C. capitata*). A larger sample of more complete descriptions of purported visual signals, including more UV measurements, are needed to better test the several hypotheses advanced to explain their evolution.

Key words

visual signal, courtship, Mediterranean fruit fly, Caribbean fruit fly

Zusammenfassung

Bohrfliegen (Tephritidae) weisen eine ganze Anzahl von Verhaltensweisen und Strukturen auf, die optisch dominierten sexuellen Verhaltensmustern oder Werbeverhalten dienen. Diese schließen umfangreiche, festgelegte Bewegungsabläufe der gemaserten Flügel bei der Karibischen Bohrfliege [*Anastrepha suspensa* (LOEW, 1862)] und der Mittelmeerfruchtfliege [*Ceratitis capitata* (WIEDEMANN, 1824)] und das weiße, geschlechtsspezifische Gesicht des Männchens von *C. capitata* ein. Reflexionen von ultravioletten Lichtanteilen (= UV) wurden bislang kaum untersucht, könnten jedoch eine besondere Bedeutung in diesen Verhaltensmustern spielen, zumal fast alle der untersuchten Tephritiden-Arten einen Peak der Empfindlichkeit für die UV-Wellenlänge von 365 nm aufweisen. Die Gesichter und Flügel der Männchen und Weibchen von *A. suspensa* und *C. capitata* wurden dahingehend untersucht, ob sie UV-Licht dieser Wellenlänge reflektieren. Das Gesicht der Männchen von *C. capitata* spiegelt mehr UV-Licht wider als das der Weibchen, wohingegen die Gesichter beider Geschlechter von *A. suspensa* die gleichen Eigenschaften hinsichtlich ihres Reflexionsvermögens aufweisen. Bei den Flügeln hängt das Vermögen UV-Licht widerzuspiegeln auch von den Reflexionseigenschaften des Untergrundes ab. Dies ist vermutlich darauf zurückzuführen, dass Teile des Flügels durchscheinend sind. Es ergaben sich signifikante Unterschiede dieses Parameters und der Durchsichtigkeit des Flügels zwischen den Geschlechtern bei beiden Arten, wenn gegen einen stark reflektierenden Untergrund gemessen wurde. Die Flügel der Männchen von *C. capitata* und der Weibchen von *A. suspensa* reflektierten UV-Anteile stärker als das jeweils andere Geschlecht. Jedoch war dieser Dimorphismus in seinem Auftreten auf solche Untergründe beschränkt, die UV-Licht stark reflektierten. Im Vergleich dazu wurde relativ wenig UV-Licht von den Blättern wichtiger Wirtspflanzen bzw. bedeutsamer Treffpunktplätze reflektiert. Mes-

sungen erfolgten an *Psidium guajava* L. (im Falle von *A. suspensa*) und *Coffea canephora* var. *robusta* L. (bei *C. capitata*). Die vermutete Funktion der optischen Reize und Merkmale muss hinsichtlich ihrer Bedeutung für die komplexen Muster und Verhaltensweisen noch viel umfassender untersucht werden, einschließlich weiterer UV-Reflexionsmessungen, um letztendlich die zahlreichen Hypothesen zu prüfen, die bezüglich der Entwicklungsgeschichte dieser komplexen Strukturen entwickelt wurden.

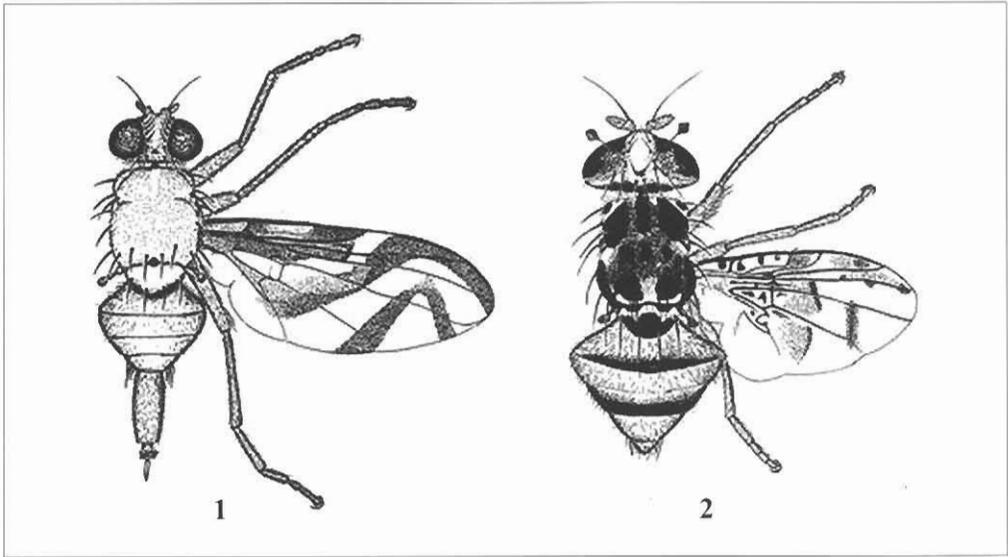
Stichwörter optische Signale, Werbungsverhalten, Mittelmeerfruchtfliege, Caribische Bohrfliege

Introduction

Purported visual signals consisting of color patterns and elaborate shapes occur widely in the Diptera, and among the acalypterate flies they are particularly numerous in the tephritoids (e.g., SIVINSKI 1997). Patterned wings are nearly universal in these families, only those of the Lonchaeidae are typically unmarked (SIVINSKI 2000). Striped, reticulate, stellate, radiate, or spotted wings may be presented in a variety of positions, including the intriguing peacock tail posture of the ulidiid (= otitid) *Callopietromyia annulipes* (MACQUART, 1855) that so struck the famous dipterist J. M. ALDRIDGE that he mounted his specimens in the display position (STEYSKAL 1979). Within the Tephritidae, the variety and complexity of wing movements that occur in interactions with potential sexual partners and rivals has generated a specialized vocabulary including terms such as *arching* (... where the tips nearly touch the substrate.), *enantion* (...extension of both wings away from the body simultaneously.), *hamation* (... movement of the wings together over the dorsum ...), *lofting* (... the wings are held parallel to each other above the dorsum ...), and *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.) (HEADRICK & GOEDEN 1994; WHITE et al. 2000).

Many *Anastrepha* spp. males supinate in the presence of females (e.g., ROBACKER & HART 1985; SIVINSKI et al. 2000). In *Anastrepha suspensa* (LOEW) courting males spend an average 35 % of their time performing such wing motions (SIVINSKI & WEBB 1986). Additional wing postures include the arrowhead position assumed by courting male *Anastrepha striata* SCHINER, 1868 (ALUJA et al. 1993). Mediterranean fruit fly [*Ceratitis capitata* (WIEDEMANN) = medfly] males (and females under laboratory conditions), rotate their wings so that the ventral surface faces forward, but any synchronous wing movements in this supinate position are typically less pronounced than those of *A. suspensa* (e.g., EBERHARD 2000). In one experiment, mated males had longer, but not wider, wings than nonmating males (HUNT et al. 2001).

In addition to patterned wings, there are other tephritid colors, structures, and movements that suggest visual signals. These range from contrastingly white, mushroom-shaped pillars of trophylactic material deposited on leaf surfaces by the African *Schistopterus moebiusi* BECKER, 1903 (FREIDBERG 1981) to the plume-like abdominal setae of male *Copiolepis quadrisquamosa* ENDERLEIN. Relatively lengthy capitate anterior-orbital setae project from the frons of males of the *C. capitata*, and are even longer in congeners such as *Ceratitis catoirii* GUÉRIN-MÉNEVILLE, 1843 (WHITE & ELSON-HARRIS 1992). In addition, the face (= prefrons) of *C. capitata* is sexually dimorphic, being bright white in the male. Eye color is also sexually dimorphic in *C. capitata*, and the combination of male colors and exaggerated setae has long suggested a visual component to courtship. Medflies kept in darkness have an order of magnitude lower insemination rate (KEISER et al. 1973). Males with a mutant eye color have reduced mating success (RÖSSLER 1980), as do those whose capitate setae are removed (MENDEZ et al. 1998). *Ceratitis capitata* missing both supra-fronto-orbital bristles were rejected by females more often than those males with one or two bristles (HUNT et al. 2001).



Figs 1, 2: Habitus images of the investigated fruit fly species. – 1: Female *Anastrepha suspensa* (LOEW, 1862); – 2: Male *Ceratitis capitata* (WIEDEMANN, 1824). Reproduced with permission from WHITE & ELSON-HARRIS (1992).

However, there are few instances in insects, and fewer in flies, where a purported visual signal has been completely described. This is due in part to the possibility of unmeasured ultra-violet (= UV) reflectance potentially visible to an insect receiver but invisible to a human observer (e.g., SILBERGLIED 1984). Visual spectral sensitivity is similar in a phylogenetically broad range of tephritids (AGEE et al. 1982). *Ceratitis capitata*, *Bactrocera oleae* (GMELIN, 1790) and *Rhagoletis cerasi* (LINNAEUS, 1758), are all particularly sensitive to wavelengths in the range of 485–500 nm (yellow-green), and to a lesser extent, 365 nm (UV). Spectral response in *Rhagoletis pomonella* (WALSH, 1867), the apple maggot, has a broad peak at 400 to 530 nm (blue-green to yellow), a secondary peak at 360 to 365 nm (UV), and a plateau at 600 to 625 nm (orange-red) (AGEE 1985). The papaya fruit fly, *Toxotrypana curvicauda* GERSTAECKER, 1860, is unusual among tephritids, and insects in general, in that it does not have a sensitivity peak in UV wavelengths, but rather has bimodal spectral sensitivity at 475 nm (blue) and 500 nm (green) (LANDOLT et al. 1988).

In the following, we have examined the UV reflectance of two surfaces on *A. suspensa* and *C. capitata* that we judged might be used in signals directed toward the opposite sex or same-sex rivals. The first were the surfaces of the wings, which are turned toward conspecifics (supination) (Figs 1, 2). Wing visible-light colorations are similar in both sexes of both species, although the pigmented areas of females' wings in *C. capitata* often appear darker. Male wings in both species are slightly more oval (SIVINSKI & DODSON 1992). The second examined surface was the face (= prefrons), which in visible light is sexually dimorphic in *C. capitata* but apparently monomorphic in *A. suspensa* (Figs 1, 2).

Methods

Origin and treatment of insects: Wings and faces were dissected from *A. suspensa* obtained from a colony maintained for over 5 years by the Florida Department of Agriculture and Consumer Services = Division of Plant Industry in Gainesville, Florida. Live individuals of *C. capitata* were taken from lots of sterile insects shipped to Florida from the MOSCAMED

rearing facility at El Pino, Guatemala. *Anastrepha suspensa* and *C. capitata* faces and wings were removed immediately after death from the flies and frozen prior to use. Additional specimens of *C. capitata*, unexposed to florescent marking powder used to identify sterile flies, were also obtained from the MOSCAMED facility but were preserved in 70 % ethanol previous to shipping. After dissection, the ethanol was evaporated at room temperature overnight and the wings and faces were then frozen prior to use. Since there were no subsequent statistical differences between the reflectance of wings / faces obtained from the powder-exposed and powder unexposed-alcohol preserved *C. capitata* samples, the data from both were pooled.

Origin and treatment of host-plant leaf surfaces: Males of both *A. suspensa* and *C. ceratitis* form mating aggregations (leks) on host plants and perform courtships on the surfaces of leaves. In order to estimate the UV present in this sexual environment and so available for transmission through the hyaline portions of the flies' wings, both surfaces of leaves of important host plants were examined for UV reflectance. These plants were *Psidium guajava* L. (common guava, a host of *A. suspensa*; NORRBOM & KIM 1988) and *Coffea canephora* var. *robusta* L. (coffee, a host of *C. capitata*; LIQUIDO et al. 1991), and were grown on the grounds of the Center for Medical, Agricultural and Veterinary Entomology in Gainesville, Florida. Leaves were collected on the day of measurement and chosen as representative on the basis of size (medium) and color (green). They were gently cleaned with a paper towel and then cut into rectangular shapes.

Spectral measurement: All spectral measurements were made using a dual wavelength flying spot scanner (CS-9000, Shimadzu Scientific Instruments, Columbia, MD). The scanner is equipped with a xenon lamp and is capable of taking spectral measurements from 200–700 nm. Operation of the scanner was tested against three externally calibrated standards, silver paint (80–100 % reflectance), black velvet (1 %), and neutral gray (18 %). Two reflective backgrounds were used for wing-reflectance measurements: the first was paper painted with silver paint [high-level of reflectance; 4 layers of Plasti-kote enamel in aluminum (B30) painted on paper], and the second was black posterboard paper (low-level of reflectance (see figure 3 for reflectance of backgrounds at 365 nm). The substrates were used to provide several different background levels of reflectance when measuring UV reflectance of the wings. Wings were placed against the respective background and then aligned under the reference beam. Due to the relatively small size of the beam, the spot measured on the wing was selected at random. Faces were placed on the glass plate only and aligned under the reference beam. The scanner was set in reflection mode, and spectral measurements were taken from 200–700 nm using a beam size of 0.05×0.5 mm. These measurements were recorded as absorbance measures and then converted to percent reflectance. Wings from 10 males and 10 females of each species were examined against each background. Face reflectance was measured from 30 male and 30 female *A. suspensa* and from 11 male and 11 female *C. capitata*.

Ten leaves, tops and bottoms, of the host plants *P. guajava* and *C. canephora* var. *robusta* were measured for reflectance against a black velvet standard in a manner similar to the above. The densitometer beam area was 1.0×2.0 mm and centered between two veins.

Statistical analysis: All statistical comparisons were made at 365 nm because all tephritids so far examined, including *C. capitata*, have sensitivity peaks at this UV wavelength. To determine whether the wing reflectance against a particular background was different than the reflectance of the background alone, 2-sample, 2-tailed t-tests were used. To assess sexual dimorphism in faces of both species, 2-sample, 2-tailed t-tests were used. All statistical analyses were performed using SYSTAT 9.0 (SPSS Inc.).

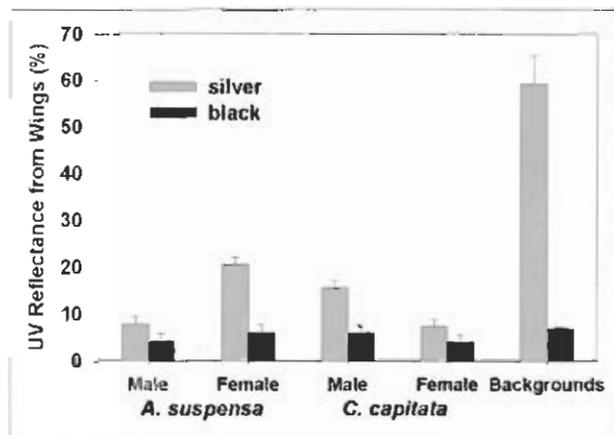


Fig 3: The mean percentages (SE) of ultraviolet reflectance at 365 nm measured on the surface of the wings of male and female *Anastrepha suspensa* (LUDW) and *Ceratitis capitata* (WILDEMANNS), and of the background materials on which the wing reflectance were measured (silver paint and black paper). The different backgrounds are examined because of the partial translucency of the wings. That is, "reflectance" is influenced by the amount of UV passing through translucent portions of the wing.

male *A. suspensa*, $df = 2.7$, $t = -8.006$, $p = 0.006$; female *A. suspensa*, $df = 2.8$, $t = -5.983$, $p = .012$; male *C. capitata*, $df = 3.1$, $t = -6.559$, $p = 0.007$; female *C. capitata*, $df = 2.0$, $t = -8.074$, $p = 0.012$) The reflectance of the wing against the black background was different from the reflectance of the black paper in male *A. suspensa* (2-tailed t-test, $df = 9.3$, $t = -2.930$, $p = 0.04$) and female *C. capitata* ($df = 9.8$, $t = -7.142$, $p < 0.001$), but was not significantly different in female *A. suspensa* ($df = 9.8$, $t = -1.536$, $p = 0.156$) or male *C. capitata* ($df = 9.3$, $t = -0.739$, $p = 0.479$).

Sexual dimorphism in UV reflectance of wings: Sexual dimorphism in UV reflectance of the wing depended on background in both species. There was a significant difference between males and females in both species when the wing was against a highly-reflective background (2-tailed t-test, *A. suspensa* wing against silver paint, $df = 18$, $t = -3.664$, $p = 0.002$; *C. capitata* wing against silver paint, $df = 9.5$, $t = 2.724$, $p = 0.022$), but not when against a low-level reflective black paper background (2-tailed t-test, *A. suspensa* wing against black paper, $df = 11$, $t = -1.68$, $p = 0.12$; *C. capitata* wing against black paper, $df = 14$, $t = -1.31$, $p = 0.21$). When against a highly reflective background, male *A. suspensa* wings were less reflective than females. Contrastingly, male *C. capitata* wings were more reflective than female wings when against the highly-reflective background.

Sexual Dimorphism of UV reflectance of the face: No sexual dimorphism was observed in the UV reflectance of the face in *A. suspensa* (2-tailed t-test, $df = 54.5$, $t = -0.636$, $p = 0.527$) (Fig. 4). The face of male *C. capitata* was significantly more UV reflective than that of the female ($df = 12.9$, $t = 2.224$, $p = 0.045$).

Between-species differences in UV reflectance: Male *C. capitata* faces reflected significantly more UV than male *A. suspensa* faces (2-tailed t-test, $p < 0.001$; Fig. 5), but there were no differences between the faces of female *A. suspensa* and *C. capitata* (2-tailed t-test,

Results

Effect of background on UV reflectance of males and female wings: Since portions of the wings of *A. suspensa* and *C. capitata* are translucent, we assessed the effect of background on UV reflectance in both male and female wings at 365 nm against a highly-reflective silver paint background and low-level reflecting black paper background. In both *A. suspensa* and *C. capitata* males and females, the level of reflectance of the wing against the background was not the same as the reflectance of the background alone. In other words, the wings were not perfectly transparent and the wing reflectance against silver paint was not the same as the reflectance of the silver paint alone (2-tailed t-test,

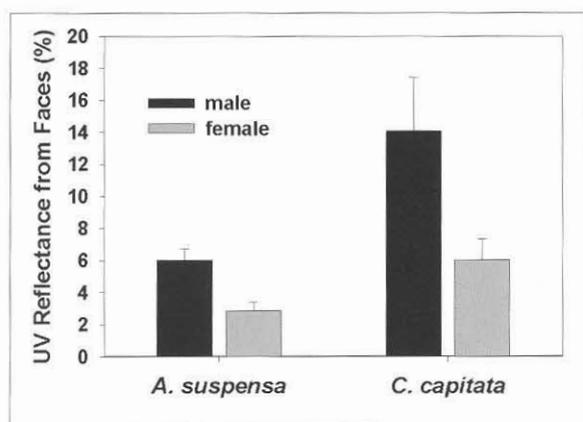


Fig. 4: Mean percentages (SE) of ultraviolet at 365 nm reflected from the faces (prefrons) of male and female *Anastrepha suspensa* (LOEW) and *Ceratitis capitata* (WIEDEMANN).

$p = 0.636$; Fig. 5). When examined against a low-level reflecting background, male *C. capitata* and *A. suspensa* wings reflect UV similarly, but there was a differences between the UV reflectance of the females = wings (males, 2-tailed t-test, black paper, $df = 18$, $t = 1.18$, $p = 0.25$; females, black paper, $df = 14$, $t = -2.44$, $p = 0.01$). When wings are examined against a highly reflective silver surface, the UV reflection of both male and female *C. capitata* and *A. suspensa* wings differ significantly (males, 2-tailed t-test, silver, $df = 17$, $t = -2.02$, $p = 0.029$; females, silver, $df = 10$, $t = 5.20$, $p < 0.0004$).

UV reflectance from the leaves of host plant / mating sites: UV reflectance from the upper and lower leaf surfaces of both *P. guajava* and *C. canephora* var. *robusta* were less than 10% (Fig. 6).

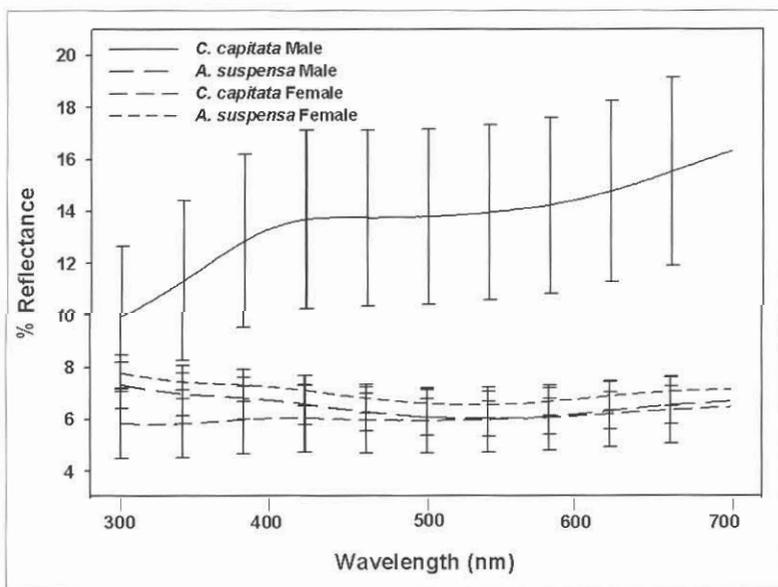


Fig. 5: Mean (SE) reflectance of ultra violet light (300–400 nm) and other, visible, wavelengths from the faces (prefrons) of male and female *Anastrepha suspensa* (LOEW) and *Ceratitis capitata* (WIEDEMANN).

Discussion

Ultraviolet reflection was greatest from the face of male *C. capitata*, the most obviously sexually dimorphic surface in visible wavelengths examined in either species. The male medfly's face is typically turned toward potential mates and sexual rivals, and its white appearance extended to its' capacity to reflect some UV as well as a broad spectrum of visible light. On the other hand, the UV reflectance of wings depended on the background against which they were viewed, as might be expected from objects consisting of mixed translucent and pigment-

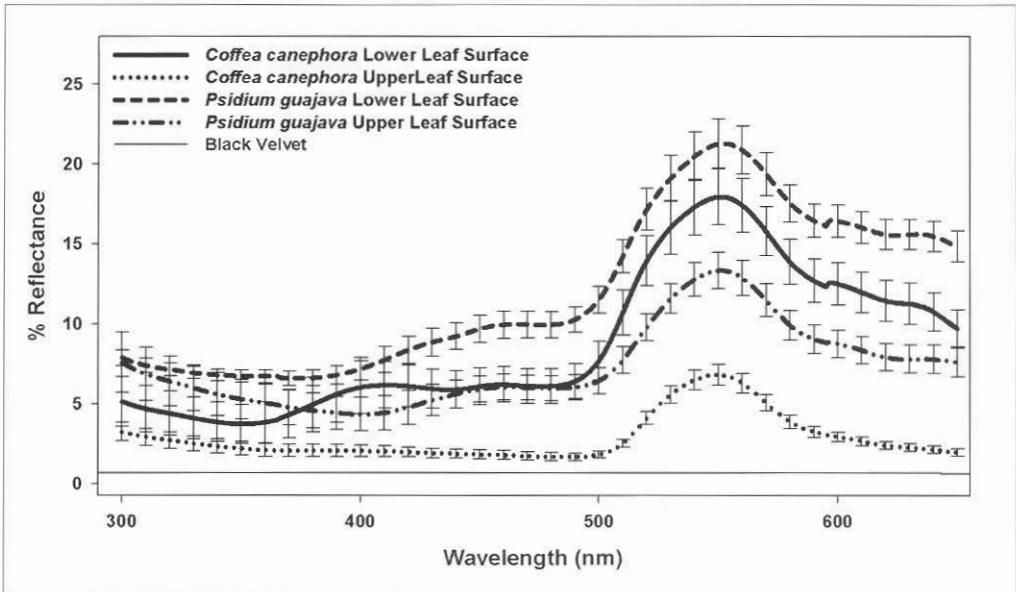


Fig. 6: Mean (SE) reflectance of ultra violet (300–400 nm) and other, visible, wavelengths from the upper and lower surfaces of important tephritid host plants and mating sites: coffee [*Coffea canephora* var. *robusta* in the case of *Ceratitis capitata* (WIEDEMANN)] and guava [*Psidium guajava* in the case of *Anastrepha suspensa* (LOEW)].

ed, more opaque, regions. There was no significant sexual dimorphism in either species when the background reflected little UV. But when wings were viewed against a highly reflective background, male *A. suspensa* wings were less transparent / reflective to UV than female wings, and male *C. capitata* wings more transparent / reflective.

There may be little adaptive significance to the sexual dimorphism in UV transparency. The wing signals of both *A. suspensa* and *C. capitata* are performed on leaf surfaces (BURK 1983; ALUJA et al. 2000; EBERHARD 2000), and many leaves reflect relatively little UV (e.g., PROKOPY et al. 1975). Neither the upper nor the bottom surfaces of coffee or guava leaves, important host-plants of *C. capitata* and *A. suspensa* respectively, reflected UV strongly. Thus, fruit fly leaf-territories and their surroundings may not offer many opportunities for sex-specific signals that exploit reflected UV passing through transparent portions of the wings; i.e., the foliage is UV “dark” and under these conditions there was little UV difference between the sexes.

The minimal sexual dimorphism of UV reflectance / transparency, if it occurs under relevant conditions in nature, adds to the ambiguity surrounding the function(s) of tephritid wing-marking patterns in general. Visible-light wing patterns in the Tephritidae are seldom sexually dimorphic (e.g., FOOTE et al. 1993) and thus not typical of insect signals directed solely by males toward females and / or rival males. There are some notable exceptions: in *Aciurina idahoensis* STEYSKAL, 1984 female wings are striped and male’s spotted (HEADRICK & GOEDEN 2000), and in the related *Aciurina bigeloviae* (COCKERELL, 1890) females’ are again striped but the males’ are fully infuscated. Similarly largely darkened male wings occur in *Trirhithrum nigrum* (GRAHAM, 1910) (WHITE & ELSON-HARRIS 1992). In addition to being uncommon, sexual dimorphisms are sometimes due to fainter markings in the male, and so perhaps the reverse of expectations (e.g., many *Trupanea* spp.; FOOTE et al. 1993 and *C. capitata*). It is

possible that female tephritids as well as males have a repertoire of wing-borne visual signals that include UV reflectance or that the patterns are directed toward heterospecific receivers. In captivity, female *C. capitata* supinate their wings and even perform the rapid wing movements that create a purported acoustic signal (ARITA & KANISHIRO 1983; SIVINSKI et al. 1989). Both sexes of *Goedenia* spp. hamanate while feeding, resting and grooming (GOEDEN 2002). On the other hand, wing patterns might be directed toward potential predators. Stripes on the wings of *Rhagoletis zephyria* SNOW, 1894 and *Zonosemata vittigera* (COQUILLET, 1899) resemble salticid jumping spiders, and protect the flies from attack (MATHER & ROITBERG 1987; GREENE et al. 1987). The papaya fruit fly, *Toxotrypana curvicauda* GERSTAECKER, is a mimic of certain vespid wasps and the dark shading on the forepart of the wing is similar in appearance to the folded wings of its wasp-models (LANDOLT 1984). In addition to mimicry, wing banding might be a form of "disruptive coloration" (COTT 1940), i.e., coloration that directs the eye and makes a common form such as a wing difficult to recognize.

While the functions of many tephritid wing patterns remain obscure it seems likely that more information on UV reflectance can only help dispel the confusion. Comparisons of UV reflectance in fruit fly males and females, their predators and mimetic-models, as well as the capacities of their predators to perceive UV, will ultimately provide the complete descriptions of coloration needed to fully test hypotheses concerning the evolution of visual signals in the family.

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