Sexual Selection on Leks: A Fruit Fly Primer

Todd E. Shelly

USDA-APHIS, 41-650 Ahiki Street, Waimanalo, HI 96795 (todd.e.shelly@aphis.usda.gov)

Subject Editor: Juan Rull

Received 28 February 2018; Editorial decision 28 April 2018

Abstract

Lek mating systems are relatively rare but occur in a diverse taxonomic array of animals, including birds, mammals, anurans, and insects. Such systems exhibit four features: 1) males provide no parental care and supply only gametes; 2) males are spatially aggregated at mating arenas (or leks); 3) males do not control access to resources critical to females; and 4) females are free to select mates at the arena. Among insects, fruit flies of the families Tephritidae and Drosophilidae display lek behavior that closely resembles the ‘classic’ lek mating systems of vertebrate species. The objective of this paper is to provide an overview of empirical findings on lek-forming tephritid and drosophilid flies. The essay is organized around a series of 19 questions, the first six of which provide background information on fruit fly leks. These questions deal with the location, persistence, and size of leks as well as pheromonal attraction of females and the nature of male–male aggression. The remaining questions touch on broader issues that are common to the study of lekking species regardless of taxonomic affiliation. For example, these questions concern skewed mating distributions among males, male signals important in female choice, the importance of male aggression and signaling position in affecting male mating success, the possibility of male choice, costs to males associated with lek displays, and evidence of direct and indirect benefits to females resulting from mate selection etc. Reflecting data availability, emphasis is on precopulatory mate choice, sperm competition and female cryptic choice are briefly addressed.

Key words: Tephritidae, Drosophilidae, female choice, courtship display, male–male aggression

While relatively rare, lek mating systems appear in a wide diversity of taxa, including mammals, birds, anurans, fish, and insects (Hoglund and Alatalo 1995). Lek mating systems exhibit four features: 1) males provide no parental care and supply only gametes; 2) males are spatially aggregated at mating arenas (or leks); 3) males do not control access to resources critical to females; and 4) females are free to select mates at the arena (Bradbury 1981). In addition, lekking males usually hold and defend symbolic territories, so-called since they contain no resources (Lederhouse 1982, Evans 1993). However, this is not always the case, and aggregated males of some species exhibit a scramble type of competition for females arriving to the lek (Droney 1992).

Because leks contain no resources, they represent extreme instances of non-resource-based sexual selection. Sexual selection is widely considered to consist of two main processes, intra-sexual selection (typically manifest as male–male aggression) and inter-sexual selection (usually involving female choice of mates) (Darwin 1871). Where males defend or control access to resources, such as food or egg-laying sites, female choice may be directed at male phenotype as well as the resources controlled. The absence of territorial resources should, in principle, facilitate investigation of mate choice in lekking species, although disentangling the relative influences of male–male aggression and male phenotype is often challenging.

The goal of this essay is to review empirical studies of lek-forming insects in the context of questions common to sexual selection and lek behavior in animals as a whole. This exercise was motivated by several factors. First, although an excellent overview of lek behavior appeared relatively recently (Hoglund and Alatalo 1995), this work was, by the authors’ own admission, biased toward vertebrates. In addition, a volume (Shuker and Simmons 2014) dedicated to updating the seminal book ‘The Evolution of Insect Mating Systems’ (Thornhill and Alcock 1983) includes very little information on lek behavior. Finally, the most recent review of insect lekking (Shelly and Whittier 1997) is two decades old and is largely a catalogue of species exhibiting this behavior.

There are several things this essay is not. It is not a review of sexual selection theory. For this, readers are directed to several comprehensive works (Bateson 1983, Bradbury and Andersson 1987, Andersson 1994). It is not a thorough exploration of all conceptual issues relevant to lekking insects. Studies of lek mating systems follow two general themes (Hoglund and Alatalo 1995), with emphasis on either the nature of the sexual selection process on leks or on the ecological and evolutionary factors that have led to the appearance of lek behavior in some species but not others. The present paper focuses almost exclusively on the former theme. In addition, emphasis is placed on precopulatory mate selection, and sperm competition and
Questions and Answers

Question 1: Where Do Fruit Fly Leks Occur?

Leks occur chiefly on flowering host trees where males aggregate, perch, and signal from the undersurfaces of leaves. For example, males of the South American fruit fly, *Anastrepha fraterculus* (Wiedemann) (Diptera: Tephritidae), form clusters and displayed most frequently on nonhost (and herbaceous) species of Asteraceae (*Iwahashi and Majima 1986*). Leks of this species were most commonly found on nonhost plants in India as well (*Mir and Mir 2016*). In the wild tobacco fruit fly, *Bactrocera cucumis* (Hering), a field-cage experiment indicated that nonhost plants containing the phenylpropanoid compound methyl eugenol, a known male attractant, serve as rendezvous sites for mating (*Raghu and Clarke 2003*). Endemic Hawaiian *Drosophila* also appear to form leks on nonhost plants. For example, males of several picture-winged species cluster and signal simultaneously on adjacent leaves (Hendrichs and Markow 1990). However, male groups and copulations occur frequently on nonhost plants. Field observations in Japan showed that, despite the presence of a preferred host, males of the melon fly, *Zeugodacus cucurbitae* (Coquillett) (Diptera: Tephritidae), aggregated and displayed most frequently on nonhost (and herbaceous) species of Asteraceae (*Iwahashi and Majima 1986*). Leks of this species were most commonly found on nonhost plants in India as well (*Mir and Mir 2016*). In the wild tobacco fruit fly, *Bactrocera cucumis* (Hering), a field-cage experiment indicated that nonhost plants containing the phenylpropanoid compound methyl eugenol, a known male attractant, serve as rendezvous sites for mating (*Raghu and Clarke 2003*). Endemic Hawaiian *Drosophila* also appear to form leks on nonhost plants. For example, males of several picture-winged species cluster and signal from tree ferns (*Spieth 1986*; see also *Shelly 1987, 1988, 1990a*). In one species of Hawaiian *Drosophila*, however, lekking males occur on trees whose fallen and decaying leaves are the larval food source as well (*Bell and Kipp 1994*).

Take home message: Fruit fly leks occur on a range of vegetation, including both larval host and non-host plant species. Where leks occur on fruiting host trees, males do not control access to fruits.

Question 2: How Are Fruit Fly Leks Defined Operationally?

Tephritid workers have adopted two approaches to identify leks in the field (*Field et al. 2002*). One defines leks by the distances between signaling males, and typical examples define alek as 3–6 males within 30 cm of one another each on a separate leaf (*Prokopy and Hendrichs 1979*), a group of ≥3 males signaling simultaneously within 10–15 cm of one another on adjacent leaves (*Hendrichs and Hendrichs 1990*), and 3–6 males, each located on a separate leaf and all within 50 cm of one another (*Morgante et al. 1983*). The distances selected presumably represent approximate distances over which a focal male could detect the sexual signals of other males (*Iwahashi and Majima 1986*), and thus male groupings represent ‘functional components of the mating system’ (*Field et al. 2002*).

The second approach defines a lek as the entire tree on which two or more calling males occur (*Shelly 1987, Whittier et al. 1992, Shelly et al. 1994*). This method thus bypasses the assumption regarding the range of male–male perception and recognizes that, owing to male movement...
among leaves, the use of intermale distances to define leks is inexact as these distances, and hence lek ‘boundaries’, may change frequently. At first glance, it appears that these two approaches might lead to different interpretations of lek dynamics (male aggression, female visitation, etc.). However, as ‘lek’ trees usually harbor only a single, tight cluster of males (Whittier et al. 1992), the distinction between the two methods is lessened. This tendency apparently reflects intra-canopy movement as males track a particular suite of microclimatic conditions (Aluja and Birke 1993, Kaspi and Yuval 1999b, Segura et al. 2007).

**Take home message:** Leks are defined either by distances among males themselves or are associated with the entire plant on which displaying males occur.

**Question 3: How Many Males Typically Comprise a Fruit Fly Lek?**

Both tephritid and drosophilid leks are small and typically contain 2–10 males as reported for *C. capitata* (Arita and Kaneshiro 1989), the Mexican fruit fly, *Anastrepha ludens* (Loew) (Aluja et al. 1983), the West Indian fruit fly, *Anastrepha obliqua* (Mascotti) (Aluja et al. 1983), the sapote fruit fly, *Anastrepha serpentina* (Wiedemann) (Aluja et al. 1989), the Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Pereira et al. 2009), *A. fraterculus* (Morgante et al. 1983), *B. dorsalis* (Shelly and Kaneshiro 1991), and *Z. cucurbitae* (Iwahashi and Majima 1986, Mir and Mir 2016). *Drosophila* leks are generally of similar size (Spieth 1986; Shelly 1988, 1990b), but larger aggregations do occur. Clusters of 20–30 lekking males were observed in *Drosophila conformis* Hardy (Shelly 1987) and *Drosophila pereosoma* Hardy (Bell and Kipp 1994), and as many as 70 males of *Drosophila mycetophaga* (Malloch) were present occurring on a single bracket fungus, which serves as the mating arena (Aspi and Hoffmann 1998).

**Take home message:** Leks involving tephritid fruit flies typically contain less than 10 individuals, whereas those of *Drosophila* species may be much larger.

**Question 4: Are Fruit Fly Lek Sites Persistent Over Time?**

Most field studies span only short intervals (from several days to 1–2 mo) and do not monitor the spatiotemporal consistency of leks. As a result, relevant data are scant, but they nonetheless indicate site persistence at least over a single season. A single lek of *B. dorsalis* was detected in a Hawaiian citrus orchard and observed for approximately 6 wk before ‘disbanding’ (Shelly and Kaneshiro 1991). Similarly, the distribution of signaling males of *C. capitata* among individual persimmon trees was stable over a 2-mo sampling interval in a Hawaiian orchard (Shelly and Whittier 1995). Lek sites of some Hawaiian picture-winged *Drosophila* have also been reported to occur at the same site for several months, although this observation was anecdotal and not supported by quantitative data (Spieth 1968).

However, systematic censuses conducted for the Hawaiian species *D. conformis* showed the persistence of a mating aggregation at the same tree for a minimum of 2 yr (Shelly 1987).

**Take home message:** Limited data suggest particular lek sites may persist through a growing season, and in aseasonal Hawaiian rain forests *Drosophila* leks may persist at the same tree for several years.

**Question 5: How Do Lekking Fruit Fly Males Attract Females to Their Perch Site?**

In the Tephritidae, sexually active males produce visual, olfactory, and acoustic signals, and of these male pheromone is likely to act over greater distances than the other modalities. Considerable attention has been devoted to the chemistry of tephritid sex pheromones, with findings summarized in several review papers (Nation 1989, Fletcher and Kitching 1995, Heath et al. 2000, Tan et al. 2014). Male pheromones are released primarily from the rectum in *Ceratitis* (Arita and Kaneshiro 1986, Quilici et al. 2002), *Bactrocera* (Fletcher 1968, Kobayashi et al. 1978, Kuba and Sokei 1988, Poramarco and Baimai 1996), and some Hawaiian *Drosophila* (Spieth 1978). Although less well-studied, pheromones in these species may also be released orally as noted for *C. capitata* (Gonçalves et al. 2006). In *Anastrepha* males, the sex pheromone is emitted from the rectum as well as pleural pouches on the abdomen and the mouthparts (Nation 1989, 1990). Pheromone release (also termed ‘calling’) is often accompanied by vigorous wing-fanning, which presumably acts to disperse the pheromone (Kuba and Sokei 1988, Nation 1989).

In addition to direct aerial release of volatile compounds, males of some species also deposit pheromone on the substrate and thus amplify and possibly prolong their olfactory signal (Sivinski et al. 1994, Dronen and Hock 1998, Shelly 2004). Interestingly, and unlike males of some other Hawaiian *Drosophila*, which release pheromone from the tip of their upturned abdomen (Tomkins et al. 1993), males of the picture-winged species *Drosophila grimshawi* Oldenberg appear to only deposit chemicals on the substrate and to not additionally emit pheromone directly from their body into the air (Spieth 1986).

Numerous studies have demonstrated the communicative function of male sex pheromones in lekking tephritids. Briefly, female attraction to live, calling males or male rectal gland extracts (or synthetic formulations of major pheromone components) has been documented using, in decreasing order of spatial scale, 1) the field using wild (Heath et al. 1991) or released females (Perdomo et al. 1975, 1976; Nakagawa et al. 1981; Shelly 2000a), 2) field cages containing potted trees (Webb et al. 1983a, Robacker and Hart 1986, López-Guillén et al. 2011), 3) wind tunnels (Robacker 1988, Jang et al. 1994, Her and Tan 1998), or 4) small cages (Kobayashi et al. 1978, Robacker et al. 1985). While there seems little question that the sex pheromones of male tephritids attract females, there is uncertainty regarding the range over which females detect and respond (either movement toward the source or arrestment) to male pheromone (see also Fitt 1981 for discussion of the unreliability of female pheromonal response in elucidating generic relationships of dacine species). Several studies, however, suggest these olfactory signals are perceived only over short distances. In the Mexican fruit fly, *A. ludens*, females offered two trees in a field cage—one with leaves treated with male pheromone and the other with leaves treated with hexane—arrived at the trees in equal numbers (Robacker and Hart 1986). Based on release distance from the trees, it was concluded that females did not detect and/or respond to male pheromone at distances >30 cm. Once on the pheromone-treated tree, however, females appear to move directly to the specific leaves bearing pheromone. Similarly, in the Queensland fruit fly, *Bactrocera tryoni* (Froggatt), females were exposed to male pheromone in a wind tunnel at a concentration estimated to be typical of distances >30 cm from a calling male and showed no response to the pheromonal signal (Pike and Meats 2003). Another study (Weldon 2007) on *B. tryoni* (conducted in 1 m³ cages) found a positive, but weak, correlation between female arrivals and numbers of calling males in male aggregations of varying size, leading the investigator to conclude that male pheromone may only attract and arrest females over very short distances. When released 1.1–1.7 m from live males in a wind tunnel, 35–50% of *Bactrocera papayae* Drew and Hancock females displayed upwind anemotaxis but only about 1% landed on the source (Hee and Tan 1998).
Many of the aforementioned experiments also measured male response to the sex pheromone of conspecific males to examine the possibility that males use the olfactory signal to locate leks. Indeed, many of these studies demonstrate male attraction to live males or rectal gland extracts whether conducted in the field (Perdomo et al. 1975, 1976; Nishida et al. 1988), field cages (Kaspi and Yuval 1999a), or wind tunnels (Hee and Tan 1998, Khoo and Tan 2000). In contrast to females, however, positive responses were not uniformly found, thus weakening the notion that the male sex pheromone functions, in part, as an aggregation cue. For example, in a field-cage test involving A. obliqua, similar numbers of males were found in traps baited with males as in empty traps (López-Guillén et al. 2011). Likewise, in a Hawaiian coffee field, released males of C. capitata arrived only rarely (<0.04%) to caged males positioned 10 m from the release point (Shelly 2000a). Lack of male response to conspecific pheromone has also been reported for A. ludens (Robacker and Hart 1986), B. dorsalis (Kobayashi et al. 1978), and Z. cucurbitae (Kobayashi et al. 1978).

**Take home message:** Displaying males attract females via release of pheromones, although their effective range may be limited (< 0.3 m). Male attraction to conspecific sex pheromone has been demonstrated in some species but not others.

**Question 6: What Is the Nature of Male–Male Aggression in Lekking Fruit Flies?**

Male fruit flies are soft-bodied and do not possess large, sclerotized weapons capable of inflicting injury; thus, it is unlikely that fighting carries any risk of physical harm (Sivinski et al. 2000). Additionally, agonistic interactions between males are usually very brief, lasting only several seconds, and even protracted interactions rarely last more than a few minutes. Thus, costs related to physical injury or time and energy expenditure appear minimal. Nonetheless, as discussed below, a male’s fighting ability may influence mating success in certain species.

Lekking male fruit flies display a great variety of aggressive displays, both within and between species (Benelli 2015), but a broad summary with selected examples includes (in order of increasing intensity):

- **Defensive posturing or threat displays.** Upon detecting an intruder, males of A. suspensa adopt a defense posture with body the pressed to the leaf, wings held close to the body, and proboscis extended directly at the other male (Dodson 1982, Burk 1983).
- **Approach and noncontact displays.** After approaching an intruder, resident males of Drosophila cneocoleana Hardy raise their wings and then make a sweeping motion of the abdomen toward the other male (Shelly 1988).
- **Approach and contact with mouthparts and/or legs.** Males of C. capitata may alternate taps with their front legs, presumably as a ‘fending’ response (Briceño et al. 1999). In Drosophila nigrospinacula Patterson and Wheeler, males touch heads with fore tarsi locked together and circle about one another for as long as 20 min (Markow 1988).
- **Lunging or chasing with or without contact.** Males of many species, including Drosophila silvestris (Perkins 1989), B. dorsalis (Shelly and Kaneshiro 1991), and C. capitata (Whittier et al. 1994), have been described as lunging or thrusting their bodies at combatants.
- **Head-buttting, body pushing, and face-offs.** Rapid lunges resulting in head-buttting occur in A. ludens (Robacker and Hart 1985), B. dorsalis (Poramarcom and Boake 1991), and B. tryoni (Tychsen 1977). In A. suspensa, head-buttting may be accompanied by aggressive songs, which are long bursts of rapid wing vibration (Webb et al. 1976). Contests involving head and/or body pushing matches have been reported for Drosophila heteroneura (Perkins) (Spieth 1981), D. percnosoma (Bell and Kipp 1994), and D. silvestris (Boake 1989). Face-offs, in which males contact their heads without visible force for as long as 5 min, have been described for C. capitata (Arita and Kaneshiro 1989).
- **Grappling or wrestling.** This intense fighting, which may end with one or both combatants falling from the substrate, has been reported for D. conformis (Shelly 1987).
- **Mounting.** Males often mount other males, but whether this action represents a copulation attempt (Prokopy and Hendrichs 1979, Morgante et al. 1983) or an aggressive behavior (Iwahashi and Majima 1986, Mir and Mir 2016) is not known definitively.

Various studies have described the importance of residency and male size in determining the outcome of aggressive encounters. A resident advantage was reported for A. obliqua (Aluja 1983), A. suspensa (Burk 1984), Procecidochares sp. (Diptera: Tephritidae) (Dodson 1986), Z. cucurbitae (Iwahashi and Majima 1986), D. cneocolea (Shelly 1988), and D. percnosoma (Bell and Kipp 1994). Residency and male size interacted in a similar way to affect outcomes in A. suspensa and D. percnosoma: when larger or the same size as intruders, residents won the great majority of encounters, but when smaller than intruders, residents won only about 33% of the encounters (Burk 1984, Bell and Kipp 1994). Similarly, D. conformis males that held preferred territories were usually larger than intruding males and generally successful in driving them away (Shelly 1987). Though residency was not considered, a size advantage in aggression was also observed in D. silvestris (Boake 1989). A resident advantage, however, is not evident in all fruit flies. In B. dorsalis (Shelly and Kaneshiro 1991) and C. capitata (Shelly 2000b), residents and intruders were equally likely to win aggressive encounters, and in another study on medfly, an intruder advantage was observed in male–male aggression (Whittier et al. 1992). Although sample size was limited, an intruder advantage was also apparent in A. ludens (Aluja et al. 1983).

**Take home message:** Male fruit flies, which appear unable to inflict physical injury, engage in a broad range of agonistic encounters, many of which are brief and involve no or very little contact. Large males usually defeat (chase away) small males, whereas a resident advantage in aggression occurs in some species but not others.

**Question 7: Do All Sexually Active Males Join and Signal in Leks?**

Available field data suggest there is much interspecific variation in the proportion of calling males that are solitary, occurring outside leks. Based on censuses in the field or field cages, the proportions of calling males seen outside of leks were 37% (Hendrichs and Hendrichs 1990) and 8% (Shelly et al. 1994) for C. capitata, 17% (Iwahashi and Majima 1986) and 15% (Mir and Mir 2016) for Z. cucurbitae, 6% for D. mycetophaga (Aspi and Hoffmann 1998), and 40% for A. obliqua (Aluja et al. 1983). In contrast, the proportion of lone callers is considerably higher for A. ludens (60%) (Aluja et al. 1983) and A. fraterculus (64%) (Segura et al. 2007). The mango fruit fly, Anastrepha striata Schiner, has been described as an ‘intermediate’ lek species, with 91% of calling males being solitary (Aluja et al. 1993), and Spieth (1986) described ‘solitary lekking’ as common in some species of Hawaiian Drosophila.
The above estimates refer to male signaling on foliage outside of leks, but males of some species may signal from fruit, awaiting the arrival of females (but see Quilici et al. 2002 for an exception in Ceratitis rosa Karsch based on fruiting phenology). However, the numbers of fruit-perching males are relatively small across all species. In the field, 100% of calling males of A. ludens and A. serpentina were sighted on leaf undersurfaces, and in A. obliqua only about 10% of calling males were on fruit (Aluja et al. 1989). In Egypt, only 1% of calling C. capitata males was on fruits (Hendrichs and Hendrichs 1990), while no calling males were evident on fruits in Hawaii (Arita and Kaneshiro 1985). In field-cage observations, 12% of male sightings were on fruit, but most of these males were not calling, and fruit-perching males comprised only 4% of the total sightings of calling males, with the remaining 96% recorded for males on the lower side of leaves (Prokopy and Hendrichs 1979; for a similar observation, see Hendrichs and Hendrichs 1999). A high incidence (approximately 50%) of males occurred on fruit in A. suspensa, but this behavior was evident in the morning well before the period of peak mating in late afternoon; by midday, the great majority (90%) of males occupied leaves (Burk 1983).

Take home message: The relative numbers of grouped vs. solitary leaf-calling males varies greatly among species. In most species, a small proportion of males are also observed calling from fruit.

Question 8: Do Solitary Males Obtain Copulations? Males occurring outside leks do achieve copulations but only rarely. In a wild population of C. capitata in Hawaii, solitary males obtained 2 of the total 55 matings observed (Whittier et al. 1992), and in an Egyptian orchard ‘copulation was initiated mostly in leks’ (Hendrichs and Hendrichs 1990). As noted above, nearly 67% of A. fraterculus males called outside leks, but only 23% of these males mated. In contrast, among males that called exclusively in leks, 83% mated one or more times (Segura et al. 2007). Males perched solitarily on fruit also mate albeit at a low rate. In A. suspensa, 10% of males occupied fruits during the time of peak mating, yet only 1 of 26 observed copulations (4%) occurred on a fruit (Burk 1983; see also Robacker and Hart 1985).

Take home message: The great majority of copulations occur within leks for all species studied.

Question 9: Within Leks, Is Mating Frequency Skewed Among Males? A mating skew, where a small proportion of males procures the majority of the copulations, is a common characteristic of lekking species (Hoglund and Alatalo 1995). Owing to their small size and mobility, field data on the mating success of individual fruit fly males are nonexistent. However, observations of marked males in laboratory cages of field cages uniformly reveal that a few males account for most of the matings and most males mate infrequently or not at all. In field-cage studies on Anastrepha species, 15% of the 33 individually marked males (followed over 20 consecutive days) obtained 73% of the 15 matings recorded in A. ludens (Robacker et al. 1991), and 46% of marked males accounted for 100% of the matings observed in A. suspensa (Hendrichs 1996, cited by Burk 1999). Four different studies involving observations of marked C. capitata males in laboratory cages yielded comparable results (Arita and Kaneshiro 1985, Whittier et al. 1994, Whittier and Kaneshiro 1995, Shelly 2000a). For example, 34% of the 50 males observed (in groups of six individuals over 6 consecutive days) accounted for 76% of the 80 total matings, while 26% of males mated only once or not at all (Whittier et al. 1994). Similarly, 15% of the 240 males observed (in groups of 16 individuals over 10 consecutive days) accounted for nearly 40% of the 421 total matings, while 49% of males mated only once or not at all (Whittier and Kaneshiro 1995). In the only data set available for Bactrocera, 10% of the 384 males of B. dorsalis observed (in groups of 12 individuals over 7 consecutive days) mated on three or more days, and nearly 50% of males did not mate at all (Porambarcom and Booze 1991). A similar pattern of nonrandom mating has been reported for D. grimshawi as well (Droney 1992, Droney and Hock 1998).

Take home message: Field data are lacking, but laboratory and field-cage data uniformly yield highly skewed distributions of male mating frequency, with a small proportion of males accounting for the majority of matings.

Question 10: Does Territory Position Influence Male Mating Success? In leks of certain vertebrate species, the position of a male’s territory is a critical determinant of its mating success. For example, males holding territories near the lek center have higher copulation frequency than males on the lek periphery (e.g., Bro-Jørgensen 2002). Among lekking fruit flies, calling location was found to play an important role in two species. In A. suspensa, for pairs of males calling within 15 cm of each other, the innermost fly (i.e., the one occupying the leaf nearest trunk) was usually larger than the outermost fly, and the innermost male obtained four of four matings observed while collecting these pairs (Sivinski 1989). Censuses of lekking D. conformis males showed that individuals occupying the lowest leaves on the tree obtained the majority of matings and were larger than intruding males (Shelly 1987). Thus, in both of these species, it appears that large males dominate small males in aggression and hold territories visited preferentially by females.

Laboratory observations purportedly indicate a position effect for C. capitata as well, but field data suggest otherwise. In one indoor study conducted in Hawaii (Arita and Kaneshiro 1985), trios of males and a single female were placed in small containers (23 cm cubes) with a plant containing seven leaves, and the locations of matings noted over 3 consecutive days. In a number of cages, matings occurred repeatedly on the same leaf, which was interpreted as evidence of a position effect. However, this interpretation is undercut by two other trends: the leaves used most frequently by males were not necessarily the same leaves on which most matings occurred, and in some cages the leaves on which males perched and matings occurred changed from day-to-day, presumably with ambient light conditions. In the second laboratory study (Niyazi et al. 2008), female arrivals were monitored for individual males caged at low, medium, and high positions in a cylindrical cage with illumination directly overhead. Female visits were most frequent for the highest male, which was taken as evidence of a position effect. However, the relevance of this result to nature is questionable, since females in this experiment were likely responding primarily to the higher light level at the cage top. In fact, under full sunshine in natural populations, medflies generally settle in lower and more shaded positions in the tree canopy (Hendrichs and Hendrichs 1990, Baker and Van der Valk 1992, Yuval and Hendrichs 2000). Moreover, within the canopy males apparently shift perching locations slightly, but continually, throughout the day as they track preferred microclimatic conditions (Aluja and Birke 1993, Yuval and Hendrichs 2000, Segura et al. 2007). Changes in perch location, coupled with the sheer abundance of available leaves in the tree canopy, likely explain the findings that, in a Hawaiian orchard, only 2 of 71 observed matings occurred on the same leaf (Whittier et al. 1992).
The preceding summary suggests a relationship between the intensity of aggressive encounters and the importance of perch location in mating success, i.e., more intense or ‘violent’ interactions may be more common in species where leaf position influences copulation success. Thus, for example, males of *D. conformis* wrestle frequently over possession of low leaves more likely to be visited by females (presumably flying upward from nearer the forest floor), whereas aggression is less intense between *C. capitata* males, and intruders actually drive residents away more often than the reverse. Correspondingly, because large *A. suspensa* males dominate in agonistic encounters (Burk 1984), they enjoy a mating advantage over small males (Sivinski 1989). In wild medflies, however, males collected in copula did not differ in size from a random sample of non-mating males (Whittier et al. 1992). Limited field observations on *B. dorsalis* indicate a situation similar to that described for medfly: agonistic encounters are brief and involve chases with or without contact, there is no resident advantage in aggression, and males change perches frequently, all of which suggest that the specific location of a signaling site is not a key determinant of male mating success (Shelly and Kaneshiro 1991). Defense of shifting ‘personal space’ was also evident in *D. mycetophaga*, and such mobile zones of defense were termed ‘moving territories’ (Aspi and Hoffmann 1995).

**Take home message:** In most species, the specific site of male calling does not appear important in determining mating success. Consistent with this view, males may move frequently among leaves without provocation, and a resident advantage is not evident in all species.

**Question 11: To What Extent Does Male Mating Success Reflect Signaling Effort?**

The few data that exist regarding the association between signaling effort and mating success for male fruit flies uniformly show that a strong positive relationship between these parameters. In *C. capitata*, males with high copulation success over 6 consecutive days spent more time pheromone calling (Shelly 2000a) and performed more courtship and mountings (Whittier et al. 1994) than males with low copulation scores. Likewise, in *B. dorsalis*, males that mated three times over 7 consecutive days spent nine times as much time pheromone calling as males that mated only once or not at all (Poramarcom and Boake 1991). Finally, mating success in *D. grimshawi* males was directly related to time spent displaying at leks (Drony 1992) as well as the intensity of ‘pheromone streaking’ (pheromone in this species is not released aerially but on the substrate via abdomen dragging, Drony and Hock 1998).

Male signaling effort appears to have a genetic component, because variation was observed in studies where males were reared under similar conditions, with a favorable abiotic environment and high-quality and readily accessible food (Poramarcom and Boake 1991, Shelly 2000a, Papadopoulos et al. 2004). Environmental factors, most notably the presence of protein in the adult diet, may affect calling levels and mating success for male medflies as well. Females of *A. suspensa* visited an average of 7.5 males before mating (Hendrichs 1986, cited by Burk 1991). In *A. striata*, male–female pairs interact in close proximity for over 20 min before mating, and 11 mating attempts, on average, precede successful copulation (Aluja et al. 1993). Likewise, only 23% and 29% of courtships ended in copulation in *D. grimshawi* (Drony 1996) and *D. silvestris* (Boake 1989), respectively.

**Take home message:** Across tephritid and Drosophilidae species, a low percentage of male–female encounters result in copulation, suggesting female discrimination among potential mates.

**Question 12: Is There Any Evidence That Females Sample Potential Mates?**

The mating skew observed among lekking male fruit flies most likely represents the influence of male–male aggression and active female choice. Evidence of the latter derives from the low incidence of courtships and/or mountings that result in copulation, a trend reported for various species. In *Z. cucurbitae*, for example, approximately 25% of male–female encounters ended in copulation in a field-cage study (Kuba and Koyama 1985), while only 2% of intersexual encounters between wild flies resulted in copulation (Mir and Mir 2016). In field-cage observations of *C. capitata*, 50% of male–female interactions led to mounting of which 74% were successful (Prokopy and Hendrichs 1979). Based on observations in laboratory cages (Whittier et al. 1994), 26% of *C. capitata* females mated with the first male encountered, but 50% were courted by five or more males before mating. Interestingly, among females courted by two or more males, 75% of females ultimately mated with the male who had the highest copulatory score (over 6 consecutive days) among those males that courted them. Mate sampling has been described for *Anastrepha* flies as well. Females of *A. suspensa* visited an average of 7.5 males before mating (Hendrichs 1986, cited by Burk 1991). In *A. striata*, male–female pairs interact in close proximity for over 20 min before mating, and 11 mating attempts, on average, precede successful copulation (Aluja et al. 1993). Likewise, only 23% and 29% of courtships ended in copulation in *D. grimshawi* (Drony 1996) and *D. silvestris* (Boake 1989), respectively.

**Take home message:** Across tephritid and Drosophilidae species, a low percentage of male–female encounters result in copulation, suggesting female discrimination among potential mates.

**Question 13: What Characteristics Are Important to Females in Selecting a Mate?**

Several of the topics considered above suggest that female fruit flies actively select among lekking males: the skewed mating success of males, the high rejection rate of courting males, indicative of mate sampling, and the low intensity of male aggression and site fidelity in a number of species. As with other taxa, teasing apart which cues influence female choice is difficult and has not been elucidated for a single fruit fly species. Considering lekking fruit flies as a whole, the evidence, in fact, is haphazard in that certain male attributes have been investigated closely in certain species but not at all in others. This renders generalizations impossible. Accordingly, the following list highlights instances where data allow reasonable assessment of the importance of different male cues across species, recognizing that even this approach is simplistic given the covariance often existing among different traits.
Although this review emphasizes empirical observations, it should be noted that, prior to listing these male cues, their evaluation gains more meaning when considered in the context of the lek paradox. This concept has two main components (Tomkins et al. 2004). First, strong female preference for male traits that indicate viability should rapidly exhaust genetic variation for viability and drive the preferred traits to fixation. Second, with depleted genetic variation, there is little chance that female choice yields genetic benefits, but genetic benefits (so-called ‘good genes’) are invoked as the explanation for that choice. Interestingly, however, sexually selected traits have been found to have additive genetic variation (Pomiankowski and Møller 1995), which is likely maintained by environmental variation in selection pressure and/or mutation-selection balance.

Regarding the latter, traits that become more elaborate or larger may involve a larger number of loci (so-called ‘genic capture’, Rowe and Houle 1996), with greater underlying variation owing to increased genetic segregation as well as increased mutational opportunities (Shuker 2014). More generally, male traits that are not ornaments per se but indicators or components of overall fitness (e.g., size, signaling and courtship vigor, age, etc.) may also be associated with large proportions of the genome and hence retain large heritable variation (Maynard Smith 1991). In sum, the ‘good genes’ argument relating to indirect fitness benefits is surely difficult to demonstrate, but empirical findings seriously question the theoretical premise that fixed alleles would eventually underlie sexually selected male traits (and thus negate any benefit of trait-based female choice).

Morphology

The importance of male body size in influencing female choice has been investigated most frequently for C. capitata, owing to the widespread use of the Sterile Insect Technique against this pest and the perceived need to mass-rear large males for sterilization and release (e.g., Churchill-Stanland et al. 1986, Orozco and Lopez 1993). Studies using wild flies or recently established colonies (derived from wild individuals), however, have yielded variable results. In Hawaii, flies emerging from two different hosts differed greatly in size, but in mating trials both large and small females preferred small over large males (Arita and Kaneshiro 1988). Data gathered in the field (Whittier et al. 1992) or laboratory cages (Whittier and Kaneshiro 1995, Norry et al. 1999, Shelly 2000a, Aquino and Joachim-Bravo 2014) found no association between male size and mating success.

Still, other studies reported higher copulatory frequency for larger males (Rodriguero et al. 2002, Anjos-Duarte et al. 2011).

Although several of these studies described size using body weight, the majority used linear measurements, primarily of wings and thorax, to gauge male size. In one case, however, both wing length and body weight were measured for individual wild flies, thus allowing description of male condition (Kaspi et al. 2000). In addition, males were provided either a protein-rich diet or sugar-only diet. Results showed that, for a given wing length, males fed the protein-rich diet contained more protein in their body, 2 weighed significantly more, and 3 obtained significantly more copulations than protein-deprived males. The higher mating frequency was associated with greater calling activity of protein-fed males as well as their tendency to initiate calling earlier in the day than protein-deprived males. These results, along with similar findings for mass-reared males (Blay and Yuval 1999, Kaspi and Yuval 2000), clearly point to the importance of adult nutrition in influencing body condition and sexual competitiveness in C. capitata. Similar results have been reported for Anastrepha spp. (Aluja et al. 2001) and D. grimshawi as well (Droney 1996).

Relatively few studies have examined the relationship between male size and mating success in other fruit fly species. Aside from A. suspensa, where large males dominate small males in aggression and hold ‘preferred’ territories (Sivinski 1989), male size has no significant effect on mating frequency in A. ludens (Robacker et al. 1991, Aluja et al. 2008), A. fraterculus (Sciurano et al. 2007, Segura et al. 2007), A. striata (Aluja et al. 2008), B. tryoni (Pérez-Staples et al. 2007), or D. silvestris (Boake 1989). A multivariate morpomorphic analysis of A. fraterculus males revealed that, while overall body size is not important, body shape is associated with mating performance, with wing width and thorax length varying significantly, albeit non-linearly, with mating success (Sciurano et al. 2007). The impact of body and head shape on female choice has also been investigated in C. capitata (Norry et al. 1999, Rodriguero et al. 2002).

The issue of fluctuating asymmetry has received limited attention in lekking fruit flies and has focused exclusively on the spatulate bristles found on the head of males of C. capitata. The role of these bristles (or sex setae) in courtship is unknown, but they are presumed to function as a visual display (Mendez et al. 1998). Data relating the right-left differences in bristle length to male mating success are inconsistent. In choice trials, both laboratory (Hunt et al. 1998) and wild males (Hunt et al. 2004) obtained copulations with lower fluctuating asymmetry in bristle length than males that failed to do so, suggesting symmetry in this character was an indicator of male genetic quality. However, experiments in which one bristle was removed showed that such males mated as successfully as control, unmodified males (Hunt et al. 2002, 2004). This result, where surgically produced, absolute asymmetry did not adversely affect male mating success, strongly suggests that bristle length asymmetry has no effect on female choice (consistent with Niyazi et al. 2008).

Courtship behavior

In many species of Anastrepha (e.g., Robacker and Hart 1985, Silva et al. 1985) and Bactrocera (e.g., Tychsen 1977), males leap upon females and attempt copulation almost immediately upon detecting them. Courtship is more prolonged in Ceratitis species, however, and in C. capitata, in particular, involves a succession of different wing and head movements. This behavioral elaboration, coupled with this species' importance as an agricultural pest and a target of the Sterile Insect Technique, has prompted considerable research comparing the characteristics of successful versus unsuccessful courtships (Eberhard 2000). Briefly, male courtship, which follows female arrival and approach, typically consists of the following stages: 1) continuous wing vibration (fanning) with the abdomen tipped downward with the pheromone droplet still present; 2) wing buzzing, in which the wings are rhythmically moved back and forth; and 3) head rocking (often occurring along with wing buzzing) in which the male's head is rotated rapidly. After these actions, the male leaps on the female, who may allow copulation or decamp.

The most detailed analysis of the courtship behavior of C. capitata involved videotaping approximately 100 courtships and comparing successful (ended in copulation) and unsuccessful (female decamped) mounts with respect to distance and angle between male and female at differing times and the durations of female immobility, wing fanning, wing buzzing, and total courtship as well as the duration and rate of individual buzzes (Briceno and Eberhard 2002). Despite this effort, large variation characterized the data for all parameters considered, such that successful courtship could be differentiated from unsuccessful ones only by having longer total duration and the male and female facing each other more directly (see also Briceno and Eberhard 2000). In a comparable, albeit less complete study (since fly distances and angles were not recorded), successful males spent
more time buzzing than their wings than unsuccessful males, but no other differences were detected (Liimatainen et al. 1997). Although neither of these studies monitored male acoustic or pheromonal signals, there is apparently no sharp demarcation in overall courtship performance between successful and unsuccessful attempts.

In contrast, a closer association between behavior and courtship success has been reported for two species of lekking Drosophila. In D. silvestris, successful males courted more persistently (without breaks) and spent more time in the head-under-wings position and in wing vibrating than unsuccessful males (Boake and Hoikkala 1995). Similarly, in D. grimshawi, two courtship components—head-under-wings—and frontal wing display—occurred at greater rates during successful than unsuccessful courtships (Droney 1996).

Acoustic cues
Males of many lek-forming tephritids rapidly vibrate or fan their wings while calling and courting, and this action produces audible signals, which could serve as cues to nearby females. Acoustical characteristics of wing vibration have been described for C. capitata males (Webb et al. 1983b), but their potential role in mate choice has been examined in only two species, A. suspensa (Webb et al. 1976, 1984) and B. tryoni (Mankin et al. 2008). By far, the most detailed work has been conducted on A. suspensa. Males of this species produce two female-directed sounds, a pulsed, calling song and a continuous, precopulatory song. The calling song is produced both to attract females over short distances (Webb et al. 1984) and during courtship, while the precopulatory song is produced after mounting but before intromission (Aluja et al. 2000). When offered a large and a small male, A. suspensa females usually selected large males as mates, and acoustic analyses showed that, although the calling songs of large and small males did not differ in fundamental frequency, those of large individuals had shorter pulse train intervals (i.e., large males produce more pulses per unit time, Burk and Webb 1983). However, a second study of similar design generated different results, with fundamental frequency of the calling song varying inversely with male size and pulse train interval varying independently of male size (Webb et al. 1984). In both studies, however, the precopulatory song, which was interpreted as the last ‘acoustic opportunity’ for males to demonstrate their quality, was more intense (louder) for large males than small males (Burk and Webb 1983, Webb et al. 1984).

Age
Robust data on the impact of male age on female choice are available for only two species, A. ludens and C. capitata. In A. ludens, ‘young’ females (13- to 23-d old) mated preferentially with ‘middle-aged’ males (28- to 39-d old) over ‘young’ males (18- to 23-d old) in two separate studies (Pérez-Staples et al. 2010, Abraham et al. 2016). However, females did not gain fitness benefits (in terms of increased fecundity, fertility, or longevity) by selecting the older males (Pérez-Staples et al. 2010). In contrast, when offered relatively young and old males, young females of C. capitata discriminated against the older males in two independent studies. In one case, 4- to 5-d-old females preferred to mate with same-age males over 20-d-old males, which may have reflected the higher calling activity of the young males (Roriz and Joachim-Bravo 2013). In the other instance, young females (10-d old) preferred young males (10-d old) over old males (30- or 40-d old) even though calling levels were similar between the age groups (Shelly et al. 2011). Interestingly, in this latter study, old females (40-d old) mated randomly with males of different ages (see also Abraham et al. 2016 for similar results). As in A. ludens, male age had no obvious direct effects on female fitness.

Sexual experience
Females may avoid mating with recently mated males, because such males have temporarily low stores of sperm and/or accessory gland products. Observations of A. suspensa are consistent with this expectation: in no-choice trials, females were less likely to mate with males that had just mated than with virgin males or males that had mated 2 or 24 h before the test (Sivinski 1984). This pattern did not reflect differences in acoustic advertisement, as just-mated males called (wing-fanned) at the same level as virgin males. However, just-mated males of A. obliqua released smaller amounts of pheromone than virgin males (López-Guillén et al. 2011), and females may discriminate against just-mated males using this cue. It should be noted that the assumption that virgin males transfer lower quantities of sperm and/or accessory gland products than mated males was not supported in A. striata (Pérez-Staples and Aluja 2004) or a genetic sexing strain of A. ludens (Arredondo et al. 2017), consequently the overall validity of this assumption merits additional investigation.

When offered a choice, females of D. silvestris (Schwartz 1991) and C. capitata (Shelly and Whittier 1993) mated indiscriminately with virgin males and males that had mated 24 h previously. In both of these species, however, females suffered a fitness cost by selecting nonvirgin males. Conversely, females of A. ludens preferred sexually experienced males over virgins, although such selection conferred no detectable fitness benefits (Pérez-Staples et al. 2010). In D. silvestris, females mating with a nonvirgin male were less likely to have sperm in their reproductive tract than females mated to virgins (Schwartz 1991). In C. capitata, females that mated with a nonvirgin male had lower fecundity and shorter life span than females that mated with a virgin male (Whittier and Kaneshiro 1991). In additional trials, C. capitata females mated to males that had mated 5 d earlier still showed lower fecundity and longevity, indicating that the absence or reduction of some compound in the ejaculate of mated males, and not sperm depletion, accounted for these trends. Although female choice was not assessed, mating with virgin over nonvirgin males conferred benefits of greater longevity to A. striata females (Pérez-Staples and Aluja 2004) and increased fertilization rate to A. obliqua females (Pérez-Staples et al. 2008).

Pheromonal signal
Removal of both antennae from females completely inhibits their mating response (Nakagawa et al. 1973, Suzuki and Koyama 1981), demonstrating the importance of olfaction in stimulating female receptivity. The most compelling evidence for the impact of male sex pheromone on female choice derives from species, particularly B. dorsalis and Z. cucurbitae, in which ingested plant-borne chemicals are incorporated into the pheromone and enhance a male’s long-range attractiveness and mating success. Males of B. dorsalis feed on plants containing the phenylpropanoid methyl eugenol (Tan and Nishida 2012), which is then converted primarily to two compounds 2-allyl-4,5-dimethoxyphenol and trans-coniferyl alcohol (Nishida et al. 1988, Tan and Nishida 1996). These compounds are then released from the rectal gland as components of the sex pheromone. Males that fed on methyl eugenol attract more females and achieve more copulations than males denied access to methyl eugenol (Tan and Nishida 1996, Hee and Tan 1998, Shelly 2001a). Similar findings have been reported for other methyl eugenol-responsive Bactrocera species (Wee et al. 2007, Orankanok et al. 2013). Similarly, Z. cucurbitae males are attracted to and feed upon plants containing raspberry ketone (Nishida 1991), which is stored unmodified in the rectal gland and released as a pheromonal component (Nishida et al. 1990). Males fed raspberry ketone attract more females and mate more often than males deprived of this compound (Shelly 2000c).
Question 14: Do Males Exhibit Alternative Mating Strategies Within Leks?

As noted above, the majority of calling males in lekking fruit flies occur within aggregations, although some males may call and court on fruits away from leks. Data on the display of alternate mating tactics within leks are sparse and not conclusive. Adopted from studies of anurans (e.g., Arak 1988) and acoustic insects (e.g., Cade 1981), the term ‘satellite males’ has been used to describe males that perch within leks but do not defend a leaf territory, do not call, and intercept females approaching calling males (Hendrichs 1986, cited by Burk 1991). Alternately, satellite males may refer to males that perch near, but outside, leks (Pereira et al. 2009). These observations are provocative but without systematically collected data on individual males, they are not particularly informative. For example, periodic censuses may include non-calling males, but without knowing the identity of the males, it is not possible to determine whether particular individuals are consistently calling versus non-calling.

It is also likely that calling, territorial males are sexually opportunistic and, upon detecting a female in an adjacent territory, will immediately leave their own leaf and attempt to mate (before his neighbor does so) or disrupt a just-started mating. Although sample sizes were small, courting/mating disruptions at natural leks were recorded for two of four female arrivals in D. percnosoma (Bell and Kipp 1994) and 3 of 15 female arrivals in D. conformis (Shelly 1987). In all cases, disruptions caused the female to depart the leaf. Thus, calling, territorial males may temporarily adopt a ‘disruption tactic’ to both prevent their neighbor from mating and insure that the female remains receptive and in search of a mate. The success of mating disruption likely varies among species. For example, in field-cage observations, unmated males of Z. cucurbitae often jump atop a mating pair and attempt to copulate, an effort that may last >10 min. However, in no instance (N = 36) have these attempts been successful (T. E. Shelly, unpublished data).

Take home message: Males are occasionally seen on fruits away from leks, but data demonstrating the presence of non-calling, satellite males within leks are lacking.

Question 15: Do Females Preferentially Visit Groups of Males Over Solitary Males, and Do Females Preferentially Visit Larger Male Aggregations Over Smaller Ones?

One explanation regarding the evolution of leks proposes that females prefer to visit and mate in male aggregations, because they facilitate comparisons of potential mates (Alexander 1975, Bradbury and Gibson 1983). Additionally, females might be expected to prefer larger male groups over smaller ones, because large aggregations offer more comparisons among males and are likely to contain higher quality males (Kokko 1997). Such female preferences would, in turn, be expected to produce greater mating rates per male for grouped over solitary males and in large over small leks.

Data from fruit flies are mixed with respect to the comparison between solitary versus grouped males. Based on laboratory observations, per capita rates of female arrivals and matings were actually higher for solitary males than grouped (4–12 males) males in D. grimshawi (Drony 1994). Similarly, in a laboratory study of B. tryoni, per capita rates of female visits (considered indicative of mating opportunities) differed significantly between solitary males and leks containing 10 males but not between lone males and leks with only five males (Weldon 2007). In contrast to these data, however, field data for D. mycetophaga reveal a much higher female encounter rate per male for aggregated males than solitary males (Aspi and Hoffmann 1998).

Data comparing leks of varying size are also inconsistent. In D. grimshawi, per capita rates of female arrivals and matings were lower at leks with 12 males than leks with four males (Drony 1994). In B. tryoni (Weldon 2007), B. dorsalis (Shelly 2001b), and A. suspensa (Pereira et al. 2009) female visits per male did not vary significantly with lek size (or, equivalently, the collective calling activity at leks). However, per capita rates of female arrivals were much higher in large leks than small leks for D. conformis (Shelly 1990b), D. mycetophaga (Aspi and Hoffmann 1998), and C. capitata (Shelly 2001b). Data from the latter two species also indicate that the increase in female encounters is not monotonic but levels off above some given lek size.

Take home message: Computed on a per male basis, rates of female arrivals and male matings are not consistently greater for grouped vs. solitary males or for large vs. small male aggregations. In two species where female arrivals increase with lek size, the trend is not monotonic, and arrival rates level off above a certain number of lekking males.

Question 16: Do Females Gain Either Direct or Indirect Fitness Benefits Through Mate Choice?

Direct fitness benefits refer to the enhancement of female fecundity, fertility, or longevity realized via nonrandom mating (Kirkpatrick and Ryan 1991). As noted earlier, female fruit flies may exhibit mate preferences without apparent gain of direct benefits (Pérez-Staples et al. 2010, Shelly et al. 2011). Other examples include female choice of protein-fed over protein-deprived males even though male diet had no effect on fecundity or fertility (Pérez-Staples and Aluja 2004, Aluja et al. 2008). In one unusual case, females of D. grimshawi prefer males that perform high levels of pheromone streaking and wing displays, yet matings with preferred males result in lower fecundity than observed for females mating with less active males (Drony 2001, 2003). Conversely, females may mate indiscriminately even though this may lead to reduced fecundity (Schwartz 1991, Whittier and Kaneshiro 1991). In a further permutation, females of A. striata mate indiscriminately with respect to male size even though mating with large males results in increased female fecundity (Aluja et al. 2008). This species represents a special case, as courtship is prolonged and involves trophallaxis, a mouth-to-mouth transfer of fluids from the male to the female (Aluja et al. 1993). The composition and function of the exchanged material are not known, but it has been proposed that the material serves as a nuptial gift (Aluja et al. 1993) and may have a positive effect on female longevity (Pérez-Staples and Aluja 2004).

The case of trophallaxis, which is rare among Tephritidae (Sivinski et al. 2000), along with the documented reduction in the
than sons of fathers that had been denied access to the attractant able to locate cue-lure sources (and thus gain a mating advantage) fed on the male attractant cue-lure produced sons that were better (Partridge 1980), females of (Papadopoulos et al. 2004, Johansson et al. 2005). In contrast, and ing success (Whittier et al. 1994), is an honest index of male quality ing father–son scores did not detect significant heritability (Whittier and Kaneshiro 1995). Thus, female choice did not appear to be based on heritable differences in mating ability among males. This finding appears at odds with the independent observation that life-time calling level and longevity are positively related in C. capitata males, suggesting that calling level, which is a predictor of male mat ing success (Whittier et al. 1994), is an honest index of male quality (Papadopoulos et al. 2004, Johansson et al. 2005). In contrast, and analogous to an earlier seminal study on Drosophila melanogaster (Partridge 1980), females of Z. cucurbitae that were free to choose their mates produced offspring with faster development (egg-to adult) and with larger body size than females given no choice of mates (Kasuya 1992). In the final relevant study, B. tryoni males that fed on the male attractant cue-lure produced sons that were better able to locate cue-lure sources (and thus gain a mating advantage) than sons of fathers that had been denied access to the attractant (Kumaran and Clarke 2014). This result suggests that female preference for cue-lure-fed males reflects heritable lure-locating behavior, such that sons of lure-fed males will inherit high lure-foraging ability and thus enjoy elevated mating success (i.e., be sexy sons).

Take home message: The evidence is inconsistent for both direct and indirect benefits. Some studies suggest constituents of male ejaculate (e.g., of virgin or lure-treated males) may boost female fecundity, indicating the importance of male-controlled resources to the female. However, these putative constituents have not been identified.

Question 17: Do Males Exhibit Pre- or Postcopulatory Mate Choice?
Female choice in lek-forming fruit fly species is—by and large—an accepted fact, but the possibility of male choice is rarely mentioned or investigated. However, several lines of evidence suggest males do not always mate indiscriminately. First, courtship does not automatically follow female arrival to a male’s territory: males departed a leaf soon after female arrival in 13% of the observations for A. ludens (Robacker et al. 1991) and 11% for A. suspensa (Hendrichs 1986, cited by Burik 1991). In addition, fighting occurs among virgin, but not among immature or mated, females of C. capitata, suggesting interference competition to gain access to high-quality males (Papadopoulos et al. 2009). Finally, when females of differing ages were presented to young C. capitata males, matings with young females were more common than expected by chance. Additional tests demonstrated that this result did not reflect differential mating propensity or responsiveness to male pheromone signals between young and old females and thus suggested that males were selecting females with greater reproductive potential (Shelly et al. 2012).

Whether or not male fruit flies vary their ejaculate among females of varying quality is largely unstudied, but the available evidence is not supportive. In C. capitata, copulation duration and sperm transfer, which varied independently of male size (Taylor et al. 2000, Aquino and Joachim-Brao 2014), were greater for large than small females of C. capitata (Taylor et al. 2000). Thus, it appears that males were engaged in longer post-insemination mate guarding and invested greater ejaculate in large females with presumably greater fecundity. However, this interpretation is confounded by the apparent lack of a positive association between female size and fecundity in this species (Whittier and Shelly 1993, Blay and Yuval 1999). In a comparative study of three Anastrepha species, the amount of sperm transferred did not vary with female size, age, or nutritional history (Pérez-Staples et al. 2014). As in C. capitata, female fecundity is not directly related to body size (Sivinski 1993, Pérez-Staples et al. 2014).

Take home message: There is scant evidence for male mate choice, although when offered females of varying age, males mated preferentially with young over old females, presumably because young females have greater reproductive potential.

Question 18: Do Calling and Courtship Impose Costs on Lekking Males?
Direct measurements of energy expenditure during calling, court ship, and mating have not been made for males of any tephritid species. Nonetheless, three lines of evidence indicate nontrivial costs of sexual signaling in C. capitata. First, capture of wild flies revealed that males actively displaying at leks were heavier and contained more protein and sugar than resting males found outside of leks (Yuval et al. 1998). Moreover, among lekking males, levels of protein, glycogen, and lipids (but not sugar) declined over the course of the day, indicating depletion of nutritional reserves. These results, along with the finding that C. capitata males provided a protein-rich diet call more actively than males provided only sugar (Kaspi et al. 2000), suggest that successful food foraging is a requisite for sexual signaling.

Second, the life span of C. capitata males presented with five females (unmodified and capable of mating) on a daily basis was significantly shorter than that of males housed with five other males (Papadopoulos et al. 2010). Furthermore, the life span of males provided five females rendered incapable of mating (by cauterizing the ovipositor) per day was 1) significantly shorter than that of males housed with other males but 2) similar to that observed for males provided unmodified females. Collectively, these trends indicate that courtship (pheromone emission plus body and wing movements), but not the act of mating per se, was responsible for the shortened life span of males. Interestingly, among males allowed to mate, those that mated at the highest rate lived longer, suggesting variation in male ability to accommodate the costs of mating activity.

Finally, while the above studies did not consider predation risks, foraging wasps (Vespidae) use olfactory cues associated with male signaling to locate and attack C. capitata males. Small, opaque cups containing mature (calling) males, immature (non-calling) males,
females, or no flies (blank control) were suspended in the canopy of host trees, and approaches and landings of Vespuca germanica (Fab.) (Hymenoptera: Vespidae) foragers were monitored. Total approaches and landings were approximately eight times greater at the cups with mature males than any other treatment (Hendrichs et al. 1994). In an additional experiment, the wings of mature males were removed to eliminate acoustic stimuli, and the same results were obtained. Subsequent observations in a field cage also revealed higher wasp predation on calling than non-calling C. capitata males (Hendrichs and Hendrichs 1998). Wasp predation has also been observed on lekking males of a Hawaiian Drosophila (Shelly 1988).

Take home message: Data are restricted to a single species, C. capitata. When provided protein-rich food in the laboratory, C. capitata males show considerable variation in calling propensity and longevity, indicating a genetic component to the level of sexual signaling. In the wild, where protein sources may be scarce or unpredictable, successful food foraging may be important in influencing lek attendance and calling level. Signaling may increase predation risk as wasps appear to locate calling males using olfactory cues associated with the male sex pheromone.

Question 19: Do Sperm Competition and Cryptic Female Choice Occur?

Some level of remating has been reported for females of all species investigated. Most estimates are based on flies from long-established laboratory colonies, with observations made in small cages. As such, these estimates appear higher than remating frequencies for wild females. In C. capitata, multiple matings have been observed for 15–76% of lab-reared females in crowded conditions, whereas wild females observed under lower densities in field cages display remating rates of 3–12% (Mossinson and Yuval 2003). Analyses of microsatellite markers of field-caught C. capitata females and their progeny indicated that 4–28% of the females from Greek populations and 50% of females from an Israeli population had mated two or more times (Bonizzoni et al. 2002, 2006; Kraaijeveld et al. 2005).

Female remating frequency appears more frequent in Bactrocera, and laboratory estimates range from approximately 30 to 67% (Harmer et al. 2006, Chinajaraiyawong et al. 2010, Ooi and Wee 2016). Again, these may overestimate the multiple mating in wild females, and a microsatellite analysis of wild-caught females generated a remating frequency of 23% for B. cucuminiata females (Song et al. 2007). To my knowledge, no data are available for wild-caught Anastrepha females, but laboratory estimates range from 25 to 45% (Aluja et al. 2009, Abraham et al. 2011, Meza et al. 2014).

As polyandry appears common, there is a strong likelihood that sperm competition occurs in many lekking fruit fly species. Data are limited, however, and available for only a few species. Based on genetic strains of C. capitata having different pupal color, estimates of $P_2$ (proportion of offspring of twice-mated female sired by the second male) were 58–67% at 10 d and 59–71% at 30 d after the second mating (Saul and McCombs 1993). Thus, the paternity advantage of the second male was stable over time. Examination of paternity trends just after the second mating showed a decrease in $P_2$ from 93% at 1 d to 65% at 8 d (Bertin et al. 2010), this latter estimate being similar to the 10-d estimate noted above. Last male sperm precedence also characterizes Z. cucurbitae, although its expression depends on the amount of time elapsed between female remating (Tsubaki and Sokei 1988, Tsubaki and Yamagishi 1991, Yamagishi et al. 1992). If the inter-mating interval is 4 d or less, $P_2$ values are near 50%. However, at intervals exceeding 16 d, the second male sired 70–95% of the offspring over 115 d after the second mating. In contrast, first male sperm precedence has been suggested for B. dorsalis (Zhao et al. 2013), but the data were not inconsistent with random mixing of sperm from the two males. Whether or not male fruit flies in the wild vary the amount of sperm transferred with the perceived risk of sperm competition is unknown, but this phenomenon has been demonstrated in the laboratory (Gage 1991, Abraham et al. 2015).

There are presently no data available on postcopulatory cryptic choice by female fruit flies. Female tephritids possess sperm storage structures that would apparently allow selective fertilization of different ejaculates. Sperm are apparently held for long-term storage in a pair or trio of spermathecae and moved to the ventral receptacle (or fertilization chamber) for fertilization (Fritz and Turner 2002, Fritz 2004,Twig and Yuval 2005). As the spermathecae are separate structures, with their own complexes of ducts and valves, they are capable of receiving, storing, and releasing sperm independently from one another. Uneven sperm storage among the different organs has been documented for several Anastrepha species (Fritz 2004, Pérez-Staples et al. 2014) and C. capitata (Taylor et al. 2000), but the relationship between storage and fertilization patterns is unknown.

Take home message: Remating has been reported for females of various tephritid species, and sperm competition is likely. Last male sperm precedence appears common, but data are limited. Whether female cryptic choice occurs is unknown, but multiple, independent organs for sperm storage suggest a mechanism for manipulating movement and fertilization of sperm from different males.

Concluding Remarks

The observations discussed here are the collective product of evolution within taxa having varying ecologies and life histories. These interspecific differences make it difficult to draw conclusions applicable to the entire suite of species considered. Although frustrating, on one hand, this reality offers the intellectually challenging opportunity of associating interspecific differences in reproductive behavior with underlying variation in natural history and demography. Making these associations was beyond the scope of this essay, which was, in fact, merely an attempt to ‘set the table’ for such comparisons by noting uniformity as well as inconsistency for empirical data on key issues related to lek behavior.

The essay touches on many key issues in sexual selection, and identifying one, or a few, topics for more intense study would be neither useful nor prudent. Though mundane, it is eminently truthful to conclude that more work is required on all aspects of fruit fly lekking, including male movements (part of a signal-search strategy) within the tree canopy; the influence of female age, mating history, and body condition on mate sampling and choice, energetic constraints on male sexual advertisement under natural conditions, and fitness benefits gained by females via choice. Another area that merits additional study is the relationship between pre- and postcopulatory selection to determine whether a positive relationship exists between male mating success and fertilization success. This issue appears particularly interesting given the high intermale variability in sperm transfer and the likely condition-dependent effects on male capability of procuring mates and fertilizing eggs.

References Cited

Abraham, S., L. Goane, J. Rull, J. Cladera, E. Willink, and M. T. Vera. 2011. Multiple mating in Anastrepha fraterculus females and its relationship with fecundity and fertility. Entomol. Exp. Appl. 141: 15–24.
Abraham, S., M. T. Vera, and D. Pérez-Staples. 2015. Current sperm competition determines sperm allocation in a tephritid fruit fly. Ethology. 121: 451–461.

Abraham, S., Y. Contreras-Navarro, and D. Pérez-Staples. 2016. Female age determines remating behavior in wild Mexican fruit flies. J. Insect Behav. 29: 340–354.

Alcock, J. 1981. Lek territoriality in the tanantula hawk wasp Hemptepis ushulata (Hymenoptera: Pompilidae). Behav. Ecol. Sociobiol. 81: 309–317.

Alexander, R. D. 1975. Natural selection and specialized courting behavior in acoustical insects, pp. 35–77. In D. Pimental (ed.), Insects, science, and society. Academic Press, New York, NY.

Aluja, M., and A. Birke. 1993. Habitat use by adults of Anastrepha obliqua (Diptera: Tephritidae) in a mixed mango and tropical plum orchard. Ann. Entomol. Soc. Am. 86: 799–812.

Aluja, M., M. Hendrichs, and M. Cabrera. 1983. Behavior and interactions between Anastrepha ludens (L.) and A. obliqua (M.) on a field caged mango tree. I. Lekking behavior and male territoriality, pp. 122–133. In R. Cavalloro (ed.), Fruit flies of economic importance. A. A. Balkema, Rotterdam, The Netherlands.

Aluja, M., C. Cabrera, J. Guillen, H. Cedeñolongo, and F. Ayora. 1989. Behaviour of Anastrepha ludens, A. obliqua, and A. serpentina (Diptera: Tephritidae) on a wild mango tree (Mangifera indica) harbouring three McPhail traps. Insect Sci. Appl. 10: 309–318.

Aluja, M. S., I. Jácome, A. Birke, N. Lozada, and G. Quintero. 1993. Basic patterns of behavior in wild Anastrepha straita (Diptera: Tephritidae) flies under field-cage conditions. Ann. Entomol. Soc. Am. 86: 776–793.

Aluja, M., J. Piñero, I. Jácome, D. Haz-Fielscher, and J. Sivinski. 2000. Behavior of flies in the genus Anastrepha (Trypetinae: Toxicotylus) II. pp. 375–406. In M. Aluja and A. L. Norrbom (eds.), Fruit flies in the genus Anastrepha (Trypetinae: Toxotrypanini), pp. 375–406. M. Aluja and A. L. Norrbom (eds.), Fruit flies in the genus Anastrepha (Trypetinae: Toxotrypanini), pp. 375–406. Martinus Nijhoff Publishers, Boston, Massachusetts.

Aluja, M., D. Pérez-Staples, J. Sivinski, A. Sánchez, and J. Piñero. 2008. Effects of male condition on mating success between males of two populations of the Mediterranean fruit fly, Ceratitis capi
taxa. Mol. Ecol. 17: 1915–1921.

Aluja, M., J. Rull, J. Sivinski, G. Trujillo, and D. Pérez-Staples. 2009. Male and female condition influence mating performance and sexual receptivity in two tropical fruit flies (Diptera: Tephritidae) with contrasting life histories. Anim. Behav. 76: 1997–2009.

Aluja, M., J. Hendrichs, and M. Cabrera. 1988. Callers and satellites in the natterjack toad: evolutionarily stable decision rules. Anim. Behav. 36: 416–432.

Arita, L. H., and K. Y. Kaneshiro. 1989. Body size and differential mating success in males of the Mediterranean fruit fly, Ceratitis capitata (Diptera: Tephritidae). J. Insect Sci. Appl. 85: 14–31.

Arita, L. H., K. Y. Kaneshiro. 1983. The evolution of leks, pp. 138–169. In K. Kawasaki, O. Iwahashi, and K. Y. Kaneshiro (eds.), Int. Symp. Biol. Control Fruit Flies. University of Ryukyus, Okinawa, Japan.

Arita, L. H., K. Y. Kaneshiro. 1981. The evolution of leks, pp. 138–169. In K. Kawasaki, O. Iwahashi, and K. Y. Kaneshiro (eds.), Int. Symp. Biol. Control Fruit Flies. University of Ryukyus, Okinawa, Japan.

Aspi, J., and A. A. Hoffmann. 1995. Distribution and spacing of Drosophila mycetophaga flies on bracket fungi used as mating arenas. Ecol. Entomol. 20: 203–207.

Aspi, J., and A. A. Hoffmann. 1998. Female encounter rates and fighting costs of males are associated with lek size in Drosophila mycetophaga. Behav. Ecol. Sociobiol. 42: 163–169.

Baker, P. S., and H. Van der Valk. 1992. Distribution and behavior of sterile Mediterranean fruit flies in a host tree. J. Appl. Entomol. 114: 67–76.

Bateson, P. 1983. Mate choice. Cambridge University Press, Cambridge, United Kingdom.

Bell, W. J., and L. R. Kipp. 1994. Drosophila perecedoma Hardy lek sites: spatial and temporal distributions of males and the dynamics of their agonistic behavior (Diptera: Drosophilidae). J. Kansas Entomol. Soc. 67: 267–276.

Benelli, G. 2015. Aggression in tephritid flies: where, when, why? Future directions for research in integrated pest management. Insects. 6: 38–53.

Bertin, S., F. Scorti, C. R. Guglielmino, M. Bonizzi, A. Bonomi, D. Marchini, L. M. Gomulski, G. Gasperi, A. R. Malacrida, and C. Matesi. 2010. Sperm storage and use in polyandrous females of the globally invasive fruitfly, Ceratitis capitata. J. Insect Physiol. 56: 1542–1551.

Blay, S., and B. Yuval. 1999. Oviposition and fertility in the Mediterranean fruit fly (Diptera: Tephritidae): effects of male and female body size and the availability of sperm. Ann. Entomol. Soc. Am. 92: 278–284.

Boake, C. B. R. 1989. Correlations between courtship success, aggressive success, and body size in a picture-winged fly, Drosophila silvestris. Ethology. 80: 318–329.

Boake, C. B. R., and A. Hoikkala. 1995. Courtship behaviour and mating success of wild-caught Drosophila silvestris males. Anim. Behav. 49: 1303–1313.

Bonizzoni, M., B. I. Katsyurany, G. Marguerie, C. R. Guglielmino, G. Gasperi, A. Malacrida, and T. Chapman. 2002. Microsatellite analysis reveals remating by wild Mediterranean fruit fly females, Ceratitis capi
taxa. Mol. Ecol. 11: 1915–1921.

Bradbury, J. W. 1981. The evolution of leks, pp. 138–169. In R. D. Alexander and D. W. Tinkle (eds.), Natural selection and social behaviour. Chiron Press, New York, NY.

Bradbury, J. W., and M. Andersson. 1987. Sexual selection: testing the alternatives. Wiley Interscience, New York, NY.

Bradbury, J. W., and R. M. Gibson. 1983. Leks and mate choice, pp. 109–138. In P. Bateson (ed.), Mate choice. Cambridge University Press, Cambridge, United Kingdom.

Briceño, R. D., and W. G. Eberhard. 2000. Possible Fisherian changes in female mate-choice criteria in a mass-reared strain of Ceratitis capitata (Diptera: Tephritidae). Anim. Entomol. Soc. Am. 93: 343–345.

Briceño, R. D., and W. G. Eberhard. 2002. Decisions during courtship by male and female medflies (Diptera: Tephritidae): correlated changes in male behavior and female acceptance criteria in mass-rearing flies. Fla. Entomol. 85: 14–31.

Briceño, D., D. Ramos, and W. G. Eberhard. 1999. Aggressive behavior in medflies (Ceratitis capitata) and its modification by mass rearing (Diptera: Tephritidae). J. Kansas Entomol. Soc. 72: 17–27.

Bro-Jorgensen, J. 2002. Overt female mate competition and preference for central males in a lekking antelope. Proc. Natl. Acad. Sci. USA. 99: 9290–9293.

Burk, T. 1981. Signaling and sex in acalypterate flies. Fla. Entomol. 64: 30–43.

Burk, T. 1983. Behavioral ecology of mating in the Caribbean fruit fly, Anastrepha suspensa (Loew). Fla. Entomol. 66: 330–344.

Burk, T. 1984. Male-male interactions in Caribbean fruit flies, Anastrepha suspensa (Loew) (Diptera: Tephritidae): territorial fights and signaling stimulation. Fla. Entomol. 67: 542–547.

Burk, T. 1991. Sex in leks: an overview of sexual behavior in Anastrepha fruit flies, pp. 177–189. In K. Kawasaki, O. Iwahashi, and K. Y. Kaneshiro (eds.), Int. Symp. Biol. Control Fruit Flies. University of Ryukyus, Okinawa, Japan.

Burk, T., and J. C. Webb. 1983. Effect of male size on calling propensity, song parameters, and mating success in Caribbean fruit flies, Anastrepha suspensa (Loew) (Diptera: Tephritidae). Ann. Entomol. Soc. Am. 76: 678–682.
Kasuya, E. 1992. Female mate preference and offspring fitness in the melon fly. Ecol. Res. 7: 277–281.

Khoo, C. C. H., and K. H. Tan. 2000. Attraction of both sexes of melon fly, Bactrocera cucurbitae, to conspecific males - a comparison after pharmacophore of cue-lure and a new attractant - zingonere. Entomol. Exp. Appl. 97: 312–320.

Kirkpatrick, M., and M. J. Ryan. 1991. The evolution of mating preferences and the paradox of the lek. Nature. 350: 33–38.

Kobayashi, R. M., K. Ohinata, D. L. Chambers, and M. S. Fujimoto. 1978. Sex pheromones of the oriental fruit fly and the melon fly: mating behavior, bioassay methods, and attraction of females by live males and by suspected pheromone glands of males. Environ. Entomol. 7: 107–112.

Kokko, H. 1997. The lekking game: can female choice explain aggregated male displays? J. Theor. Biol. 187: 57–64.

Kraaijeveld, K., B. I. Katsyoyannos, M. Stavriniades, N. A. Koulousis, and T. Chapman. 2005. Remating in wild females of the Mediterranean fruit fly, Ceratitis capitata. Anim. Behav. 69: 771–776.

Kuba, H., and J. Koyama. 1985. Mating behavior of wild melon flies, Dacus cucurbitae Coquillett (Diptera: Tephritidae) in a field cage: courtship behavior. Appl. Entomol. Zool. 20: 365–372.

Kuba, H., and Y. Sokei. 1988. The production of pheromone clouds by spraying in the melon fly Dacus cucurbitae (Diptera: Tephritidae). J. Ethol. 6: 105–110.

Kumaran, N., and A. R. Clarke. 2014. Indirect effects of phytochemicals on offspring performance of Queensland fruit fly, Bactrocera tryoni (Diptera: Tephritidae). J. Appl. Entomol. 138: 361–367.

Kumaran, N., S. Balagavi, M. K. Schutze, and A. R. Clarke. 2013. Evolution of lure response in tephritid fruit flies: phytochemicals as drivers of sexual selection. Anim. Behav. 85: 781–789.

Landolt, P. J., and J. Sivinski. 1992. Effects of time of day, adult food, and host fruit on incidence of calling by male Caribbean fruit flies (Diptera: Tephritidae). Environ. Entomol. 21: 382–387.

Lederhouse, R. C. 1982. Territorial defense and lek behavior of the black swallowtail butterfly, Papilio polyxenes. Behav. Ecol. Sociobiol. 10: 109–118.

Liimatainen, J., A. Hoikkala, and T. Shelly. 1997. Courtship behavior in Ceratitis capitata (Diptera: Tephritidae). J. Ethol. 6: 105–110.

López-Guillén, G., L. Cruz López, E. A. Malo, and J. C. Rojas. 2011. Olfactory courting in extreme longevity reduction. J. Insect Physiol. 56: 283–287.

Mankin, R. W., M. Lemon, A. M. T. Harmer, C. S. Evans, and P. W. Taylor. 1983. Distribution and activity of the supra-fronto-orbital bristles of male medflies (Diptera: Tephritidae). Fla. Entomol. 66: 234–241.

Malavasi, A., J. Sivinski, and R. J. Wood. 2008. Male position and calling effort together influence male attractiveness in leks of the medfly, Ceratitis capitata (Diptera: Tephritidae). J. Ethol. 26: 129–132.

Mossinson, S., B. Yuval. 2003. Regulation of sexual receptivity of female Mediterranean fruit flies: old hypotheses revisited and a new synthesis proposed. J. Insect Physiol. 49: 561–567.

Makarova, S., G. J. Farias, D. Suda, and D. L. Chambers. 1973. Mating behavior of the Mediterranean fruit fly following excision of the antennae. J. Econ. Entomol. 66: 583–584.

Nagakawa, S., L. F. Steiner, and G. J. Farias. 1981. Response of virgin female Mediterranean fruit flies to live mature normal males, sterile males, and trimedullin in plastic traps. J. Econ. Entomol. 74: 566–567.

Nakagawa, S., R. K. Tan, M. Serit, N. H. Lajis, A. M. Sukari, S. Takahashi, and H. Fukami. 1988. Accumulation of phenylpropanoids in the rectal glands of males of the oriental fruit fly, Dacus dorsalis. Experientia. 44: 534–536.

Nishida, R., K. H. Tan, S. Takahashi, and H. Fukami. 1990. Volatile components of male rectal glands of the melon fly, Dacus cucurbitae Coquillett (Diptera: Tephritidae). Appl. Entomol. Zool. 25: 105–112.

Niyazi, N., D. M. Shuker, and R. J. Wood. 2008. Male position and calling effort together influence male attractiveness in leks of the medfly, Ceratitis capitata (Diptera: Tephritidae). J. Ethol. 26: 129–132.

Ooi, Y. T., and S. L. Wee. 2016. Sexual maturation, mating propensity and remating incidence of Zeugodacus tau (Walker) (Diptera: Tephritidae). J. Asia Pac. Entomol. 19: 451–457.

Orankanok, W., S. Chinvijikul, A. Savatwangkhoung, S. Pinkaw, and S. Orankanok. 2013. Methyl eugenol and pre-release diet improve mating performance of young Bactrocera dorsalis and Bactrocera correcta males. J. Appl. Entomol. 137(Suppl. 1): 200–209.

Partridge, L. 1991. Theories of sexual selection. Trends Ecol. Evol. 6: 356–362.

Papadopoulos, N. T., B. I. Katsyoyannos, N. A. Koulousis, A. P. Economopoulos, and J. R. Carey. 1998. Effect of adult age, food, and time of day on sexual calling incidence of wild and mass-reared medflies. Ann. Entomol. Soc. Am. 91: 571–577.

Papadopoulos, N. T., B. I. Katsyoyannos, N. A. Koulousis, J. R. Carey, H. G. Müller, and Y. Zhang. 2004. High sexual signalling rates of young individuals predict extended life span in male Mediterranean fruit flies. Oecologia. 138: 127–134.

Pereira, R., J. Sivinski, and P. E. Teal. 2009. Influence of methoprene and dietary protein on male Anastrepha suspensa (Diptera: Tephritidae) mating aggregations. J. Insect Physiol. 55: 328–335.
Poramarcom, R., and C. R. Boake. 1991. A resolution of the lek paradox. 

Rowe, L., and D. Houle. 2001. The relevance of age and nutrition on the mating competitiveness of medfly males (Diptera: Tephritidae): influence of time of day, sex and airborne pheromone. Bull. Entomol. Res. 93: 173–178.

Pomiankowski, A., and A. P. Müller. 1995. A resolution of the lek paradox. Proc. R. Soc. Lond. Ser. B. 260: 21–29.

Poramarcom, R., and V. Baimai. 1996. Sexual behavior and signals used for mating of Bactrocera correcta, pp. 51–58. In B. A. McPherson and G. J. Steck (eds.), Fruit fly pests: a world assessment of their biology and management. St. Lucie Press, Delray Beach, FL.

Poramarcom, R., and C. R. B. Boake. 1996. Behavioural influences on male mating success in the oriental fruit fly, Dacus dorsalis Hendel. Anim. Behav. 42: 453–460.

Prokop, R. J. 1980. Mating behavior of frugivorous Tephritidae in nature, pp. 37–46. In J. Koyama (ed.), Proc. Symp. Fruit Fly Problems. XVI Intl. Cong. Entomol., Kyoto, Japan.

Prokop, R. J., and J. Hendrichs. 1979. Mating behavior of Ceratitis capitata on a field-cages host tree. Ann. Entomol. Soc. Am. 72: 642–648.

Prokop, R. J., R. Poramarcom, M. Suntawong, R. Dokmaihom, and J. Hendrichs. 1996. Localization of mating behavior of released Bactrocera dorsalis flies on host fruit in an orchard. J. Insect Behav. 9: 133–142.

Quilici, S., A. Franck, E. Puppuy, E. Dos Reid Corrìa, C. Mouniama, and F. Blard. 2002. Comparative studies of courtship behavior of Ceratitis spp. (Diptera: Tephritidae) in Reunion Island. Fla. Entomol. 85: 138–142.

Raghu, S., and A. R. Clarke. 2003. Spatial and temporal partitioning of behaviour by adult dactines: direct evidence for methyl eugenol as a mate rendezvous cue for Bactrocera cucumis. Physiol. Entomol. 28: 173–184.

Robacker, D. C. 1988. Behavioral responses of female Mexican fruit flies, Anastrepha ludens, to components of male-produced sex pheromone. J. Chem. Ecol. 14: 1715–1726.

Robacker, D. C., and W. G. Hart. 1985. Courtship and territoriality of laboratory-reared Mexican fruit flies, Anastrepha ludens (Diptera: Tephritidae), in cages containing host and nonhost trees. Ann. Entomol. Soc. Am. 78: 488–494.

Robacker, D. C., and W. G. Hart. 1986. Behavioral responses of male and female Mexican fruit flies, Anastrepha ludens, to male-produced chemicals in laboratory experiments. J. Chem. Ecol. 12: 39–47.

Robacker, D. C., S. J. Ingle, and W. G. Hart. 1985. Mating frequency and response to male-produced pheromone by virgin and mated females of the Mexican fruit fly. Southwestern Nat. 10: 215–221.

Robacker, R. L. Mangan, D. S. Moreno, and A. M. Tarshis Moreno. 1991. Mating behavior and male mating success in wild Anastrepha ludens (Diptera: Tephritidae) on a field-caged host tree. J. Insect Behav. 4: 471–487.

Rodrigueiro, M. S., J. C. Vilardi, M. T. Vera, J. P. Cayol, and E. Rial. 2002. Morphometric traits and sexual selection in medfly (Diptera: Tephritidae) under field cage conditions. Fla. Entomol. 85: 143–149.

Rozier, A. K., and I. S. Joachim-Bravo. 2013. The relevance of age and nutritional status on the mating competitiveness of medfly males (Diptera: Tephritidae). Zoologica. 30: 506–512.

Rove, L., and D. Houle. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. Proc. R. Soc. Lond. Ser. B. 263: 1415–1421.

Saul, S. H., and S. D. McCombs. 1993. Dynamics of sperm use in the Mediterranean fruit fly (Diptera: Tephritidae): reproductive fitness of multiple-mated females and sequentially mated males. Ann. Entomol. Soc. Am. 86: 198–202.

Schwartz, J. M. 1991. Effect of sexual experience on male mating success in Drosophila silvestris. Anim. Behav. 42: 1017–1019.

Sciurano, R., D. Segura, M. Rodrigo, P. Gómez Cendrà, A. Allingham, J. L. Cladera, and J. Vilardí. 2007. Sexual selection on multivariate phenotypes in Anastrepha fraterculus (Diptera: Tephritidae) from Argentina. Fla. Entomol. 90: 163–170.

Segura, D., N. Petit-Marry, R. Sciurano, T. Vera, G. Calcagno, A. Allingham, P. Gómez Cendrà, J. Cladera, and J. Vilardí. 2007. Lekking behavior of Anastrepha fraterculus (Diptera: Tephritidae). Fla. Entomol. 90: 154–162.

Shelly, T. E. 1987. Lek behaviour of a Hawaiian Drosophila: male spacing, aggression and female visitation. Anim. Behav. 35: 1394–1404.

Shelly, T. E. 1988. Lek behaviour of Drosophila neoclopestris in Hawaii. Ecol. Entomol. 13: 51–55.

Shelly, T. E. 1990a. Observations on the lek behavior of Drosophila imparisetae (Diptera: Drosophilidae) in Hawaii. J. Kansent Entomol. Soc. 63: 652–655.

Shelly, T. E. 1990b. Waiting for mates: variation in female encounter rates within and between leks of Drosobila coniformis. Behaviour. 107: 34–48.

Shelly, T. E. 2000a. Male signalling and lek attractiveness in the Mediterranean fruit fly. Anim. Behav. 60: 245–251.

Shelly, T. E. 2000b. Aggression between wild and laboratory-reared sterile males of the Mediterranean fruit fly in a natural habitat (Diptera: Tephritidae). Fla. Entomol. 83: 105–108.

Shelly, T. E. 2000c. Effects of raspberry ketone on the mating success of male melon flies (Diptera: Tephritidae). Proc. Hawaiian Entomol. Soc. 34: 163–167.

Shelly, T. E. 2001a. Feeding on methyl eugenol and pukenkeni flowers increases long-range, female attraction by male oriental fruit flies, Bactrocera dorsalis (Diptera: Tephritidae). Fla. Entomol. 84: 634–640.

Shelly, T. E. 2001b. Lek size and female visitation in two species of tephritid fruit flies. Anim. Behav. 62: 33–40.

Shelly, T. E. 2003. Starvation and the mating success of wild male Mediterranean fruit flies (Diptera: Tephritidae). J. Insect Behav. 16: 171–179.

Shelly, T. E. 2004. Scent marking by males of the Mediterranean fruit fly, Ceratitis capitata. J. Insect Behav. 17: 709–722.

Shelly, T. E., and K. Y. Kaneshiro. 1991. Lek behavior of the oriental fruit fly in Hawaii. J. Insect Behav. 4: 235–241.

Shelly, T. E., and S. S. Kennelly. 2007. Settlement patterns of Mediterranean fruit flies in the tree canopy: an experimental analysis. J. Insect Behav. 20: 453–472.

Shelly, T. E., and T. S. Whittier. 1993. Effect of sexual experience on the mating success of males of the Mediterranean fruit fly, Ceratitis capitata (Wiedemann) (Diptera: Tephritidae). Proc. Hawaiian Entomol. Soc. 32: 91–94.

Shelly, T. E., and T. S. Whittier. 1995. Lek distribution in the Mediterranean fruit fly: influence of tree size, foliage density, and neighborhood. Proc. Hawaiian Entomol. Soc. 32: 113–121.

Shelly, T. E., and T. S. Whittier. 1997. Insect lek behavior, pp. 273–293. In J. C. Choe and B. J. Crespi (eds.), The evolution of mating systems in insects and arachnids. Cambridge University Press, Cambridge, United Kingdom.

Shelly, T. E., T. S. Whittier, and K. Y. Kaneshiro. 1994. Sterile insect release and the natural mating system of the Mediterranean fruit fly, Ceratitis capitata (Diptera: Tephritidae). Ann. Entomol. Soc. Am. 87: 470–481.

Shelly, T. E., J. Edu, and E. Palio. 2011. Female medflies mate selectively with young males but gain no apparent fitness benefits. J. Insect Behav. 24: 55–66.

Shelly, T. E., J. Edu, and E. Palio. 2012. Male choice by lekking males: evidence from the Mediterranean fruit fly from field cage trials (Diptera: Tephritidae). Anim. Entomol. Soc. Am. 105: 368–376.

Shuker, D. M. 2014. Sexual selection theory, pp. 20–41. In D. M. Shuker and L. W. Simmons (eds.), The evolution of insect mating systems. Oxford University Press, Oxford, United Kingdom.

Shuker, D. M., and L. W. Simmons. 2014. The evolution of insect mating systems. Oxford University Press, Oxford, United Kingdom.
