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Authors: Rodriguero, M. S., Vilardi, J. C., Vera, M. T., Cayol, J. P., and Rial, E.

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MORPHOMETRIC TRAITS AND SEXUAL SELECTION IN MEDFLY (DIPTERA: TEPHRITIDAE) UNDER FIELD CAGE CONDITIONS

M. S. Rodriguero[1], J. C. Vilardi[1], M. T. Vera[2], J. P. Cayol[3] and E. Rial[4]
Laboratorio de Genética de Poblaciones, Departamento de Ciencias Biológicas, Facultad
Cs. Exactas y Naturales, Universidad de Buenos Aires, (1428) Buenos Aires, Argentina

Instituto de Genética, "Ewald Favret", INTA Castelar, CC25, (1712) Buenos Aires, Argentina

West Asia Section, Technical Cooperation Division, IAEA
Wagramerstrasse 5, P.O. Box 100, A-1400 Vienna, Austria

Laboratorio Central Programa Moscafrut Patagonia, EEA Alto Valle INTA
CC782 (8332) General Roca, Rio Negro, Argentina

Abstract

The effects of male size and other morphometric traits as determinants of male mating success were evaluated under field cage conditions. Males of the laboratory Seib6-96 strain were released into field cages with males and females of a wild population from the Patagonian region. Mating pairs were classified as 'successful', while unmated flies were labeled as 'unsuccessful'. Five morphometric traits were measured in a sample of 141 unsuccessful and 149 successful males: eye length (EL), head width (HW), thorax length (TL), face width (FW), and wing length (WL). An exploratory non-parametric Spearman's rank correlation test indicated that mated males were in average larger for all traits ($P < 0.01$) except FW, indicating that with the exception of FW all traits are positively correlated with mating success. Step-wise multiple regression and principal component analysis + logistic regression indicated that the most likely targets of selection were TL, EL, and FW. The two former are positively correlated, while FW is negatively correlated with the fitness component analyzed here (male mating success). In previous studies where male-male interaction had been removed experimentally, EL was shown to be associated with female choice and no effect relative to mating success was detected on TL. On the basis of that study and the present results it is tempting to suggest that body size (TL) might be important in intra-sexual selection. However, size was found to be strain dependent and flies from the wild were on average bigger than laboratory ones. Size selection might then be correlated with copulatory success, as a side effect due to selection of wild males over lab males due to differential sexual activity or other causes. The potential importance of both intra-sexual selection (male-male interactions) and inter-sexual selection (mate choice) on the morphology of *Ceratitis capitata* is discussed on the basis of the results presented here and previous works.

Key Words: male-male competition, female choice, morphometric traits, genetic sexing strain

Resumen

Se evaluaron los efectos del tamaño y otros rasgos morfométricos del macho como determinantes del éxito copulatorio en condiciones de jaulas de campo. Se liberaron en jaulas de campo machos de la línea de laboratorio Seib6-96 junto con machos y hembras de una población salvaje de la región Patagónica. Las parejas en cópula se clasificaron como "exitosas", mientras que las moscas que no se aparearon se marcaron como "no exitosas". En una muestra de 141 machos no exitosos y 149 exitosos se midieron 5 rasgos morfométricos: longitud del ojo (LO), ancho de la cabeza (ACb), longitud del tórax (LT), ancho de la cara (ACr) y largo del ala (LA). Un análisis exploratorio no paramétrico utilizando la correlación de rangos de Spearman indicó que los machos apareados eran en promedio más grandes para todos los rasgos ($P < 0.01$), salvo para ACr, indicando que, con la excepción de ACr, todos los rasgos están positivamente correlacionados con el éxito copulatorio. Análisis de regresión múltiple de a pasos ("step-wise") y análisis de componentes principales (ACP) seguido de regresión logística indicaron que los blancos más probables de la selección eran LT, LO y ACr. Los dos primeros están correlacionados positivamente, mientras que ACr está correlacionado negativamente con el componente de aptitud analizado en este trabajo (éxito copulatorio de los machos). En estudios previos donde la interacción entre machos había sido removida experimentalmente, LO había mostrado asociación con la elección de la hembra, mientras que no se habían detectado efectos de LT sobre el éxito copulatorio. Sobre la base de aquel y del presente estudio es tentador sugerir que el tamaño corporal (LT) podría ser importante en la selección intrasexual. Sin embargo, se comprobó que el tamaño es dependiente de la línea y que las moscas salvajes eran en promedio más grandes que las de laboratorio. La selección del tamaño podría, por lo tanto, estar correlacionada con el éxito copulatorio como un efecto colateral, debido a la ventaja de los machos salvajes sobre los de laboratorio, por una actividad sexual diferencial o alguna otra causa. La importancia potencial tanto de la selección intrasexual (interacciones entre machos) como de la selección intersexual (elección de la pareja) sobre la morfología de *Ceratitis capitata* se discute sobre la base de los resultados presentados aquí y de trabajos previos.

Sexual selection was proposed by Darwin (1859, 1871) to explain extraordinary sexually dimorphic characters troublesome to his concept of natural selection. Two different kinds of processes could account for the evolution of such traits (Thornhill & Alcock 1983, Alcock & Gwynne 1991). Male-male competition for mates, or intrasexual selection, is where those males with the most exaggerated trait are supposed to be able to fight and win fights over other males for access to mates. The second process is active choice of individuals of one sex by individuals of the other, usually female choice of mates, namely inter-sexual selection. Again, males with the most exaggerated (Moller & Pomiankowski 1993), most symmetric (Moller 1990), or most attractive traits are assumed to be at a selective advantage because they are more likely to be chosen by a female and they should therefore experience higher mating success. For some species, finding the direct targets of sexual selection can be a difficult task and may frequently lead to misinterpretations. Moreover, the relative role of male-male competition and female choice in sexual selection has been assessed in only few cases, but there is little doubt that while male combat is of overwhelming importance in some species, mate choice predominates in others (Bradbury & Davies 1987).

A good knowledge of sexual selection mechanisms is required for the successful implementation of the sterile insect technique (SIT) developed by Knipling (1955) to control insect pest populations (Burk & Calkins 1983). Sexually selected traits are usually a good reflection of male fitness and are thus a representation of both its genotype and phenotype. Mass-rearing conditions can be controlled to improve male quality in order to promote the occurrence of sexually selected phenotypes in a high frequency. Moreover, directed selection events may be used to select genotypes with high mating success.

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) has a well-established lek mating system (Prokopy & Hendrichs 1979, Arita & Kaneshiro 1989, Hendrichs & Hendrichs 1990, Whittier et al. 1992). Leks generally take place on the underside of leaves of trees, where males establish territories and release a pheromone to attract females (Féron 1962, Prokopy & Hendrichs 1979, Arita & Kaneshiro 1989). After the arrival of a female, the male begins courtship (Féron 1962) and finally jumps onto the female and attempts to copulate. If unreceptive, the female either leaves before the male jumps or drops from the leaf when the male has already jumped and is trying to copulate (Whittier & Kaneshiro 1995). Females discriminate among potential mates at a lek and reject most courtships (Whittier et al. 1992, Whittier et al. 1994), leading to differential copulatory success within males. The common finding that copulatory success is highly variable among lekking males has led to the predominant view that mate choice is of great importance for sexual selection in such mating systems (Whittier et al. 1992, Whittier et al. 1994, Norry et al. 1999). Despite this disparity of male mating success within leks, male-male interactions may result in the males sorting themselves by territory location or position in a dominance hierarchy as reported for other dipterans (Shelly 1987, Sivinski 1989). As a consequence many traits could be correlated with copulatory success without being mate-choice cues. Male mating activity and aggressive behavior are examples of intra-sexually selected traits in many lek-mating species. According to Whittier et al. (1992) and Whittier et al. (1994) *C. capitata* males defend their territories very weakly, and there does not appear to be any relationship between territory location and mating success. However, male-male interactions are commonly observed both in the laboratory and in the field (though probably not very well documented).

Mating success in *C. capitata* males has been associated with nutritional level (Blay & Yuval 1997); decreasing fluctuating asymmetry of male supra-orbital bristles (Hunt et al. 1998); body size (Churchill-Stanland 1986, Orozco & Lopez 1993); eye length and mating activity (Norry et al. 1999). However, as yet there is still no unifying theory. In particular some studies have found an important role of male size (Orozco & Lopez 1993, Blay & Yuval 1997) while others have shown that body size itself is not a direct target of sexual selection (Hunt et al. 1998, Norry et al. 1999). Body size has been associated with male mating success in many studies of sexual selection (Davies & Halliday 1979, Berven 1981), particularly in some Diptera (Ewing 1961, Borgia 1981, Partridge et al. 1987), but this association might be explained by male-male competition (Partridge et al. 1987) and even to differential survival associated with size (Hasson et al. 1993).

Most of the studies on sexual selection of *C. capitata* have been done under laboratory conditions or with laboratory adapted strains, so the potential role of male-male interactions and female mate choice in the field is still poorly understood. The aim of the present work was to examine sexual selection based on morphometric traits of males of *C. capitata* from both a genetic sexing strain sterilized with irradiation and a wild population controlled with SIT under field cage conditions.

MATERIALS AND METHODS

Biological Materials

The laboratory strain used in this work was the Seib 6-96. This genetic sexing strain carries a white pupae (*wp*) mutation (Rössler 1979). A translocation T(Y:5) 2-22 (Franz et al. 1994) produces females with a white puparium and wild type males, enabling sorting of the sexes at this stage. Currently this strain is being reared at the Bioplanta Km8 (Mendoza, Argentina) for its use in a SIT program. Pupae were air-shipped to the testing area after irradiation. Wild flies were obtained from infested figs and peaches from the Alto Valle Region, Patagonia, Argentina. Fruits collected in the field and yards were taken to the laboratory and placed in trays on sand litter. Sand was checked periodically to collect wild pupae and land-shipped to the testing area. Once at the testing site pupae were placed in flasks until emergence. Virgin adults were aspirated from the flask within 24 h. after emergence in order to separate the sexes. Once sexed, the flies were kept in separate rooms until they reached sexual maturity at the age of 6-8 days for lab flies and 8-10 days for wild flies.

Field Cage Tests

The test was carried out at Estación Experimental Agroindustrial Obispo Colombres, Tucumán, Argentina. Field cages were used to analyze both sexual compatibility between strains and sexual selection based on male morphology. For sexual compatibility test results and procedures see Cayol et al. (1999). Outdoor cylindrical field cages (2.0 m high and 2.9 m diameter, saran screen 20 by 20 mesh) with a young host tree (*Citrus* sp.) inside were used to score male mating success under a mass selection experiment. Individuals from different strains were identified with water based paint labels painted on their notothorax. Each test consisted of the release of 30 wild males and 30 Seib 6-96 sterile males at dawn, about 7:00 AM. Half an hour later, 30 wild females were released into the cage. During a 7-h observation period, mating pairs were scored and gently removed from the cage as they formed with the aid of a vial. Male strain was determined and couples were placed in the shade until the end of copulation. Mated males were labeled as 'successful' while those males which were not able to copulate during the test were labeled as 'unsuccessful'.

Morphometric Analyses

Five body size related traits were measured in a sample of 141 unsuccessful and 149 successful males: eye length (EL), head width (HW), thorax length (TL), face width (FW), and wing length (WL) (Fig. 1). Measurements were performed with a binocular microscope fitted with an ocular micrometer. More details can be found in Norry et al. (1999).

Data Analysis

In the current study we use the term fitness to mean copulatory success. Successful individual fitness was coded 1, while unsuccessful individual fitness was 0. All morphometric measures were standardized to have mean zero and unit variance before the analyses were carried out. In a first exploratory approach, non-parametric Spearman's rank correlation tests were performed to estimate the correlation of male origin and fitness with each trait. As the results obtained from such analysis should be taken with caution due to possible correlation among traits, two statistical alternative approaches were applied: Step-wise multiple regression and principal component analysis + logistic regression. Principal Component Analyses (PCA) was used to identify major factors of variation within traits. To maximize the explained variance and obtain orthogonal variables, the factors (PCs) were rotated using VARIMAX method as done in previous works (Norry & Vilardi 1996, Norry et al. 1999).

RESULTS

Approximately 50% of the flies mated in each cage. Descriptive statistics for the traits measured are given on Table 1. It can be seen that for

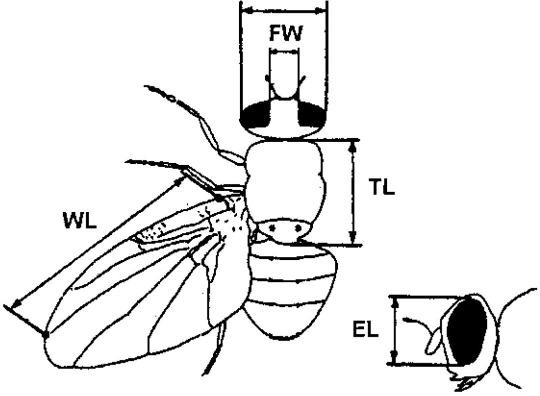

Fig. 1. Description of measured traits. WL, wing length; TL, thorax length; HW, head width; FW, face width; EL, eye length.

TABLE 1. DESCRIPTIVE STATISTICS (IN MM) FOR THE MORPHOMETRIC TRAITS ANALYZED IN MATED AND UNMATED SEIB6-96 (LAB) AND WILD MALES.

	Patagonia				Seib 6-96			
	Successful (N = 114)		Unsuccessful (N = 59)		Successful (N = 34)		Unsuccessful (N = 83)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Eye length	0.950	0.038	0.928	0.047	0.933	0.035	0.919	0.044
Face width	0.544	0.023	0.550	0.027	0.540	0.021	0.543	0.020
Head width	1.715	0.050	1.716	0.056	1.679	0.047	1.670	0.049
Thorax length	2.244	0.103	2.217	0.109	2.121	0.096	2.089	0.083
Wing length	3.571	0.111	3.559	0.112	3.415	0.115	3.387	0.111

all traits Patagonia males were larger than Seib 6-96 males. Moreover, in both strains successful males showed higher average values than unsuccessful males for all traits except FW.

In order to test the observed trends statistically, Spearman's rank correlations were estimated between 1) morphological traits and strain origin and 2) morphological traits and fitness (Table 2). Significant differences were observed between strains for all traits but FW. This analysis also showed that all traits except FW were positively and significantly correlated with fitness.

The identification of the actual target of sexual selection requires the possible correlation among traits to be removed. This was done by means of a Step-wise multiple regression analysis (Table 3). The three variables that showed a high association ($P < 0.01$) with fitness were TL, FW and EL (enumerated according to the relevance order), while the effect of WL was non-significant ($P = 0.086$). According to these results, the apparent lack of effect of FW on fitness in the original Spearman's correlation might be a consequence of its correlation with the other size related traits.

TABLE 2. SPEARMAN'S RANK ORDER CORRELATION OF MORPHOMETRIC TRAITS WITH FITNESS AND STRAIN. IN ALL CASES R ESTIMATES ARE BASED ON 290 INDIVIDUALS. *P*: SIGNIFICANCE.

	Spearman R	N	*P*
Fitness			
Eye length	0.254	290	0.000
Face width	-0.068	290	0.248
Head width	0.157	290	0.007
Thorax length	0.332	290	0.000
Wing length	0.294	290	0.000
Male strain			
Eye length	0.219	290	0.000
Face width	0.086	290	0.143
Head width	0.399	290	0.000
Thorax length	0.588	290	0.000
Wing length	0.611	290	0.000

In order to obtain completely uncorrelated (orthogonal) variables a principal component analysis (PCA) was performed with the morphometric traits analyzed. Three PCs were obtained from the factor analyses, which account for 90% of the total variance, and are explained respectively by TL and WL (PC1), FW (PC2), and EL (PC3). Factor loadings and eigen values are detailed in Table 4.

Since in the current experiment fitness was a dichotomic variable, a logistic (instead of a linear) regression analysis of fitness on the three axes from the PCA was performed. All the obtained axes showed a highly significant association with fitness (probability of mating in Table 4). It should be noted that the logistic regression coefficient for FW was negative, suggesting again that those males with smaller traits have the highest mating success.

DISCUSSION

In the present study head traits, eye length (EL) and face width (FW), and male size, thorax length (TL), have been revealed as targets of sexual selection. EL had previously been reported as a predictor of mating success under laboratory conditions with two different strains and in outdoors field cage tests with a long established laboratory strain (Norry et al. 1999). These authors have shown the occurrence of sexual selection on head morphology even in the absence of male competition, suggesting female choice. Results from the present study performed under a different testing protocol (wild females and outdoors field cages) are highly consistent. Also, EL appeared to be associated with mating success for both wild and Seib 6-96 males when each strain was analyzed separately (data not shown). These results can be interpreted as further evidence of the importance of mate choice over male-male competition in the sexual selection process acting on EL, and probably other head associated traits

TABLE 3. STEP-WISE REGRESSION.

Variable	R^2	Variable order	β	SE	*P*
Thorax length	0.541	1	0.248	0.078	0.002
Face width	0.249	2	-0.331	0.061	0.000
Eye length	0.318	3	0.232	0.064	0.000
Wing length	0.542	4	0.134	0.078	0.086

as well. Discrimination among potential mates on the basis of the male head morphology probably takes place when the female approaches the wing-fanning and head rocking male (Féron 1962, Calcagno et al. 1999) face to face (Norry et al. 1999). Hunt et al. (1998) have reported an association between male supra-orbital bristle fluctuating asymmetry and mating success, another example of head traits also identified as targets of sexual selection.

The finding that TL was associated with mating success suggests that male size may be another trait subjected to sexual selection. Pupal weight, as an adult size related trait, has been reported as a determinant of mating success in field cage studies of sexual selection with laboratory irradiated and wild flies (Orozco & Lopez 1993). Additionally pupal weight has been proved as a key determinant of both male and female mating activity (Churchill-Stanland et al. 1986), though these results account more for assortative mating rather than sexual selection towards male size. Blay & Yuval (1997) using wing length as a determinant of male size have found that for matings taking place within the first 1.5 h after release of females, variation in copulatory success could be explained by variation in wing length for both protein-fed and protein deprived males. When whole day observation data was pooled this effect disappeared for protein-fed males but remained for protein deprived males. Wing length can only be environmentally influenced at the larval stage and not after imaginal molt, and the experimental design followed by these authors determined the difference among protein-fed and protein-deprived males at the adult stage. It is thus tempting to conclude that the variation in mating success of these males is probably a consequence of differential mating activity, and not necessarily due to any possible effect of male size. Male size might be indirectly associated with mating activity as a consequence of nutritional reserves passed from the larvae to the adult, bigger adults being best nourished at the larval stage than the smaller ones.

TABLE 4. FACTOR ANALYSES COUPLED WITH LOGISTIC REGRESSION ANALYSES.

Variable	PC1	PC2	PC3
Eye length	0.265	0.229	**0.935**
Face width	0.178	**0.948**	0.172
Head width	0.586	0.633	0.332
Thorax length	**0.876**	0.194	0.201
Wing length	**0.877**	0.204	0.202
Eigenvalue			
% Variance	39.6	28.6	21.9
Cumulative %	39.6	68.2	90.1
Probability of mating			
$\chi^2_{(1)}$	34.07	10.82	16.78
P	0.000	0.001	0.000
β	0.732	-0.398	0.501

In the case of the present study TL seems to be associated directly with copulatory success. This view is supported by the step-wise regression analysis (Table 3) and the significant correlation of PC1, which accounted for body size only, with probability of mating (Table 4). The non-significant effect of wing length (WL) in the step-wise regression (Table 3) indicates that wing size even when included on PC1 (Table 4) is a trait associated with mating success only as a side effect of its high correlation with TL. This is a clear example of the power of the combination of step-wise regression plus factor analysis coupled with regression analysis (either logistic or linear). These approximations succeed in removing WL as a target under selective pressure contrary to the first exploratory Spearman's rank correlation analysis (Table 2).

On the contrary, Whittier et al. (1994) found no correlation between male body weight and copulatory success, but they did detect a high correlation for number of attempted copulations, i.e., mating activity. Similar results have been found by Norry et al. (1999) in relation to WL and TL and by Hunt et al. (1998) for WL. These studies have been done under laboratory conditions, and the field cage test results reported by Norry et al. (1999) where no male size advantage was detected was carried out with a laboratory strain (approximately 30 generations under lab conditions). To summarize, the work by Orozco & Lopez (1993) was the only evidence to date of sexual selection favoring male size of lab males mated to wild females under field cage conditions. No evidence had been detected when females belonged to a lab strain even when tests were performed in outdoor field cages (Norry et al. in press), or when flies were tested under laboratory conditions

(Hunt et al. 1998, Blay & Yuval 1997, for the case of pooled data, Norry et al. 1999). A close look at this apparent contradiction reveals that for the indoor and lab strain tests percentages of mating were very high (ranging from 69 to 86%) compared with percentages of mating found for wild females (50%, the present work). Such percentages imply that highly receptive yet low discriminating lab females may be responsible for hiding the effect of male size or size related traits on sexual selection. Rearing conditions may also represent a different environment where lek formation might not be so important as in nature.

Another possible cause for the lack of detectable size effects on sexual selection is that size can account for nutritional level only in those cases where food quality has been the same and any size variation is only a consequence of lesser consumption. Arita & Kaneshiro (1988) have found that flies emerging from coffee beans copulated more frequently even being significantly smaller than flies emerging from cherry beans. Orozco & Lopez (1993) also reported smaller size for flies emerging from coffee berries but no effect on mating activity was detected. In the current study, the advantage of bigger males was observed in both strains (the interaction fitness × origin was non significant), and the wild males, which were shown to have higher success (Cayol et al. 1999), were on average bigger than their mass-reared counterparts.

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