

Comparative Allometry and Sexual Behavior of Four Fruit Fly Species in the Tribe Ceratitidini (Diptera: Tephritidae)

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ABSTRACT: Sexual dimorphisms in four related species of tephritid flies were shown to be associated with differences in sexual behavior. In two species, *Ceratitis capitata* and *C. catoirii*, males and females approach closely head to head and apparently touch aristae, and the male buzzes his wings, probably fanning pheromone toward the female; the males were found to have longer aristae with fewer microsetae, and larger posterior areas of their wings than do females. These dimorphisms were absent in the other two species, *C. rosa* and *Neoceratitis cyanescens*, which court at a longer distance and in which the male does not fan pheromone toward the female prior to mounting. All three pairs of legs were proportionally longer in the males of all four species. None of the other sexually dimorphic male signalling traits showed the positive allometric slopes predicted by some theories.

KEY WORDS: *Ceratitis*, *Neoceratitis*, sexual dimorphism, sexual selection, courtship

Sexual selection often results in differences between male and female traits. In some cases the proportional sizes of traits remain the same, and it is only the overall body size that differs between males and females. In others, the proportional sizes of traits differ. Male structures that are used as signaling devices and as weapons are frequently not only larger in males than females, but also proportionally larger in larger males of a given species (Huxley, 1972; Petrie, 1988, 1992; Alatalo *et al.*, 1988; Green, 1992; Baker and Wilkinson, 2001). The proportional size of a trait is often expressed as the slope of the log-log regression of that trait vs. the overall body size in mature conspecific individuals: when the slope is >1.0 (“positive allometry”), larger-sized individuals have proportionally larger structures.

The reason why sexually selected traits tend to show positive allometry is not certain (Huxley, 1972; Petrie, 1988, 1992; Green, 1992). Baker and Wilkinson (2001) suggested that sexually selected traits which serve as ornaments or weapons are relatively small in smaller individuals because small individuals have less to gain from investing in such structures. Otte and Stayman (1979) proposed a related, “overflow” model, in which larger individuals have proportionally greater reserves of material which they can dedicate to sexually selected traits. Petrie (1988) argued that only structures used as signaling devices in intraspecific aggression should show positive allometry, and that weapons should not show positive allometry. This idea is not supported empirically, however. Positive allometry is commonly observed in the horns of mammals and beetles and the cerci of earwigs, which are known to function as weapons in intraspecific battles between males. In some of these groups behavioral details and the settings of interactions suggest that they function as weapons rather than in displays (Huxley, 1972; Eberhard, 1979; Brown, 1980; Eberhard and Gutierrez, 1991; Briceño and Eberhard, 1985; Eberhard *et al.*, 1998, 2000). Bonduriansky and Day (2003) suggested that positive allometry is expected in both signals and weapon traits only under certain sets of conditions.

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Behavioral observations of how particular structures are used are needed to interpret their allometric patterns of morphology. Very little is known regarding the sexual biology of flies in the genus *Ceratitis*, aside from that of the widespread pest species, *C. capitata* [Wiedemann] (reviewed in Eberhard, 2000). In *C. capitata*, males lure females to leks with pheromones, and court them face-to-face at close range, apparently utilizing visual and chemical stimuli, as well as tactile stimulation with their antennal arista (Eberhard, 2000; Briceño and Eberhard, 2002b). Quilici *et al.* (2002) gave brief descriptions of some aspects of courtship in the Mascarene fruit fly, *C. catoirii* Guérin-Mèneville, and the Natal fruit fly *C. rosa* Karsch. In this paper we present further details of the sexual behavior of three species of Ceratitidini that damage crops on Reunion Island: two polyphagous species (*C. catoirii* and *C. rosa*), and the stenophagous Tomato fruit fly, *Neoceratitis cyanescens* (Bezzi), which attacks wild and cultivated Solanaceae. We also correlate these observations with patterns of sexual dimorphism.

Methods

Flies of *C. rosa* and *N. cyanescens* used for behavioral and morphological observations were first generation descendants of wild flies from Reunion Island. Adults from a recent lab-rearing were used for the more rare *C. catoirii*. Measurements of *C. capitata* were made using flies from an approximately five year-old mass-reared strain derived from wild flies in Costa Rica. Video recordings of courtship behavior of *C. catoirii*, *C. rosa*, and *N. cyanescens* strains that had been in captivity only a few (<5) generations were made on Reunion Island with an analogue video camera using standard techniques (e.g., Briceño and Eberhard, 2002a), and were analyzed frame by frame.

Measurements of legs, wings, and bristles (Fig. 1—terminology of White *et al.*, 2000) were made by mounting structures flat on microscope slides in Hoyer's medium, and photographing them using a Sanyo VCC-3912 camera mounted on a compound microscope and connected to a Genius Video Wonder Series II card in a computer. Measurements were made employing the Scion image program (© 1998 Scion Image Corp.). Thorax length and head width were measured in dorsal view when the posterior edge of the thoracic scutellum just obscured the posterior edge of the mediotergite (terminology of White *et al.*, 2000). When all measurements were repeated on 20 individuals of *C. capitata* to test measurement precision, correlations between first and second measurements ranged from 0.93 to 1.0.

Tests for differences in log-log plots of different traits against thorax length were performed by first testing for differences in male and female centroids with Wilk's Lambda tests. Differences in male and female slopes and elevations of ordinary least squares (OLS) regressions were tested as described by Zar (1999). OLS regressions were used instead of reduced major axis (RMA) regressions, which generally give somewhat higher slopes (Green, 1999; Eberhard *et al.*, 1999). RMA analyses are preferred by some authors (Green, 1999), but are not clearly more appropriate for the type of analysis performed here (see discussion by Eberhard *et al.*, 1999). Means are followed by \pm one standard deviation.

Results

Behavior

Ceratitis catoirii

Males in field cages apparently called females pheromonally in the morning, inflating their abdominal pleura and everting a spherical body at the tip of the abdomen

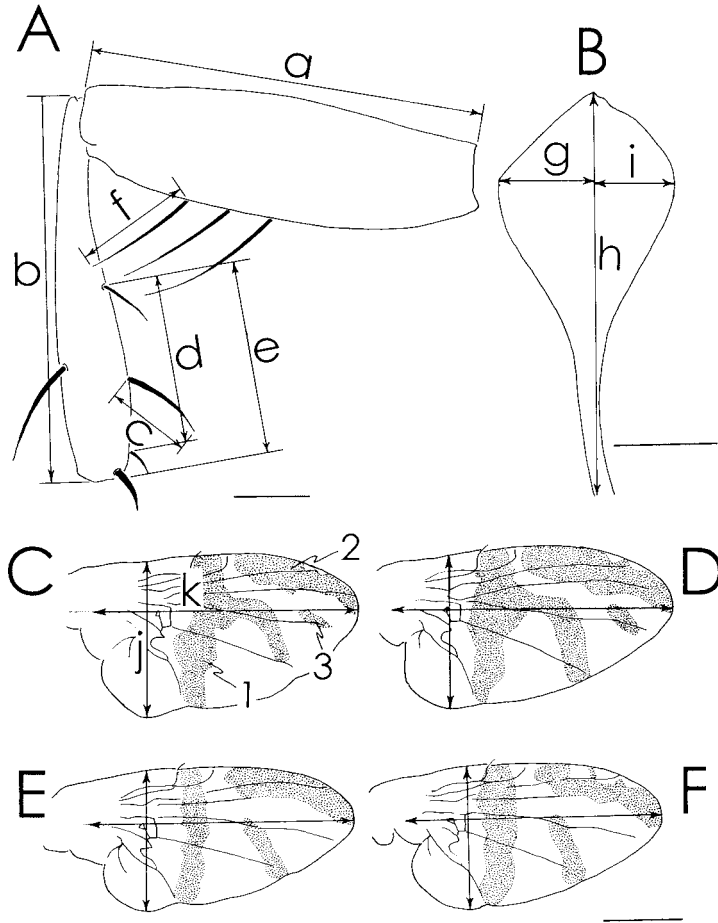


Fig. 1. Dimensions of measured structures: (A) (a–f) leg; (B) (g–i) supra-fronto-orbital (SFO) seta (of male *C. capitata* and *C. catoirii*); and (j–k) wings of male (C) and female (D) *C. catoirii*, and male (E) and female (F) *C. rosa*. a—length femur; b—length tibia; c—length longest tibial seta; d—length brush of tibial setae (only the most basal, most distal, and longest setae are drawn); e—length tibia from base of brush; f—length longest femoral seta; g—widest portion of tip on left side of center line; h—length of seta; i—widest portion of tip on right side of center line (width of tip = g + i); j—width of wing; k—length of wing. The area of the discal (DB) + apical band (SAB) (1) on the wing was measured; two other bands, the anterior apical band (2) and the posterior apical band (3) were not measured. Scale bars are 0.2 mm for leg (A), 0.1 mm for bristle (B), and 1.0 mm for wings (C–F).

(presumably the inflated rectal epithelium, as in *C. capitata*). Courtship began when a female approached a calling male. Nine video recordings of courtships in which the male eventually mounted the female were analyzed. As noted by Quilici *et al.* (2002), male behavior resembled that of male *C. capitata*, and included continuous wing vibration while the male faced the female early in courtship, and intermittent wing buzzing later after the female approached closer. The flies approached closely, to within about 0.25 body lengths, before the male jumped onto the female. This was close enough for contact to occur between their arista, as in *C. capitata* (Briceño and Eberhard, 2002b), but the arista were not visible in the video recordings. Head rocking behavior similar to that of *C. capitata* did not occur. As in *C. capitata*, the female turned to look more directly at the male during the

Table 1. Comparison of courtship behavior in *C. catoirii* (this study) and successful courtships of wild male *C. capitata* (A from Briceño and Eberhard, 2002a, $N = 34$; B from Briceño and Eberhard, 1998, $N = 22$). Differences in experimental settings and small sample sizes make statistical comparisons inappropriate.

	<i>C. catoirii</i>	<i>C. capitata</i>
Durations (sec)		
Continuous vibrate wings	5.15 ± 4.21	18.7 ± 23.8 (A)
Intermittent buzzing wings	17.0 ± 10.2	10.7 ± 6.6 (A)
Number of buzzes/courtship	35.8 ± 9.9	41.8 ± 39.0 (B)
Rate of buzz (number/sec)	2.34 ± 0.56	4.5 ± 1.7 (B)
Total courtship before mount	21.5 ± 13.2	23.2 ± 22.2 (A)
Female immobile before mount	4.87 ± 1.57	5.78 ± 3.63 (A)
Distances (fraction of male length)		
Start of continuous wing vibration	1.50 ± 2.08	1.36 ± 0.81 (A)
Start of intermittent wing buzz	0.45 ± 0.14	0.30 ± 0.12 (A)
Jump onto female	0.25 ± 0.07	0.14 ± 0.02 (A)
Angles		
Male orientation toward female ^a		
Start of continuous vibration	7.4 ± 8.8°	10.2 ± 9.2° (A)
Start of intermittent buzzing	4.3 ± 5.3°	2.8 ± 3.6° (A)
Moment of jump	3.1 ± 5.9°	1.1 ± 2.1° (A)
Female orientation toward male ^b		
Start of continuous vibration	31.5 ± 37.8°	52.6 ± 33.2° (A)
Start of intermittent buzzing	8.9 ± 13.5°	7.3 ± 9.9° (A)
Moment of jump	4.1 ± 6.9°	3.9 ± 4.2° (A)
<i>N</i>	9	34, 22

^a 0° = male facing directly toward female.

^b 0° = female facing directly toward male.

latter stages of courtship. Durations, distances, and angles at different stages of courtship, which reflect both male courtship and female responses (Briceño and Eberhard, 2002a), were at least generally similar in the two species (Table 1).

Ceratitis rosa

Male *C. rosa* in field cages formed small groups (usually 2–5 males), especially late in the afternoon, either on fruit where females might oviposit, or on leaves. They appeared to call females pheromonally, inflating their abdominal pleura and everting a tri-lobed rectal ampulla. Fourteen video recordings confirmed the general descriptions of Quilici *et al.* (2002). The male responded to an approaching female by performing continuous wing vibration. Males did not perform intermittent wing buzzes or head rocking as in *C. capitata*, but the male faced toward the female ($8.0 \pm 13.6^\circ$) while the female faced less directly toward the male ($18.1 \pm 18.2^\circ$) just before he jumped. The male extended his middle legs laterally very briefly (0.1–0.2 sec) just before jumping onto the female. In ten cases the male first extended one leg, withdrew it, and then extended both legs just before jumping. In two others he twice extended both legs briefly, and in two others he extended each one, in alternation, just before jumping. The distance between male and female at the moment the male jumped was larger than that in *C. capitata* and *C. catoirii* (mean = 1.3 ± 0.5 body lengths, $N = 9$).

Neoceratitis cyanescens

Only three courtship sequences were taped, and only two of these led to mounting. In all three the male made rhythmic, small amplitude anterior-posterior synchronous movements with his wings (low amplitude “enanation” in the terminology of White *et al.*, 2000) while the female was several body lengths away, and in two of the three it was clear that there was a brief burst of low amplitude buzzing each time the wings moved anteriorly. At no time did the male perform either continuous wing vibration or intermittent buzzing similar to that seen in the other species. In one case the female approached the male even though (in sharp contrast with the other species) he did not turn to face toward her (the male’s angle was about 90° when he jumped). The distance between the two flies at the moment the male jumped onto the female was between two and three body lengths, much greater than ever seen in several hundred mounts we have observed in published and unpublished studies of *C. capitata*. The male did not extend any of his legs laterally before jumping, as in *C. rosa*.

Morphology—Sexual Dimorphism and Allometry

Tables 2a–d present measurements of male-female dimorphism in overall size and allometry, and Table 3 summarizes the sexual dimorphisms in the different species. Female body size (estimated by thorax length) was larger than that of males in *C. capitata* and *C. rosa*, but not in *C. catoirii* and *N. cyanescens*.

The expanded supra-frontal-orbital (SFO) bristles of males differed between *C. capitata* and *C. catoirii*. Those of *C. capitata* were much shorter (means were 0.38 ± 0.03 and 1.15 ± 0.10 mm respectively), and had narrower expansions at their tips (mean widths were 0.22 ± 0.02 and 0.76 ± 0.06 mm respectively) (both $P < 0.01$ with *t*-tests). The log-log slopes of length and width on body size were relatively low in both species (respectively, 0.28 and 0.26 in *C. capitata*, and 0.27 and 0.42 in *C. catoirii*; only the final value was statistically significant, $P = 0.03$).

The length of the longest dark setae on the dorsal or the ventral side of the tibia II in the tibial brush of male *C. rosa* were not significantly related to male body size. The log-log slopes on body size were 0.24 and 0.48 respectively ($P > 0.2$ in both cases). The length of the brush, measured at the bases of the setae on the dorsal surface of the tibia (d in Fig. 1A) had a weak, positive relationship with body size (log-log slope = 0.51, $P = 0.02$).

Discussion

Several patterns in the most highly significant male-female differences in morphology ($P < 0.001$ and < 0.0001 in Tables 2 and 3) are in accord with apparent differences in sexual behavior (increased behavioral samples, especially in *N. cyanescens*, are needed to confirm the patterns we note here). In the two species in which males and females approached each other head-to-head to within about 0.25 body lengths before the male mounted (*C. capitata* and *C. catoirii*), the length of the male’s arista was greater than that of the female, and the male arista had fewer microsetae (as also found in *C. capitata* by Miranda, 2000). Tactile stimulation from the male arista is apparently important to induce female *C. capitata* to mate (Briceño and Eberhard, 2002b), and the similar allometry of male arista in *C. catoirii* suggests that they play a similar role in this species. The arista were not sexually dimorphic in *C. rosa* and *N. cyanescens*, in which males and females did not approach close enough prior to mounting for their arista to touch.

Table 2. Male-female differences (linear measurements in mm; area measurements in mm² (***) = $P \leq 0.0001$; **** = $P \leq 0.0001$; ***** = $P \leq 0.0001$; ** = $P \leq 0.01$; * = $P \leq 0.05$).

	Mean ± SD	Significance of difference between means	Log-log regression on length of thorax			Significance of Wik's Lambda	Significance of differences between slopes	Significance of differences between elevations
			Slope	Significance of slope	Intercept			
a. <i>C. capitata</i> (N = 24–30 males, 29–30 females)								
length thorax	male 2.06 ± .07							
	female 2.14 ± .05	***						
width head	male 1.74 ± .14	**	0.90	***	-0.03			
	female 1.77 ± .04		0.45	*	0.11	*		ns
length arista	male 1.15 ± .09	***	0.85	*****	-0.27			
	female 1.10 ± .05		0.57	*****	-0.27	ns		****
number dorsal setae arista	male 19.14 ± 3.93	***	0.28	ns	0.68			
	female 31.73 ± 4.31		0.31	ns	0.89	ns		****
number ventral setae arista	male 5.38 ± 3.13	***	0.14	ns	0.18			
	female 11.97 ± 4.51		-0.27	ns	2.66	ns		***
length wing	male 3.30 ± .09	**	0.49	**	0.38			
	female 3.28 ± .54		0.62	****	0.32	*		
width wing	male 2.06 ± .36	***	0.61	****	0.05			
	female 2.03 ± .07		0.55	****	0.04	ns		****
posterior area wing	male 1.60 ± .13	*	0.68	*****	-0.33			
	female 1.51 ± .10		0.68	*****	-0.45	ns		****
total area wing	male 3.28 ± .23	ns	0.46	*	0.21			
	female 3.20 ± .15		0.64	****	-0.81	ns		****
area wing bands DB + SAB	male 0.53 ± .03	ns	0.43	*	-0.53			
	female 0.54 ± .03		0.68	****	-0.80	ns		****
length femur I	male 1.03 ± .03	ns	0.38	*	-0.08			
	female 1.02 ± .03		0.26	ns	-0.12	**		**
length seta femur I	male 0.35 ± .02	***	0.14	ns	-0.53			
	female 0.30 ± .02		0.43	*	-0.88	ns		****
area setae femur I	male 1336 ± 253	ns	0.32	ns	2.50			
	female 1265 ± 276		0.20	ns	2.36	*		*
number setae femur I	male 11.57 ± 1.7	*	0.15	ns	0.82			
	female 10.40 ± 1.5		0.00	ns	1.01	*		*

Table 2. Continued.

		Mean \pm SD	Significance of difference between means	Log-log regression on length of thorax			Significance of Wilk's Lambda	Significance of differences between slopes	Significance of differences between elevations
				Slope	Significance of slope	Intercept			
length tibia I	male	1.00 \pm .02		0.46	*	0.70			
	female	0.98 \pm .02	*	0.57	***	-0.18	****	****	
length femur II	male	1.27 \pm .04		0.51	**	0.02			
	female	1.25 \pm .02	*	0.37	*	0.003	****	****	
length tibia II	male	1.34 \pm .04		0.59	***	-0.03	ns	ns	
	female	1.33 \pm .03	ns	0.56	**	-0.07	ns	ns	
length femur III	male	1.20 \pm .03		0.32	ns	0.32	****	****	
	female	1.20 \pm .03	ns	0.40	*	-0.06	****	****	
length tibia III	male	1.18 \pm .05		0.60	**	-0.12	ns	ns	
	female	1.19 \pm .03	ns	0.66	****	-0.14	ns	ns	
b. <i>C. catovirii</i> (N = 26-30 both male and female)									
length thorax	male	2.53 \pm .09							
	female	2.14 \pm .98	ns						
width head	male	1.69 \pm .59		0.78	****	-0.10	ns	ns	
	female	1.57 \pm .72	ns	0.70	****	-0.04	ns	ns	
length arista	male	1.31 \pm .15		0.13	ns	-0.05	****	****	
	female	1.17 \pm .11	***	0.45	*	-0.29	****	****	
number dorsal setae	male	7.64 \pm 6.82		-0.17	ns	2.22	****	****	
	female	26.37 \pm 7.78	***	0.20	ns	0.73	****	****	
number ventral setae	male	0.00							
	female	5.10 \pm 3.38	***	-0.16	ns	1.56	—	—	
length wing	male	4.2 \pm .5	***	-0.33	ns	0.74	****	****	
	female	4.4 \pm .1	***	0.64	****	0.36	****	****	
width wing	male	2.77 \pm .42	***	-0.18	ns	0.50	****	****	
	female	2.38 \pm .10	***	0.58	**	0.09	****	****	
posterior area wing	male	2.55 \pm .22	***	-0.47	*	0.84	****	****	
	female	2.15 \pm .17	***	0.66	****	-0.26	****	****	
total area wing	male	5.24 \pm .39	***	0.68	****	0.78	****	****	
	female	4.81 \pm .35	***	0.52	*	0.31	****	****	

Table 2. Continued.

	Mean ± SD	Significance of difference between means	Log-log regression on length of thorax				Significance of differences between elevations
			Slope	Significance of slope	Intercept	Significance of Wilk's Lambda	
area wing bands DB + SAB	male	1.10 ± .08	ns	-0.14	ns	0.17	ns
length femur I	female	1.12 ± .09	ns	0.10	ns	-0.03	ns
	male	1.41 ± .06	****	0.65	****	-0.13	ns
length seta femur I	female	1.26 ± .05	***	0.50	*	-0.13	ns
	male	0.57 ± .03	****	0.33	ns	-0.43	ns
area seta femur I	female	0.44 ± .04	****	0.36	ns	-0.72	****
	male	2796 ± 395	**	0.22	ns	3.09	ns
number seta femur I	female	2209 ± 350	***	0.29	ns	2.77	****
	male	14.00 ± 1.60	****	-0.22	ns	1.41	****
length tibia I	female	10.15 ± 1.26	****	0.19	ns	0.69	ns
	male	1.23 ± .10	****	0.32	ns	-0.16	ns
length femur II	female	1.09 ± .07	****	0.62	****	-0.39	ns
	male	1.51 ± .04	****	0.49	****	0.03	****
length tibia II	female	1.45 ± .07	**	0.60	****	-0.09	ns
	male	1.66 ± .06	****	0.31	ns	-0.09	ns
length femur III	female	1.56 ± .05	****	0.53	**	0.02	ns
	male	1.42 ± .05	ns	0.37	ns	0.006	ns
length tibia III	female	1.42 ± .05	ns	0.56	**	-0.10	ns
	male	1.37 ± .06	ns	0.39	*	-.04	ns
	female	1.34 ± .04	ns	0.58	**	-0.12	**

c. <i>C. rosae</i> (N = 28-30 for females, 22-30 for males)							
length thorax	male	2.43 ± .08	****	0.69	****	0.07	ns
	female	2.55 ± .11	****	0.77	****	0.07	ns
width head	male	1.93 ± .05	**	0.27	ns	-0.51	ns
	female	1.98 ± .06	*	0.25	ns	-0.27	ns
length arista	male	0.97 ± .12	ns	0.23	ns	1.25	ns
	female	0.99 ± .11	ns	0.16	ns	1.41	ns
number dorsal setae arista	male	41.87 ± 5.51	ns				ns
	female	41.27 ± 5.47	ns				ns

Table 2. Continued.

		Mean \pm SD	Significance of difference between means	Log-log regression on length of thorax			Significance of Wilk's Lambda	Significance of differences between slopes	Significance of differences between elevations
				Slope	Significance of slope	Intercept			
number ventral setae arista	male	27.33 \pm 3.44		0.02	ns	1.39			
	female	28.93 \pm 4.33	ns	-0.03	ns	1.50	ns	ns	
length wing	male	4.19 \pm .14	****	0.71	****	0.33			
	female	4.28 \pm .12	**	0.66	****	0.46	ns	ns	
width wing	male	2.39 \pm .11	****	0.57	****	0.06			
	female	2.43 \pm .08	ns	0.59	****	0.22	ns	ns	
posterior area wing	male	1.95 \pm .16	*	0.63	****	-0.35			
	female	2.07 \pm .12	*	0.50	**	0.05	ns	ns	
total area wing	male	4.54 \pm .37	****	0.68	****	-0.03	ns	ns	
	female	4.75 \pm .27	*	0.66	****	0.32	ns	ns	
area wing bands DB + SAB	male	0.50 \pm .04	*	0.45	*	-0.73	****	****	
	female	0.66 \pm .06	****	0.28	ns	-0.44	ns	****	
length femur I	male	1.22 \pm .05	**	0.40	*	-0.09	****	****	
	female	1.17 \pm .057	**	0.55	**	-0.18	****	****	
length seta femur I	male	0.29 \pm .02	****	0.25	ns	-0.82	ns	*	
	female	0.31 \pm .02	****	0.31	ns	-0.68	ns	*	
area setae femur I	male	1220 \pm 300	****	0.30	ns	2.01	**	**	
	female	1580 \pm 240	****	0.40	*	2.61	ns	ns	
number setae femur I	male	8.10 \pm 1.27	ns	-0.04	ns	0.98	ns	ns	
	female	8.47 \pm 1.50	ns	-0.05	ns	0.98	ns	ns	
length tibia I	male	1.10 \pm .04	****	0.53	**	-0.16	****	****	
	female	1.03 \pm .14	****	0.14	ns	-0.02	****	****	
length femur II	male	1.60 \pm .06	ns	0.70	****	-0.10	****	****	
	female	1.59 \pm .06	ns	0.67	****	-0.04	****	****	
length tibia II	male	1.65 \pm .05	****	0.69	****	-0.04	****	****	
	female	1.51 \pm .26	****	-0.03	ns	0.27	****	****	
width tibia II	male	0.26 \pm .02	****	0.21	ns	-0.75	ns	****	
	female	0.24 \pm .01	****	0.15	ns	-0.67	ns	****	
length femur III	male	1.51 \pm .05	*	0.50	**	-0.02	****	****	
	female	1.48 \pm .06	*	0.44	*	0.02	****	****	

Table 2. Continued.

	Significance of difference between means	Mean ± SD	Log-log regression on length of thorax			Significance of differences between slopes	Significance of differences between elevations
			Slope	Significance of slope	Intercept		
length tibia III							
male	ns	1.38 ± .05	0.68	****	-0.14		
female	ns	1.38 ± .07	0.54	**	-0.09	*	
d. <i>Neoceratitis cyanescens</i> (N = 27-30 for females, 24-30 for males)							
length thorax							
male	ns	1.76 ± .51					
female	ns	1.99 ± .26					
width head							
male	ns	1.66 ± .13	0.98	****	1.60	**	
female	ns	1.45 ± .62	0.98	****	1.53	**	
length arista							
male	ns	0.93 ± .07	0.89	****	-0.24		
female	ns	0.95 ± .12	0.82	****	-0.26	ns	
number dorsal setae arista							
male	ns	37.67 ± 4.37	0.30	ns	1.47	*	
female	ns	36.97 ± 6.85	0.84	****	1.21	*	
number ventral setae arista							
male	ns	25.70 ± 3.34	0.34	ns	1.27	ns	
female	ns	26.5 ± 4.83	0.77	****	1.09	ns	
length wing							
male	*	3.30 ± .25	0.78	****	0.33	ns	
female	*	3.45 ± .39	0.94	****	0.30	ns	
width wing							
male	ns	1.75 ± .14	0.77	****	0.06	ns	
female	ns	1.83 ± .22	0.94	****	0.01	ns	
posterior area wing							
male	*	1.12 ± .26	0.77	****	-0.34	ns	
female	*	1.30 ± .28	0.95	****	-0.35	ns	
total area wing							
male	*	2.80 ± .40	0.80	****	0.08	ns	
female	*	3.07 ± .67	0.95	****	0.002	*	
length femur I							
male	ns	1.11 ± .09	0.87	****	-0.18	****	
female	ns	1.08 ± .13	0.93	****	-0.23	****	
length seta femur I							
male	*	0.30 ± .03	0.59	**	-0.73	**	
female	*	0.34 ± .04	0.84	****	-0.73	**	
area setae ventral femur I							
male	ns	2150 ± 490	0.79	****	2.75	ns	
female	ns	2240 ± 560	0.89	****	2.77	ns	
number seta femur I							
male	ns	9.79 ± 1.22	0.37	ns	0.83	ns	
female	ns	9.37 ± 1.21	0.63	****	0.78	*	

Table 2. Continued.

	Mean ± SD	Significance of difference between means	Log-log regression on length of thorax			Significance of Wilk's Lambda	Significance of differences between slopes	Significance of differences between elevations
			Slope	Significance of slope	Intercept			
length tibia I	male 1.00 ± .10		0.88	*****	-0.27			
	female 0.96 ± .12	ns	0.94	*****	-0.26	ns	****	
length femur II	male 1.21 ± .28		0.80	*****	-0.18			
	female 1.26 ± .15	ns	0.88	*****	-0.14	ns	****	
length tibia II	male 1.31 ± .12		0.68	***	-0.08			
	female 1.32 ± .16	ns	0.94	*****	-0.14	ns	*****	
length femur III	male 1.25 ± .09		0.85	*****	-0.10			
	female 1.26 ± .15	ns	0.95	*****	-0.16	ns	***	
length tibia III	male 1.16 ± .11		0.89	*****	-0.20			
	female 1.18 ± .14	ns	0.95	*****	-0.19	ns	**	

Table 3. Summary of statistically significant differences between males and females of the four species of *Ceratitis* and *Neoceratitis* (“+” = male values higher than those of similarly sized females, from inspection of graphs; “el” = significant difference in elevation; “sl” = significant difference in slope) (**** = $P \leq 0.0001$; *** = $P \leq 0.001$; ** = $P \leq 0.01$; * = $P \leq 0.05$).

	<i>C. capitata</i>	<i>C. catoirii</i>	<i>C. rosa</i>	<i>N. cyanescens</i>
width head	NO	NO	NO	* (+ el)
length arista	**** (+, el)	**** (+, el)	NO	NO
number dorsal setae arista	**** (-, el)	**** (-, el)	NO	* (-, sl, el)
number ventral setae arista	**** (-, el)	**** (-, el)	NO	NO
length wing	* (+, el)	*** (-, sl, +, el) ^a	NO	NO
width wing	**** (+, el)	**** (+, sl, el)	NO	NO
posterior area wing	**** (+, el)	**** (+, sl, el)	NO	NO ^b
total area wing	**** (+, el)	**** (+, el)	NO	NO ^c
area wing bands DB + SAB	NO	NO	**** (-, el)	—
length femur I	** (+, el)	**** (+, el)	**** (+, el)	**** (+, el)
length seta femur I	**** (+, el)	**** (+, el)	* (-, el)	** (-, el)
area seta femur I	* (+, el)	**** (+, el)	** (-, el)	NO
number seta femur I	* (+, el)	**** (+, el)	NO	* (+, el)
length tibia I	**** (+, sl, el)	**** (+, el)	**** (+, el)	**** (+, el)
length femur II	**** (+, el)	**** (+, el)	**** (+, el)	**** (+, el)
length tibia II	**** (+, el)	**** (+, el)	**** (+, el)	**** (+, el)
length femur III	*** (+, el)	NO	**** (+, el)	** (+, el)
length tibia III	NO	** (+, el)	* (+, el)	* (+, el)

^a Male slope not statistically significant.

^b Wilk’s lambda barely significant ($P = 0.03$), but neither slope nor elevation significantly different (respectively, $P = 0.70, 0.09$).

^c Wilk’s lambda barely significant ($P = 0.03$), but neither slope nor elevation significantly different (respectively, $P = 0.14, 0.72$).

Similarly, in the two species in which males performed intermittent wing buzzing while facing females at close range, the male’s wing was wider than that of the female, due to an expansion of the posterior wing area. The details of wing movements in *C. capitata* indicate that the male uses the posterior area of his wing to waft pheromones toward the female (Briceño and Eberhard, 2000), and presumably the same occurs in *C. catoirii*. Wing width was not sexually dimorphic in *C. rosa* and *N. cyanescens*, in which males did not buzz their wings this way at close range. The greater similarity between *C. capitata* and *C. catoirii* is in accord with recent taxonomic studies: these two species are in the same clade within the subgenus *Ceratitis* s.s., while *C. rosa* is in a different subgenus which is not closely related (DeMeyer, 2000). The biological significance of the sexual differences in the size of wing markings in *C. rosa* is less clear. Perhaps visual stimuli from the wings are used in courtship.

The absolute values of the allometric slopes of several display traits (aristae, head bristles, and posterior wing area in *C. capitata* and *C. catoirii*, middle tibiae and their brushes of setae in *C. rosa*) were all well below 1.0 (Tables 2a–c), in contrast to the theoretical predictions discussed above (Otte and Stayman, 1979; Baker and Wilkinson, 2001). Perhaps emphasis on the value 1.0 in previous discussions of allometry and sexual selection was not justified (Eberhard, 2002; Bonduriansky and Day, 2003). Simple utilitarian arguments may explain why some of these traits have relatively low slopes. For instance, an overly long male arista might bring the male into contact with the female’s aristae before he was close enough to launch an effective jump. A similar argument based on mechanical design is not applicable,

however, for the SFO setae of *C. capitata* and *C. catoirii*, or the brush of setae on tibia II of *C. rosa*. The reduced frequency of female acceptance during courtship in *C. capitata* when the SFO setae were removed (Mendez *et al.*, 1998), and the sharp difference between the sizes and colors of SFO setae in *C. capitata* and *C. catoirii*, suggests that they may be under sexual selection; nevertheless their allometric slopes were especially low, and were not even statistically significant in three of four measures. The sizes of the SFO setae are thus poor indicators of male size, and seem more likely to have evolved under female choice for “arbitrary” traits rather than as indicators of male size. There are further sexual dimorphisms in some of these species (greater pilosity on the front femur of males of *C. capitata* and *C. catoirii*, larger frontal bristles in male *C. catoirii*): evaluation of their possible significance (e.g., visual stimuli, dispersers of chemical stimuli, threats during male-male interactions) must await further behavioral studies.

Most sexual dimorphisms resulted from male-female differences in elevation ($N = 52$ cases) rather than slope ($N = 5$ cases). Perhaps changes of elevation require less reorganization of developmental programs than do changes in slope, and are thus easier to evolve.

Acknowledgments

RDB and WGE thank Eddy Camacho for technical help, Bernal Burgos and Hernan Camacho for specimens of wild Costa Rican flies, Jorge Lobo and Federico Bolaños for help with statistics, and the International Atomic Energy Agency, the Smithsonian Tropical Research Institute, and the Vicerrectoría of the Universidad de Costa Rica for financial support.

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