

FORUM

Do Mediterranean Fruit Flies Lek? Does It Matter?

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Abstract: Saul and McCombs (1995) recently argued that existing data do not support the accepted notion that the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), exhibits lek behavior. In particular, these authors claimed that 1) the mating system of *C. capitata* is resource-based and 2) *C. capitata* males are not spatially aggregated. Here, I review field observations that are consistent with lek behavior in this species and hence contrary to these claims. Also, contrary to the view of Saul and McCombs (1995), knowing that the Mediterranean fruit fly leks stimulates many questions of interest from both basic and applied viewpoints.

Keywords: *Ceratitis capitata*, leks, male aggregations, mating behavior

Bradbury (1977,1981) listed four principle characteristics of lek mating systems: absence of paternal care (the male provides nothing but gametes to females), spatial clustering of males in mating arenas (or leks), male defense of territories that contain no resources vital to females, and female capability to freely select a mate. These criteria have been widely accepted and have been used to identify lek mating systems in a diverse array of animal taxa, including mammals (Apollonio et al., 1989), birds (Hoglund and Lundberg 1987), frogs (Robertson 1986), and insects (Alcock and Smith 1987). The only modification to the original concept has come from Bradbury (1985) himself, who suggested that the presence or absence of resources in male territories per se was perhaps less important than whether or not males actively regulated female access to critical resources.

In a recent Forum article in this journal, Saul and McCombs (1995; abbreviated SM hereafter) criticize studies of lek behavior in the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), on both empirical and conceptual fronts. First, and most importantly, SM argue that the existing data do not support the accepted view that the Mediterranean fruit fly exhibits lek behavior. SM appear to consider lek behavior not an accurate depiction of the natural mating system of *C. capitata* but an unproven notion used primarily as a “rhetorical tool to question the effectiveness of mass rearing technologies”. Second, SM argue that lek behavior has failed as a model for *C. capitata* in not (i) identifying new parameters for study or (ii) generating testable hypotheses.

In this rejoinder, I show that the empirical data demonstrating lek behavior in the Mediterranean fruit fly are far stronger than SM purport. Specifically, I will show that their criticisms are based on basic misconceptions of the mating behavior of *C. capitata* in some instances and on misinterpretation of the data in others. Regarding the perceived failure of the lek model, I will suggest that knowing that *C. capitata* males form leks stimulates many interesting questions (from both basic and applied viewpoints), and a brief list of testable hypotheses is provided. SM deal only with two of Bradbury’s (1977,1981) criteria: the role of resources and the existence of male aggregations. Correspondingly, my discussion will be restricted to these two factors.

According to SM, the observation that male Mediterranean fruit flies signal from host as well as non-host trees (cited Hendrichs and Hendrichs 1990; Whittier et al. 1992; see also Arita and Kaneshiro 1998; Hendrichs et al. 1991; Shelly et al. 1994) violates the stipulation regarding the absence of essential resources in male territories. This argument is invalid because it uncritically equates “sex near resources” with “sex in exchange for resources” and thus completely ignores the real nature of male behavior on host trees. Even on host trees, males typically perch and call from leaf undersurfaces (not from fruit) and such leaves are not necessarily near fruit. Moreover, territorial defense is restricted to the occupied leaf, and in no way do males regulate female access to fruits. For example, working in both a mixed fruit orchard and a coffee field, Arita and Kaneshiro (1989) found high numbers of *C. capitata* males on leaves of host trees but did not observe any male calling or matings on host fruit. Similarly, Hendrichs and Hendrichs (1990) reported that, even on fruiting host trees, only about 1% of calling males and matings, respectively, were observed on fruit. Finally, over several seasons of field work in a mixed orchard on Maui (Shelly et al. 1993, 1994), less than 1% of male sightings and zero matings were recorded on host fruit. In short, male behavior on host trees appears identical to that on non-host trees: in neither case do male territories contain resources vital to females or males control female access to resources in return for matings.

The erroneous perception of a mating system based on resource defense undermines SM’s discussion of the purported contradiction between the occurrence of leks on host trees and Calkin’s (1989) suggestion following [Prokopy (1980) and Burk (1981)] regarding the evolution of lek behavior in *Anastrepha*. According to this idea, lek behavior is more likely to arise in polyphagous than monophagous species owing to the spatial and temporal unpredictability of host fruits, which, in turn, renders male defense of resources an untenable tactic for encountering females. SM suggest that this hypothesis is flawed, because “in contrast to the definitions of leks presented above [presumably a reference to Hendrichs and Hendrichs (1990) and Whittier et al. (1992) and the occurrence of leks on host trees], the unpredictability of host distribution and abundance means that males are not able to defend host fruit from other males nor restrict female access to it in exchange for mating opportunities”. This argument is spurious, however, because males simply do not engage in these behaviors. The fact that male Mediterranean fruit flies may aggregate on host trees does not negate the Prokopy-Burk notion but indicates that such sites may be environmental “hotspots” with high female traffic (Bradbury et al. 1986).

In addition to suggesting male defense of resources, SM question whether *C. capitata* males actually aggregate. In fact, field data indicate that males aggregate at two distinct spatial scales. First, several studies (Hendrichs and Hendrichs 1990; Hendrichs et al. 1991; Whittier et al. 1992; Shelly et al. 1993, 1994; Shelly and Whittier 1995) show that males are not distributed randomly among trees but instead prefer to aggregate on certain trees over others. For example, Hendrichs and Hendrichs (1990) found 54% of calling males on orange trees, although orange trees accounted for only 12% of all trees in the study area. Similarly, Whittier et al. (1992) reported that, in an area containing 118 trees, 80% of all male sightings were made on only 10 trees (of three different species). Second, males tend to form aggregations within the canopy of individual trees (Arita and Kaneshiro 1989; Hendrichs and Hendrichs 1990; Hendrichs et al. 1991; Whittier et al. 1992). For example, Hendrichs and Hendrichs (1990) reported that nearly 66% of calling males were within 15 cm of another calling male(s).

SM concern themselves only with the smaller spatial scale - male spacing within individual trees - and focus specifically on the data presented by Hendrichs and Hendrichs (1990). These workers reported that the location of male groups within a tree varied over time in apparent response to changing light and wind conditions. Based on this observation,

SM propose that, as an “alternate model”, males may actually be randomly distributed within regions of the canopy with favorable environmental conditions. As support for this “alternate model”, SM analyzed the size frequency distribution of male groups (based on counts of males within 15 cm of a reference male) for another tephritid species, the melon fly *Bactrocera cucurbitae* (Coquillett), on the plant *Bidens pilosa* L. (Table 1 in Iwahashi and Majima 1986). SM found that these data form a random (Poisson) distribution and claimed this result contradicted Iwahashi and Majima’s (1986) conclusion [and by inference that of Hendrichs and Hendrichs (1990)] that males lek.

There are several serious flaws with SM’s critique of male spacing. First, and most generally, by focusing solely on male dispersion within trees, SM ignore the common observation that *C. capitata* males are nonrandomly distributed among trees. Because leks can, in certain circumstances, be associated with entire trees rather than specific volumes or distances within trees (Shelly et al. 1994), omitting this larger spatial scale greatly weakens their objection. Second, Bradbury’s (1977, 1981) criterion on male spacing deals exclusively with the presence or absence of male aggregations and says nothing about either the factors leading to the formation of these aggregations or the dispersion patterns of males within aggregations. Thus, the likely possibility that *C. capitata* males gather independently (and not via mutual attraction) in particular sections of the canopy with favorable microclimatic conditions is irrelevant to the definition of lek. Similarly, if males are clumped in suitable patches of the canopy, the spacing of males within these patches is interesting but unimportant in terms of lek criteria.

Finally, SM’s analysis of Iwahashi and Majima’s (1986) data does not address the question of random spacing within the plant but examines the size frequency distribution of male groups. Their finding that the observed distribution does not differ from that expected by chance simply indicates that neither very small nor very large groups were represented disproportionately in the sample of all groups. Essentially, their analysis fails as a test of random spacing, because their index of male dispersion (group size) is not independent of male spacing to begin with. In other words, SM’s analysis implicitly assumes the existence of groups - the very thing they are trying to discredit! A more appropriate test of random spacing would involve dividing the plant into sections of equal volume, scoring the number of males in each section, and then comparing the observed dispersion pattern with a Poisson distribution. Alternatively, an analysis of nearest neighbor distances (for three dimensions) could be performed.

The points raised here regarding *C. capitata* also apply to SM’s dismissal of lek behavior in *Bactrocera* species. Although fewer data are available for this genus, they nonetheless are consistent with Bradbury’s (1977, 1981) lek criteria, and SM’s statement that the lek model was distorted to fit field observations of *B. dorsalis* (Shelly and Kaneshiro 1991) is unjustified. In this study, males (1) provided no nuptial gifts or resources to females during copulation, (2) were aggregated in the interior section of a single tree in a citrus orchard, (3) defended leaf territories that contained no resources, and (4) females were free to choose among potential mates. SM do not specify which of Bradbury’s (1977, 1981) conditions was distorted, and given these observations, it appears that, in reality, none were.

I agree with SM that the lek definition should not be applied to mating systems that do not adhere to Bradbury’s (1977, 1981) criteria. I also maintain that the use of the term lek follow some consistent level of stringency across taxa. Thus, it is ironic the SM question the term lek for the Mediterranean fruit fly but accept it without reservation for Hawaiian Drosophilidae, citing this taxon as one “for which it [the “lek model”] was constructed”. This phrase raised two immediate problems. First, and most apparent, the term lek did not originate from studies of Hawaiian Drosophilidae but was first used by Selous (1906, 1907) in his studies of avian reproduction. Second, the field data for *C. capitata* are at least as

comprehensive as those for Hawaiian *Drosophilidae*. To my knowledge, quantitative field data are available for only a handful of Hawaiian *Drosophila* (Shelly 1987, 1988, 1991; Bell and Kipp 1994), and these studies were all conducted at the same location over short periods of time. Thus, if the term lek is considered appropriate for the Hawaiian *Drosophilidae*, it should certainly be suitable for the Mediterranean fruit fly as well.

Finally, contrary to the claim of SM, the term lek stimulates many testable hypotheses. Some of these include: 1. Leks occur independently with respect to tree species. 2. Leks occur independently with respect to physical characteristics of trees. 3. Leks occur in the same trees within and between flight seasons. 4. Matings occur independently with respect to lek location. 5. Matings in leks occur independently with respect to leaf position. 6. Males in leks are the same size as solitary males. 7. Males in leks call the same amount as solitary males. 8. In leks, male mating success varies independently with respect to fighting success. 9. Females are equally attracted to leks of different sizes. 10. Individual males attend leks for equal amounts of time both within and between days. 11. Predation risks to males vary independently of lek size. 12. Sterile males distribute themselves independently with respect to lek location. 13. Solitary and lek-joining sterile males have equivalent mating success. 14. Sterile and wild males are equal competitors in aggressive contests. 15. Among leks of equal size, females are equally attracted to leks comprised of sterile males and wild males respectively.

To answer the two questions posed in the title of this article, (1) the Mediterranean fruit fly does lek, and (2) this matters on one hand but not the other. The chief characteristic of the mating system of *C. capitata* is that females apparently choose mates on the basis of male phenotype and not on the basis of male-controlled resources. Regardless of whether males aggregate (form leks), this basic fact places a premium on releasing sterile males that can compete successfully in epigamic competition with wild males. The additional fact that males aggregate should serve primarily to focus our attention on identifying characteristics of lek sites and ensuring that sterile males are successful at locating and competing within natural leks.

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