

Sexual Dimorphism in *Anastrepha suspensa* (Loew) and Other Tephritid Fruit Flies (Diptera: Tephritidae): Possible Roles of Developmental Rate, Fecundity, and Dispersal

John M. Sivinski^{1,2} and Gary Dodson²

Accepted November 5, 1991; revised December 20, 1991

Larger male Caribbean fruit flies are more likely to be chosen as mates and defeat rivals in territorial contests. Yet males are smaller than females. Adaptive explanations for relatively small male size include (1) acceleration of male development to maximize female encounter rates, (2) selection for greater female size to increase fecundity, and (3) selection for body sizes most suitable for sexually dimorphic degrees of mobility, speed, and distance flight. None of these unambiguously accounts for the degree of sexual dimorphism. Male development is not accelerated relative to that of females. On average, males remain in fruit longer than females and those males with extended development periods are smaller than more rapidly developing individuals. There is no evidence that female enlargement alone, presumably for greater fecundity, has generated the degree of dimorphism in the Caribbean fruit fly or other fruit flies. The relationship between dimorphism and mean female body size in 27 species of Tephritidae is the opposite of what would be predicted if differences in dimorphism were due to differences in unilateral female enlargement. Larger size in a species or in one sex of a species may be an adaptation for extensive flight. In general, among 32 species of fruit flies, as body size increases, wing shape becomes progressively more suited for distance flight. However, there are important exceptions to this correlation. Both sexual selection and nonadaptive allometries may contribute to the range of dimorphisms within the family.

¹Insect Attractants, Behavior, and Basic Biology Research Laboratory, Agricultural Research Service, U.S. Department of Agriculture, Gainesville, Florida 32604.

²Department of Biology, Ball State University, Muncie, Indiana 47306.

³To whom correspondence should be addressed at USDA/ARS, P.O. Box 14565, Gainesville, Florida 32604.

KEY WORDS: sexual selection; body size; wing aspect ratio; *Ceratitis*; *Dacus*; *Bactrocera*; *Rhagoletis*; *Urophora*.

INTRODUCTION

The different reproductive organs and behaviors of males and females can influence the evolution of their body sizes (Darwin, 1871). For instance, the relatively large size of males in some polygynous species is frequently ascribed to a history of competition and confrontation with sexual rivals (e.g., Alexander *et al.*, 1979). An extreme example is the huge and combative male of the southern elephant seal *Mirounga leonina* (Linn.), which can be up to eight times heavier than his mate (Bryden, 1969). However, as noted by Reiss (1989), there are more ambiguous cases. In the Weddell seal (*Leptonychotes weddelli* Lesson), another aggressive harem-forming pinniped, males are actually smaller than females. In fact, relatively small polygynous males are found in a number of bats and anurans and are the rule in insects (citations by Reiss, 1989).

Males of the Caribbean fruit fly *Anastrepha suspensa* (Loew) benefit from being larger than sexual competitors. Bigger males are better able to defeat adversaries in territorial disputes within mating aggregations (Burk, 1984), they produce acoustic signals that elicit female responses more frequently than smaller males (Sivinski *et al.*, 1984), and they are more likely to be chosen as mates than are smaller males (Burk and Webb, 1983). While both intra- and intersexual selection seem to favor increased male size, males weigh only 80% as much as females (Sivinski and Calkins, 1990).

There are two general types of adaptationist explanation for "unexpectedly" small males. The first is that some factor favors small male size. For example, female discrimination against larger males can influence the evolution of male size. Female *Drosophila subobscura* find the slower stops and accelerations in the courtship dances of bigger males less attractive (Steele and Partridge, 1988). In another instance, the amplexus position of larger male *Uperoleia laevigata* frogs is mechanically less suitable (Robertson, 1990). Females prefer males that are about 70% their own length. The second type of explanation for relatively small males is that there is even greater selection for increased female size than there is for male size. More bulk in females is often considered an adaptation to increase fecundity or enhance ability to rear offspring (e.g., Ralls, 1976). In species in which females rather than males are territorial, females may be disproportionately selected for large size (e.g., Fairbairn, 1990).

Both perspectives, the "small male" and the "big female," are addressed in this investigation of sexual dimorphism in *Anastrepha suspensa* and other tephritid fruit flies. The particular topics considered are (1) the relationship between adult body size and development times inside host fruit, (2) the role of

female fecundity in the evolution of female size, and (3) the influence of body size on dispersal ability and mobility.

METHODS

Developmental Period

To determine if time spent as a larva influences adult body size, *A. suspensa* larvae hatched from eggs collected over a 24-h period were reared by the method described by Sivinski and Calkins (1990). Larvae under these conditions typically mature over a 3- to 4-day period. Larvae leaving the diet during the first and third days of this maturation period were separated and allowed to pupate on moistened vermiculite. As adults emerged, the sexes were separated, and the dorsal length of the thorax of each fly was measured from the anterior margin of the prothorax to the posterior margin of the scutellum with an optical micrometer with 20 × magnification. Statistical comparisons were by *t* test (SAS Institute, 1987).

Fecundity

Comparison of sexual dimorphism in different species could reveal patterns that would indicate the importance of fecundity in the evolution of body size. Body size in 32 species of tephritids was quantified through measurements of thoracic length (see above). This measurement was chosen over dry weight since specimens preserved in alcohol tend to lose soft tissue over time and the length of preservation differed among species. Thoracic length was preferred over the frequently used wing length since there were clear differences in the relative development of wings between species and even between the sexes of certain species (see Dispersal and Agility, below). It is our impression that the thorax showed relatively little specialization in any of the species and was the most generalized and monomorphic of the rigid body structures that could be conveniently measured.

Specimens of various species preserved in alcohol were obtained from colleagues around the world. Conspecific individuals reared from different hosts can vary in size (personal observation). When possible, attempts were made to measure individuals reared in the laboratory or taken in the field from a particular site over a relatively short period of time. It was assumed in the first case that selection under domestication did not have a substantial effect on dimorphism.

The following species (in alphabetical order) and numbers of specimens were examined: *Aciurina bigeloviae* (Cockerell), 15 males, 14 females, G. Dodson, collected on III-90; *Anastrepha bistrigata* Bezzi, 16 males, 25 females, Brazil, A. Malavasi, I-91; *A. distincta* Greene, Finca Tempinque, Antigua,

Guatemala, from McPhail trap in Inga; *A. fraterculus* (Wiedemann), 25 males, 25 females, laboratory colony, USDA-ARS, Mission, TX, D. Robacker, 1988; *A. grandis* (Maquart), 12 males, 12 females, Brazil, A. Malavasi, I-91; *A. ludens* (Loew), 25 males, 25 females, laboratory colony, USDA-ARS, Mission, TX, D. Robacker, III-90; *A. obliqua* (M.), 25 males, 25 females, laboratory colony, USDA-ARS, Mission, TX, D. Robacker, 20-III-90; *A. serpentina* (Wiedemann), 8 males, 10 females, Finca Brilantos, Retalhuleu, Guatemala, from McPhail trap in mango, 8-VI-89; *A. striata* Schiner, 21 males, 25 females, Finca Brilantos, Retalhuleu, Guatemala, McPhail trap in guava; *A. suspensa*, 25 males, 25 females, laboratory colony, IABBBRL, Gainesville, FL, J. Sivinski, III-90; *Bactrocera alyxiae* (May), 15 males, Bamaga, Australia, E. Hamacek, 16-IV-90, from cue-lure trap; *B. bryoniae* (Tryon), 3 males, 9 females, Munduberra, Australia, E. Hamacek, 2-V-90, from *Diplocyclas palmatas*; *B. cucumis* French, 14 males, 14 females, laboratory colony, Brisbane, Australia, T. A. Heard, 2-V-90; *B.* (= *Dacus*) *cucurbitae* (Coquillett), 20 males, 20 females, Waimanaia, HI, M. Ramadan, 14-III-90; *B. dorsalis* (Hendel), 20 males, 20 females, Oahu, HI, M. Ramadan, 4-IX-90, from Surinan cherry; *B. frauenfeldi* (Schiner) 19 males, Bamaga, Australia, E. Hamacek, 16-IV-90, from cue-lure trap; *B. jarvisi* Tryon, 6 males, laboratory colony, Brisbane, Australia, T. A. Heard, 2-V-90; *B. musae* (Tryon), 14 males, Bamaga, Australia, E. Hamacek, 16-IV-90, from methyl eugenol trap; *B. neohumeralis* (Hardy), 25 males, 25 females, laboratory colony, Brisbane, Australia, T. A. Heard, 2-V-90; *B. peninsularis* (Drew & Hancock) 22 males, Bamaga, Australia, E. Hamacek, 16-IV-90, from cue-lure trap; *B. tryoni* (Frogg) 21 males, 25 females, from laboratory colony, Brisbane, Australia, T. A. Heard, 2-V-90; *Ceratitidis capitata* (Wiedemann), 12 males, 18 females, laboratory colony, Guatemala, J. Sivinski; *Dacus oleae* (Gmelin), 19 males, 19 females, laboratory colony, Demokritos, Greece, A. Manoukas, 13-XI-90; *Paracantha gentilis* (Hering), 3 males, 3 females, Albuquerque, NM, G. Dodson, III-90; 1987; *Phytalmia mouldsi* MacAlpine & Schneider, 9 males, 7 females, Iron Range, Queensland, Australia, G. Dodson III-90; *Procecidochares* sp., 8 males, 11 females, Albuquerque, NM, G. Dodson; *Rhagoletis completa* Cresson, 25 males, 21 females, Jeff Davis County, TX, R. Wharton, 19-VIII-87; *R. pomonella* (Walsh), 25 males, 25 females, Urbana, IL, IX-86, from *Crategus mallis*; *R. suavis* (Loew), 12 males, 8 females, Muncie, IN, G. Dodson, XI-90; *Toxotrypana curvicauda* (Gerstaecker), 18 males, 25 females, Dade County, FL, P. Landolt, VII-90; *Urophora affinis* (Fröhd), 12 males, 12 females, Ravalli County, MT, W. Good, 17-VIII-90; *U. quadrifasciata*, 12 males, 12 females, Ravalli County, MT, W. Good, 17-VIII-90.

Statistical analysis was by regression of log-transformed data (SAS Institute, 1987). Since both variables were measured with equal error, slopes calculated by least-squares regression were transformed to reduced-major-axis

regression values by dividing the slope by the correlation coefficient r (Reiss, 1989).

Dispersal and Agility

Wing structure can influence flight ability (e.g., Norberg and Raynor, 1987). If body size were also influenced by the extent and type of flight performed by a species, then body size and wing shape might change together in a predictable pattern. Wing shapes and sizes were determined in the 32 species of Tephritidae listed in the previous section. All individuals whose thoracic length was measured also had their wings examined in the following manner. A wing was dissected away from the body and placed on a glass slide, and its image projected onto a piece of paper through the use of a microprojector (Bausch and Lomb). Measurements of the drawing were made with a digital tablet and the software package Sigmascan (Borland). Length was defined as the distance from the wing tip to a line perpendicular to the long axis of the wing that began on the most proximate point of the axillary cell. The area of wing, again bounded proximally by the axillary cell line, was obtained in a similar manner. Wing aspect ratios were calculated from the above dimensions. Aspect ratio (AR) is a means of quantifying wing shape and is a ratio of wing length to width expressed as $AR = 4 \text{ length}^2 \cdot \text{area}^{-1}$ (e.g., Betts and Wooton, 1988). Analysis was by regression with log-transformed size measurements (SAS Institute, 1987). Means were compared by t test (SAS Institute, 1987).

RESULTS

Developmental Period

Males that are smaller might mature more quickly and have more opportunity to encounter mates than will larger flies (Thornhill and Alcock, 1983). In fruit flies, there is an additional reason to mature as quickly as possible. Fruit has evolved to be eaten and its palatability poses a danger to the inhabitants of a fruit that might be eaten with it. By abandoning hosts at what would otherwise be a less than optimal size, male larvae may be more able than females to sacrifice adaptively adult size for greater safety. If either argument were true for the Caribbean fruit fly, males would be expected to leave fruit earlier than females of equal age. This is not the case. In fact, females tend to mature earlier and leave fruit prior to males (Sivinski and Calkins, 1990). Nor is there any evidence that males might sometimes extend larval feeding periods in order to "risk" becoming a larger adult. In the laboratory, eggs laid over a period of 24 h typically result in a cohort of larvae that mature over a period of 3–4 days (Sivinski and Calkins, 1990). While the majority of early developers is female,

and the majority of late developers male, there are some of each sex in both classes. There was no difference in the thoracic length of females that leave diets on the first and third days of emergence (day 1, $n = 144$, $\bar{X} = 2.37$ mm, $SE = 0.04$ mm, vs day 3, $n = 97$, $\bar{X} = 2.36$ mm, $SE = 0.04$ mm; $t = 0.36$, $df = 239$ $P = 0.72$). In males, day 1 individuals were actually larger than day 3 individuals (day 1, $n = 34$, $\bar{X} = 2.30$ mm, $SE = 0.07$ mm, vs day 3, $n = 123$, $\bar{X} = 2.19$ mm, $SE = 0.04$ mm; $t = 2.60$, $df = 155$, $P = 0.01$).

Fecundity

Larger female insects often, but not always, produce more offspring than smaller conspecifics (citations by Thornhill and Alcock, 1983). All other things being equal, reproductive competition between females in such cases will select larger individuals. When adult females neither feed nor disperse long distances, they can become relatively enormous, a graphic example being certain larviform cantheroid beetles (e.g., Tiemann, 1967).

It is possible that selection for fecundity has created the larger-female dimorphism of *A. suspensa*. There is considerable variance among the lifetime egg productions of *A. suspensa* females. However, the maximum numbers of eggs per day that females in six size categories laid are significantly correlated with their thoracic length [$r = 0.86$ (Sivinski, unpublished manuscript)]. Thus, the potential fecundity of females increases with size.

Given the potential for increased egg production with greater body size, what might indicate that selection for fecundity has actually generated the degree of dimorphism found in *A. suspensa* or any other tephritid? One means of examining this possibility is to look for a particular pattern of dimorphism within a group of species. If there is variation in the relative sizes of males compared to females, and if that variation is ascribed solely to selection in certain species for greater female fecundity/size than in others, then the variation in female size among species should be greater than the variation in male size among species. What is more, the relative difference in male size to female size should increase as females become larger. That is, if all other things are equal, males of different species should be relatively homogeneous in size compared to females, so that the larger the female of a species, the greater the difference between male and female size. An illustrative example is found in the stick insects (Phasmatodea). There are a number of giant female forms with enlarged abdomens that give the impression of being selected to produce either large eggs or large numbers of eggs. A regression of log-male body length over log-female body length in 152 species resulted in a statistically significant line with a slope of 0.84 [$F = 836.8$, $P = 0.0001$, $r^2 = 0.85$; body lengths from citations by Sivinski (1978)]. A slope of 1 would have shown that as females increased in body size, males increased proportionately. A slope of less than 1 demonstrates a tendency for

species with larger females to have relatively smaller males. Thus, a prediction of the argument that differences in dimorphism are due in part to greater selection in some species for female size/fecundity is fulfilled.

When the same analysis is applied to the thoracic lengths of male and female Tephritidae, the reduced-major-axis slope is 1.12 (least-squares slope = 1.11) and significantly *greater* than 1 ($t = 3.67$, $P < 0.01$; Fig. 1). Not all groups within the family show the same pattern of dimorphism. The Dacinae, composed in this sample of the genera *Bactrocera*, *Dacus*, and *Phytalmia*, yield a slope of 0.99 that is statistically indistinguishable from 1 ($t = 0.04$, $n = 8$, $P > 0.90$). However, in the genus *Anastrepha* there is a pronounced tendency to find comparatively large males in species with large females ($b = 1.22$, $t = 2.2$, $P < 0.05$; Fig. 2; least-squares slope = 1.20). This pattern is the opposite of what would be expected were differences in sexual dimorphism among species of *Anastrepha* due solely to differing degrees of selection acting on females to increase their fecundity.

Dispersal and Agility

Males and females often have different patterns of movement and different locomotory organs. For example, in insects, including Diptera, there are species with winged males and wingless females (e.g., Capella and Whitworth, 1973); wingless males are rarer (Hamilton, 1979). There might be less obvious sexual differences in adaptations for movement, and perhaps body size is one of these. If so, differences in mobility could underlie the evolution of sexual dimorphism in size.

It is supposed, all other things being equal, that a larger fruit fly is capable of covering a greater distance at a higher velocity than a smaller individual (see Peters, 1983; Calder, 1984; Fairbairn, 1990). On the other hand, smaller insects might have greater agility and be better able to maneuver around sexual rivals or potential mates. Small males may enjoy such advantages in both Diptera and Lepidoptera (McLachlan, 1986; McLachlan and Allen, 1987; Marshall, 1988; McLachlan and Neems, 1989).

Sexual dimorphism in flight and dispersal has not been widely examined in the Tephritidae. In one closely observed species, the Mediterranean fruit fly, *Ceratitis capitata*, females spend more time foraging for nitrogen-rich foods and travel considerably farther than males (Hendrichs and Hendrichs, 1990). Female *C. capitata* are significantly larger than males, as are the females of 16 of the 27 species in which both sexes were measured (Table I; only in the antlered fly *Phytalmia mouldsi* are males larger than females).

If species of flies that are believed to travel substantial distances are larger than more sedentary species, this might give some credence to the possibility that differences between the sexes in any particular species could evolve because

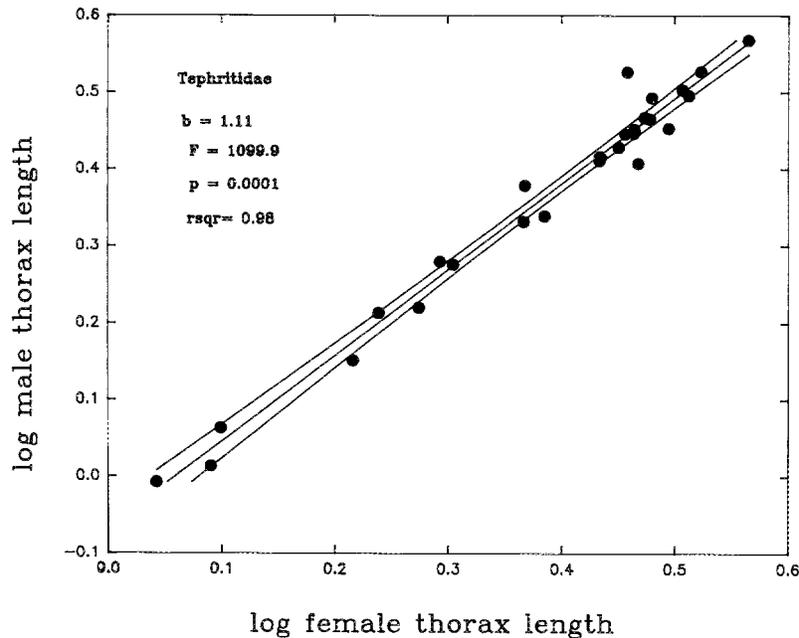


Fig. 1. The least-squares relationship between mean log-male thoracic length and mean log-female thoracic length in 27 species of Tephritidae. Boundary lines represent 95% confidence limits.

of differences in their patterns of movement. Flies that are believed to travel extensively, *Toxotrypana curvicauda* (Landolt and Hendrichs, 1983), *Phytalmia mouldsi* (G. Dodson, personal observation), *Bactrocera* (= *Dacus*) *tryoni*, *B. dorsalis*, *B. cucurbitae* (Fletcher, 1989), and *Anastrepha ludens* (Fletcher, 1989), are larger than species that are known or suspected to be relatively sedentary, such as *Procecidocares* sp. (Dodson, 1986) *Aciuria bigeloviae* (Dodson, 1986), *Rhagoletis pomonella* (Fletcher, 1989), *Urophora quadrifaciata* and *affinis* (Fletcher, 1989), and *Dacus oleae* (Fletcher, 1989) (see Table I). Unfortunately, there are phylogenetic and ecological complications with such a comparison. The sedentary species are either "gall"-forming Tephritinae or Trypetinae that specialize in small fruits. The highly mobile Dacinae and Trypetinae often infest larger fruit. Perhaps limited availability of food in a gall or small fruit, rather than adult mobility per se, could be responsible for the sedentary species relatively small size.

Is there any further evidence that body size could be an adaptation for mobility? It would be useful if size could be correlated with some other feature that is suspected of influencing the amount and speed of movement. Wing size and shape are such characteristics.

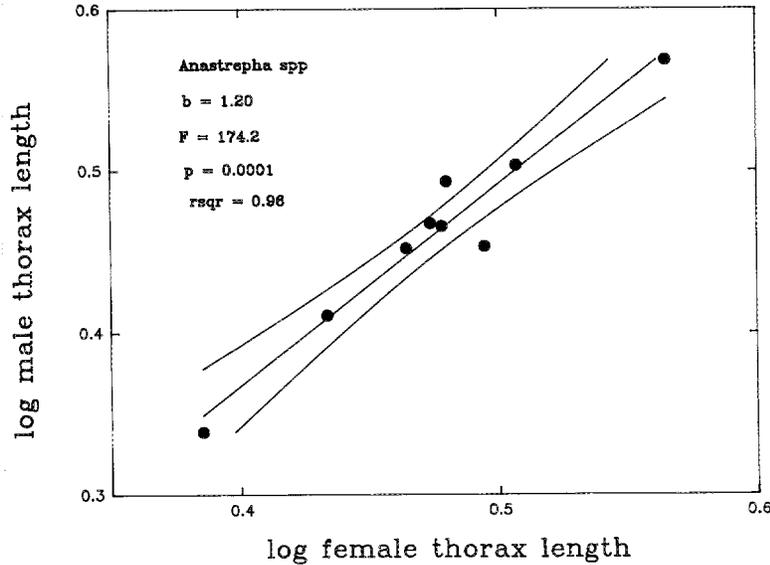


Fig. 2. The least-squares relationship between mean log-male thoracic length and mean log-female thoracic length in nine species of *Anastrepha*. Boundary lines represent 95% confidence limits.

Wings of various sizes and shapes perform differently in flight. These aerodynamic relationships have been most thoroughly explored in vertebrates, e.g., the work of Norberg and Rayner (1987) on bats, but similar conclusions have been reached with insects (e.g., Chai and Srygley, 1990; McLachlan and Allen, 1987). In essence, wings that are both long and narrow (i.e., have a high aspect ratio) are efficient but do not produce high speeds. They are associated with long, even migratory-scale, flights. Short, high-aspect ratio wings are capable of generating high rates of extended speed. Broad (low aspect ratio) and short wings and hence short wing span can be important to an agile insect maneuvering through cluttered vegetation. Broad, long wings would be effective in maneuverable flight or, particularly, efficient takeoffs (Norberg and Rayner, 1987).

In this sample, only one type of tephritid, the female papaya fruit fly, *Toxotrypana curvicauda*, has wings that are both more than 1 SD narrower than average and more than 1 SD longer than average (length here being relative, i.e., the ratio of wing length to thorax length; Table I). These long narrow wings would be expected to be found on a fly that does a substantial amount of traveling. *T. curvicauda* is unusual in that it roosts and perhaps mates off the host (Landolt and Hendrichs, 1983), making trips between forested areas and papaya (M. Alvja, personal communication). Another species believed to forage

Table 1. Mean Thoracic Length (SE), Mean Wing Length (SE), and Mean Wing Aspect Ratio (SE) in Males and Females of Various Species of Tephritidae^a

	Thorax (mm)		Wing length (mm)		Wing aspect ratio	
	Male	Female	Male	Female	Male	Female
<i>Actinina bigeloviae</i>	1.42 (0.04)	1.65 (0.04)a	2.86 (0.05)	3.33 (0.05)	9.69 (0.15)	9.38 (0.10)
<i>Anastrepha bistrigata</i>	3.02 (0.02)	3.12 (0.06)	5.95 (0.08)	6.00 (0.10)	9.51 (0.06)	9.72 (0.09)
<i>Anastrepha distincta</i>	2.84 (0.04)	2.92 (0.04)	5.08 (0.07)	5.43 (0.04)	9.00 (0.05)	9.29 (0.06)a
<i>Anastrepha fraterculus</i>	2.94 (0.02)	2.98 (0.02)	5.14 (0.03)	5.29 (0.03)	8.84 (0.04)	8.95 (0.06)
<i>Anastrepha grandis</i>	3.68 (0.06)	3.71 (0.06)	7.81 (0.07)	8.08 (0.10)	10.42 (0.06)	10.29 (0.08)
<i>Anastrepha ludens</i>	2.85 (0.04)	3.13 (0.03)a	5.70 (0.04)	6.21 (0.05)	9.22 (0.09)	9.42 (0.05)a
<i>Anastrepha obliqua</i>	2.59 (0.05)	2.72 (0.04)a	5.17 (0.07)	5.42 (0.05)	9.02 (0.06)	9.08 (0.04)
<i>Anastrepha serpentina</i>	3.19 (0.05)	3.22 (0.06)	5.78 (0.11)	6.20 (0.05)	9.37 (0.13)	9.53 (0.07)
<i>Anastrepha striata</i>	2.93 (0.04)	3.01 (0.04)	5.61 (0.05)	5.71 (0.06)	9.38 (0.07)	9.46 (0.06)
<i>Anastrepha suspensa</i>	2.19 (0.03)	2.43 (0.04)a	4.32 (0.04)	4.74 (0.04)	8.58 (0.09)	8.99 (0.05)a
<i>Bactrocera alysiata</i>	2.46 (0.05)	—	4.14 (0.05)	—	9.99 (0.09)	—
<i>Bactrocera bryoniae</i>	3.13 (0.07)	3.26 (0.02)a	5.17 (0.15)	5.49 (0.03)	10.01 (0.08)	9.97 (0.06)
<i>Bactrocera cucumis</i>	2.56 (0.03)	2.94 (0.05)a	4.15 (0.02)	5.09 (0.05)	9.41 (0.06)	9.68 (0.12)
<i>Bactrocera cucurbitae</i>	2.68 (0.03)	2.83 (0.03)a	4.93 (0.03)	5.34 (0.03)	9.63 (0.05)	9.61 (0.04)
<i>Bactrocera dorsalis</i>	2.80 (0.03)	2.91 (0.03)a	4.84 (0.03)	5.03 (0.03)	9.39 (0.08)	9.45 (0.08)
<i>Bactrocera fravenfeldi</i>	2.73 (0.05)	—	3.95 (0.05)	—	9.26 (0.06)	—
<i>Bactrocera jarvisa</i>	2.88 (0.03)	—	4.83 (0.03)	—	10.16 (0.17)	—
<i>Bactrocera musae</i>	2.88 (0.30)	—	4.72 (0.05)	—	10.13 (0.08)	—
<i>Bactrocera neohumeralis</i>	2.80 (0.03)	2.86 (0.02)	4.63 (0.04)	4.79 (0.03)	9.86 (0.05)	9.80 (0.06)
<i>Bactrocera peninsularis</i>	2.43 (0.05)	—	4.16 (0.07)	—	9.74 (0.08)	—
<i>Bactrocera tryoni</i>	2.61 (0.04)	2.72 (0.04)	4.48 (0.03)	4.69 (0.04)	9.82 (0.06)	9.96 (0.04)a
<i>Ceratitis capitata</i>	1.64 (0.03)	1.74 (0.03)a	3.31 (0.06)	3.46 (0.03)	7.13 (0.07)	7.58 (0.05)a
<i>Dacus oleae</i>	1.91 (0.02)	1.97 (0.02)a	3.57 (0.02)	3.71 (0.03)	9.90 (0.08)	10.00 (0.09)
<i>Paracantha gentilis</i>	2.17 (0.22)	2.33 (0.12)	4.57 (0.20)	4.55 (0.16)	8.08 (0.20)	8.06 (0.09)
<i>Phytomyia moulti</i>	3.38 (0.12)	2.89 (0.11)a	6.45 (0.20)	5.89 (0.14)	13.53 (0.25)	13.31 (0.16)
<i>Procecidochares</i> sp.	1.04 (0.04)	1.24 (0.05)a	2.16 (0.04)	2.64 (0.04)	8.36 (0.10)	8.53 (0.10)
<i>Rhagoletis completa</i>	1.67 (0.03)	1.89 (0.03)a	2.78 (0.04)	3.09 (0.04)	8.90 (0.09)	8.77 (0.07)
<i>Rhagoletis pomonella</i>	1.89 (0.03)	2.02 (0.03)a	3.18 (0.03)	3.63 (0.06)	8.34 (0.10)	8.31 (0.04)
<i>Rhagoletis suavis</i>	2.42 (0.01)	2.34 (0.09)	4.26 (0.16)	4.33 (0.13)	9.15 (0.07)	8.88 (0.09)a
<i>Toxotrypana curvicauda</i>	3.39 (0.09)	3.34 (0.02)	7.42 (0.16)	8.10 (0.07)	10.31 (0.06)	11.10 (0.06)a
<i>Urophora affinis</i>	1.16 (0.01)	1.26 (0.02)a	2.29 (0.04)	2.56 (0.05)	9.30 (0.14)	9.41 (0.12)
<i>Urophora quadrifasciata</i>	0.98 (0.01)	1.10 (0.03)a	1.99 (0.04)	2.27 (0.04)	9.27 (0.18)	9.00 (0.16)

^aSpecies are in alphabetical order. An ‘‘a’’ after either the female thorax length or the female wing aspect ratio of a particular species denotes a statistically significant sexual dimorphism in this trait.

widely for scattered oviposition sites, *Phytalmia mouldsi* (G. Dodson, personal observation), also has very narrow wings, but their relative length is within 1 SD of the mean. Both species are unusually large for tephritids. *Bactrocera* (= *Dacus*) *cucurbitae*, like the papaya fruit fly, mates and roosts off hosts (Iwahashi and Najima, 1986). However, neither is it unusually large nor does it bear peculiarly elongated or narrow wings. Other *Bactrocera* species that are believed to undertake extensive dispersal, *B. tryoni* and *B. dorsalis*, have wings and body sizes within 1 SD of average. The closely related *Dacus oleae* is sedentary compared to other species of the *Bactrocera/Dacus* lineage (Fletcher, 1988) and actually has narrower wings than its more dispersive relations, albeit it is a smaller insect. The extremely sedentary gall-forming *Urophora* species likewise have wings of average shape. As noted previously they are very small flies, but again, this might be the result of restrictions imposed by diet or some other aspect of their parasitic relationship with flower seed-heads, rather than the lack of demand for mobility. Given these numerous exceptions, there is still a positive correlation between wing aspect ratio and log thorax length for both tephritids in general ($F = 13.4$, $P = 0.0006$, $r^2 = 0.19$; Fig. 3) and the genus *Anastrepha* in particular ($F = 49.5$, $P = 0.0001$, $r^2 = 0.76$).

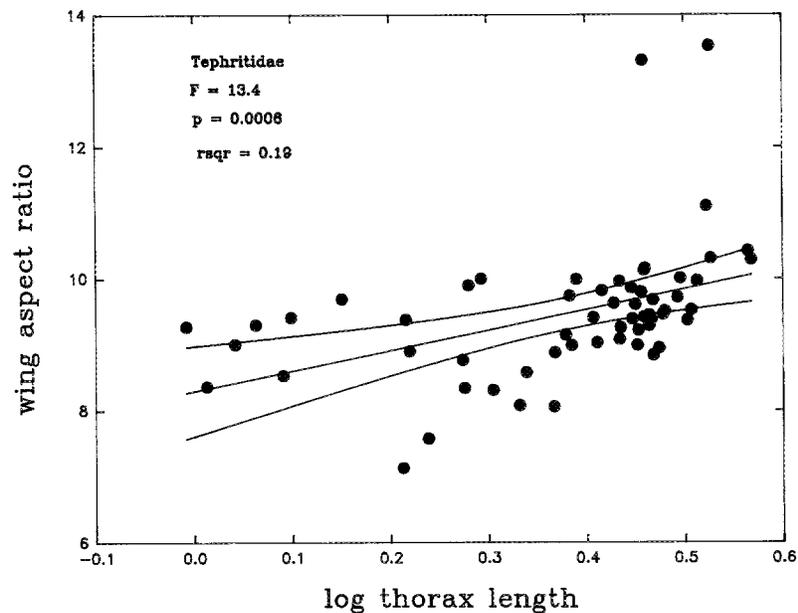


Fig. 3. The least-squares relationship between wing aspect ratio and mean log thoracic length in both sexes of 32 species of Tephritidae. Boundary lines represent 95% confidence limits.

There is no species in the sample that has the very narrow and very short wings of the high-speed fliers. However, the male apple maggot (*Rhagoletis pomonella*) has wings that are shorter than average by more than a standard deviation and are broader by more than a standard deviation as well. Such a fly would be predicted to be maneuverable in cluttered vegetation. There seems to be no evidence that the apple maggot is peculiarly agile or any reason why it should have such extreme wing development. Males of two species from North America, the gall-forming *Procecidocares* sp. and the flower head-infesting *Paracantha gentillis* have extremely long broad wings. This would suggest unusually maneuverable flight and/or efficient takeoffs. *P. gentilis* lives on a treacherous substrate of thistle spines over which it scrambles gingerly (G. Dodson, personal observation). Perhaps this delicacy of movement carries over into its flight about host plants. What is noteworthy about these particularly broad-winged flies, regardless of their wing length, is that they are male. There are seven instances of significant sexual dimorphism in wing shape in the sample (four in the genus *Anastrepha*). In six of these, the male has broader wings. A prediction might be that males in a variety of species engage in slower, more maneuverable flight, perhaps as they search within foliage for potential mates and for microhabitats from which to broadcast sexual signals (see Sivinski, 1989; Hendrichs and Hendrichs, 1990). Such males might also increase maneuverability by reducing body size, although in only three of these six species are males significantly smaller than conspecific females.

There is an alternative explanation for sexual dimorphism in wing shape. Male wings may be specialized to produce acoustical signals. Speculations have been made that the broader wings of male *Anastrepha suspensa*, *Ceratitis capitata*, and *Toxotrypana curvicauda* and the braconid parasite of Tephritidae, *Diachasmimorpha longicaudata*, serve a communicative role (Sivinski and Webb, 1985a,b, 1989). Subsequent recordings of similar acoustic signals from species without statistically significant wing dimorphism, such as *Anastrepha serpentina*, *A. grandis*, *A. fraterculus*, and *A. striata*, weaken this argument (Sivinski and Malavasi, personal observation). Male *B. cucurbitae*, *B. dorsalis*, and *B. tryoni* all signal acoustically but only *tryoni* bears dimorphic wings (e.g., Kuba *et al.*, 1984). Female *C. capitata*, whose wings are significantly narrower than those of males, produce a repertoire of songs similar to that of the male (Webb *et al.*, 1983).

DISCUSSION

None of the presumed adaptive factors examined so far, duration of the larval stage, female fecundity, and differences in mobility, unambiguously accounts for the larger-female sexual size dimorphism typical of Tephritidae. Males of *A. suspensa* in general are not trading valuable adult size for safety

or earlier access to mates by shortening the time they spend in fruit. On average, they inhabit fruit for a longer period of time than females. Moreover, those male *A. suspensa* with longer developmental durations are actually smaller than the more rapidly maturing members of their cohort. Thus, later-emerging males are not "gamblers" that remain in a dangerous environment to acquire the resources to become unusually attractive and competitive adults. The pattern of female first emergence, and presumably shorter larval life, occurs in fruit flies other than *A. suspensa*. Interestingly, it is found in species both where females are larger than males [*Rhagoletis completa* (Boyce, 1934)] (Table I) and where males are larger than females [*Phytalmia mouldsi* (G. Dodson, personal observation)] (Table I).

Competition between female insects in terms of fecundity can yield striking sexual dimorphisms. However, the comparative evidence in the Tephritidae does not support the argument that the different degrees of dimorphism among species are due to different degrees of unilateral female enlargement. If females of some species were under greater selection for fecundity than others, then on average the larger these high-fecundity females become, the more dimorphic their species should become. While this is the tendency in taxa such as the stick insects and cantheroid beetles, it is not true of fruit flies. As females of Dacinae become larger, males increase in size at an identical rate. In the genus *Anastrepha*, males become relatively larger as females become absolutely larger.

Body size may influence movement and it is possible that a sexual dimorphism in patterns of movement is the evolutionary cause of dimorphisms in size. Comparative evidence on this is ambiguous. If larger size is an adaptation to cover distance better, then fruit flies that disperse widely should be larger than more sedentary species. This is often the case, but comparisons are complicated by phylogenetic and ecological differences between the two groups. Another approach is to correlate body size with some other structure that clearly influences movement. Wing size and shape have been found to be adapted to patterns of movement in vertebrates and other insects. While there is a tendency for wings progressively more suited for extended flight to be found on increasingly larger flies, there are numerous exceptions to the rule, so that the argument is only weakly supported. In the end, it cannot be discounted that some fruit flies are larger in order to engage in longer flights or that females of particular species may be larger to undertake their more substantial foraging or dispersal. It also remains possible that males may sacrifice size for greater agility, but corroborative behavioral observations are unavailable. It should be noted that if body size is an important component of flight and if large size is an adaptation for "migration," it might be favored in both sexes (Fairbairn, 1990). The result would be reduced sexual dimorphism in large species. This is the pattern displayed in the genus *Anastrepha*.

There are other presumably adaptive factors that might account for variance

in sexual dimorphism within the Tephritidae. Differing degree of sexual selection is certainly a candidate. For example, the unique greater-male size of the antlered fly *Phytalmia mouldsi* could be due to a history of intense confrontation between males as they compete for control of rare, but highly defensible, oviposition sites in fallen timber (G. Dodson, personal observation; see Borgia, 1979). Males of two species of *Rhagoletis*, *R. completa* and *R. suavis*, also engage in fierce fights as part of resource defense mating systems (G. Dodson, personal observation). In *R. suavis*, but not *R. completa*, males are as large as females. Intersexual selection might also be of importance in determining dimorphism. Female *C. capitata* prefer males from certain populations even when they are smaller than their rivals (Arita and Kaneshiro, 1988). In this instance, female choice acts contrary to intrasexual selection, which favors larger males.

However, recent investigations into sexual dimorphism in taxa as disparate as primates and water striders have shown that nonadaptive factors influence relative body size. These factors include phylogenetic constraints and allometry. While allometries can arise through natural selection (as argued earlier for the pattern of sexual dimorphism in stick insects), they can also come about through apparently nonadaptive mechanisms (Lentenegger, 1978; Chaverud *et al.*, 1985; Fairbairn, 1990). One commonly repeated allometric pattern is the increase in relative male size as females become larger (citations by Fairbairn, 1990). This can be found in taxa where males are generally smaller than females or in groups where males are generally larger than females. Species of *Anastrepha* fit this pattern and its repetition in taxa with widely divergent ecologies invites speculation that some commonly encountered nonadaptive factor may be responsible.

ACKNOWLEDGMENTS

Many colleagues, including A. Malavasi, P. Landolt, D. Robacker, E. Hamacek, T. A. Heard, M. Ramadan, W. Good, and A. Manoukas, kindly provided us with specimens. Pat Graham and Eve Singleton spent many hours measuring flies. Pat Wilkerson cheerfully prepared the often-trying manuscript. Ted Burk, Jim Lloyd, and T. J. Walker suggested a number of important improvements in early drafts.

REFERENCES

- Alexander, R. D., Hoogland, J. L., Howard, R. O., Noonan, K. M., and Sherman, P. W. (1979). Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates, and humans. In Chagnon, N. A., and Irons, W. (eds.), *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, Duxbury Press, North Scituate, Mass., pp. 402-435.
- Arita, L. H., and Kaneshiro, K. (1988). Body size and differential mating success between males of two populations of the Mediterranean fruit fly. *Perif. Sci.* **42**: 173-177.

- Betts, C. R., and Wootton, R. J. (1988). Wing shape and flight behavior in butterflies (Lepidoptera: Papilionoidea and Hesperioidea): A preliminary analysis. *J. Exp. Biol.* **138**: 271-288.
- Borgia, G. (1979). Sexual selection and the evolution of mating systems. In Blum, M., and Blum, N. (eds.), *Sexual Selection and Reproductive Competition in Insects*, Academic Press, New York, pp. 19-80.
- Boyce, A. M. (1934). Bionomics of the walnut husk fly *Rhagoletis completa*. *Hilgardia* **8**: 363-579.
- Bryden, M. M. (1969). Growth of the southern elephant seal, *Microunga leonina* (Linn.). *Growth* **33**: 431-536.
- Burk, T. (1984). Male-male interactions in Caribbean fruit flies, *Anastrepha suspensa* (Loew) (Diptera: Tephritidae): Territorial fights and signalling stimulation. *Fla. Entomol.* **67**: 542-548.
- Burk, T., and Webb, J. C. (1983). Effect of male size on calling propensity, song parameters, and mating success in Caribbean fruit flies *Anastrepha suspensa* (Loew). *Ann. Entomol. Soc. Am.* **76**: 678-682.
- Calder, W. A. (1984). *Size, Function and Life History*, Howard University Press, Cambridge, Mass.
- Capella, K. J., and Whitworth, T. L. (1973). The distribution and avian hosts of *Carnus hemopterus* (Diptera: Milichidae) in North America. *J. Med. Entomol.* **10**: 525-526.
- Chai, P., and Srygley, R. B. (1990). Predation and the flight, morphology, and temperature of neotropical forest butterflies. *Am. Nat.* **135**: 748-765.
- Cheverud, J. M., Dow, M. M., and Lenteneger, W. (1985). The quantitative assessment of phylogenetic constraints in comparative analyses: Sexual dimorphism in body weight among primates. *Evolution* **39**: 1335-1341.
- Darwin, C. (1971). *The Descent of Man and Selection in Relation to Sex*, John Murray, London.
- Dodson, G. (1986). Lek mating system and large male aggressive advantage in a gail-forming tephritid fly (Diptera: Tephritidae). *Ethology* **72**: 99-108.
- Dodson, G. (1987). Biological observations on *Aciurina trixa* and *Valentibulla dodsoni* (Diptera: Tephritidae) in New Mexico. *Ann. Entomol. Soc. Am.* **80**: 494-500.
- Fairbairn, D. J. (1990). Factors influencing sexual size dimorphism in temperate water striders. *Am. Nat.* **136**: 61-86.
- Fletcher, B. S. (1989). Movements of Tephritid fruit flies. In Robinson, A. S., and Hooper, G. (eds.), *Fruit Flies: Their Biology Natural Enemies and Control, Vol. 3B*, Elsevier, Amsterdam, pp. 209-219.
- Hamilton, W. D. (1979). Wingless and fighting males in fig wasps and other insects. In Blum, M. S., and Blum, N. A. (eds.), *Sexual Selection and Reproductive Competition in Insects*, Academic Press, New York, pp. 167-220.
- Hendrichs, J., and Hendrichs, M. A. (1990). Mediterranean fruit fly (Diptera: Tephritidae) in nature: Location and diel pattern of feeding and other activities on fruiting and nonfruiting hosts and nonhosts. *Ann. Entomol. Soc. Am.* **83**: 632-641.
- Iwahashi, O., and Najima, T. (1986). Lek formation and male-male competition in the melon fly *Dacus cucurbitae* Coquillett (Diptera: Tephritidae). *Appl. Entomol. Zool.* **21**: 70-75.
- Kuba, H., Koyama, J., and Prokopy, R. (1984). Mating behavior of wild melon flies, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae) in a field cage: Distribution and behavior of flies. *Appl. Entomol. Zool.* **19**: 367-373.
- Landolt, P. J., and Hendrichs, J. (1983). Reproductive behavior of the papaya fruit fly *Toxotrypana curvicauda* Gerstaecker (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* **76**: 413-417.
- Lenteneger, W. (1978). Scaling of sexual dimorphism in body size and breeding system in primates. *Nature* **272**: 610-611.
- Marshall, L. D. (1988). Small male advantage in mating in *Parapediasia teterella* and *Agsiphila plumbifimbriella* (Lepidoptera: Pyralidae). *Am. Midl. Nat.* **119**: 412-419.
- McLachlan, A. J. (1986). Survival of the smallest: Advantages and costs of small size in flying animals. *Ecol. Entomol.* **11**: 237-240.
- McLachlan, A. J., and Allen, D. F. (1987). Male mating success in Diptera: Advantages of small size. *Oikos* **48**: 11-14.

- McLachlan, A., and Neems, R. (1989). An alternative mating system in small male insects. *Ecol. Entomol.* **14**: 85-91.
- Norberg, V. M., and Rayner, J. M. V. (1987). Ecological morphology and flight in bats (Mammalia: Chiroptera): Wing adaptations, flight performance, foraging strategy and echo location. *Phil. Trans. Roy. Soc. Lond.* **B316**: 335-427.
- Peters, R. H. (1983). *The Ecological Implications of Body Size*, Cambridge University Press, Cambridge, Mass.
- Ralls, K. (1976). Mammals in which females are larger than males. *Q. Rev. Biol.* **51**: 245-276.
- Reiss, M. J. (1989). *The Allometry of Growth and Reproduction*, Cambridge University Press, Cambridge.
- Robertson, J. G. (1990). Female choice increases fertilization success in the Australian frog *Uperoleia laevis*. *Anim. Behav.* **39**: 639-645.
- SAS Institute (1987). *User's Guide: Statistics*, SAS Institute, Cary, N.C.
- Sivinski, J. (1978). Intrasexual aggression in the stick insects *Diaperomera veliei* and *D. covilleae* and sexual dimorphism in the Phasmatodea. *Psyche* **85**: 395-405.
- Sivinski, J. (1989). Lekking and the small-scale distribution of the sexes in the Caribbean fruit fly *Anastrepha suspensa* (Loew). *J. Insect Behav.* **2**: 3-13.
- Sivinski, J., and Calkins, C. O. (1990). Sexually dimorphic developmental rates in the Caribbean fruit fly (Diptera: Tephritidae). *Environ. Entomol.* **19**: 1491-1495.
- Sivinski, J., and Webb, J. C. (1985a). Sound production and reception in the Caribfly, *Anastrepha suspensa*. *Fla. Entomol.* **68**: 273-278.
- Sivinski, J., and Webb, J. C. (1985b). The form and function of acoustic courtship signals of the papaya fruit fly *Toxotrypana curvicauda*. *Fla. Entomol.* **68**: 634-641.
- Sivinski, J., and Webb, J. C. (1989). Acoustic signals produced during courtship in *Diachasmimorpha* (Biosteres) *longicaudata* (Hymenoptera: Braconidae) and other Braconidae. *Ann. Entomol. Soc. Am.* **82**: 116-120.
- Sivinski, J., Burk, T., and Webb, J. C. (1984). Acoustic courtship signals in the caribfly *Anastrepha suspensa*. *Anim. Behav.* **32**: 1011-1016.
- Steele, R. H., and Partridge, L. (1988). A courtship advantage for small males in *Drosophila subobscura*. *Anim. Behav.* **36**: 1190-1197.
- Thornhill, R., and Alcock, J. (1983). *The Evolution of Insect Mating Systems*, Harvard University Press, Cambridge, Mass.
- Tiemann, D. L. (1967). Observations on the natural history of the Western banded glowworm *Zarhipis integripennis* (Le Coate) (Coleoptera: Phengodidae). *Proc. Calif. Acad. Sci.* **35**(12): 235-264.
- Webb, J. C., Calkins, C. O., Chambers, D. L., Schwienbacher, W., and Russ, K. (1983). Acoustical aspects of behavior of Mediterranean fruit fly, *Ceratitidis capitata*: Analysis and identification of courtship sounds. *Entomol. Exp. Appl.* **33**: 1-8.