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WHY DO CALLING MEDFLIES (DIPTERA: TEPHRITIDAE) CLUSTER? ASSESSING THE EMPIRICAL EVIDENCE FOR MODELS OF MEDFLY LEK EVOLUTION

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ABSTRACT

Recent years have seen a proliferation both in theoretical approaches to understanding lek evolution and in empirical work on the lek mating system in the Mediterranean fruit fly. This paper aims to integrate these two lines of research and to identify practical insights of relevance to those engaged in medfly research. We begin by considering the definition of a medfly lek and recognize the existence of male aggregations at two distinct spatial scales: entire trees, or groups of trees within a given habitat; and small areas (ca 30 cm diameter) within the canopy of a given tree. After summarizing the assumptions and predictions of the main candidate models for lek evolution (predation avoidance, hotspot, hotshot and female preferences) we review empirical evidence from previous and ongoing research that is relevant to medfly lek evolution at both spatial scales. Far from being attributable to a single cause, we conclude that the evolution and selective maintenance of lekking behavior in the medfly can be attributed to a complex mosaic of interacting ecological pressures. We recognize that much more empirical work is needed to resolve outstanding questions on medfly lek evolution, and highlight potential benefits from the interaction between pure and applied lines of research on medfly mating behavior.

Key Words: medfly, *Ceratitis capitata*, lek, model, evolution

RESUMEN

En años recientes se ha visto una proliferación tanto en aproximaciones teóricas para entender la evolución del comportamiento en la selección del lugar de apareamiento y en trabajos empíricos sobre los sistemas de selección de los lugares de apareamiento en la mosca del Mediterráneo. Este trabajo está dirigido hacia la integración de estas dos líneas investigativas y hacia la determinación de información practica y de relevancia para las personas envueltas en la investigación de la mosca del Mediterráneo. Comenzamos por considerar la definición de el método de selección del lugar de apareamiento de la mosca del mediterráneo y en reconocer la existencia de grupos de machos en dos escalas espaciales diferentes: árboles completos, o grupos de árboles dentro de un hábitat dado; y pequeñas áreas (30 cm de diámetro) dentro del área foliar de un árbol determinado. Después de resumir las suposiciones y predicciones del candidato como modelo principal para la evolución del comportamiento en la selección del lugar de apareamiento (evitar depredación, punto clave, personaje y preferencias de la hembra) se analizó la evidencia empírica proveniente de investigaciones anteriores y aún en proceso, que son relevantes para la evolución del comportamiento en la selección del lugar de apareamiento de la mosca del Mediterráneo en ambas escalas espaciales. Lejos de poderse atribuir a una sola causa, concluimos que la evolución y mantenimiento selectivo del comportamiento en la selección del lugar de apareamiento de la mosca del Mediterráneo puede ser atribuido a un complejo mosaico de presiones interactivamente ecológicas. Reconocemos que es necesario mucho más trabajo empírico para contestar las sobresalientes preguntas en cuanto a la evolución del comportamiento en la selección del lugar de apareamiento de la mosca del Mediterráneo, y para destacar los beneficios potenciales de la interacción entre líneas puras y aplicadas de investigación en el comportamiento de apareamiento de la mosca del Mediterráneo.

WHAT IS A MEDFLY LEK?

Animals from a wide range of taxa, with a diverse array of life-histories, are classified as having a lek mating system (Hoglund & Alatalo 1995). Although the term 'lek' has been used by ornithologists for over a century, only recently have attempts been made to give it a rigorous ecological definition (see Hoglund & Alatalo 1995). Bradbury (1977, 1981, 1985) suggested four crite-

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ria: 1) the absence of male parental contribution; 2) most mating occurs at a specific site(s) where males aggregate and display; 3) the display sites contain no significant resources required by females; 4) females have the ability to choose a mate when visiting the display site. However, in light of numerous exceptions and ambiguities, Hoglund & Alatalo (1995) advocated a more relaxed definition based simply on the presence of aggregations of males and the absence of pair bonding and paternal care. This definition, "aggregated male display that females attend primarily for the purpose of fertilization", nearly reverts to that previously proposed by Emlen & Oring: "communal display area where males congregate for the sole purpose of attracting and courting females and to which females come for mating". Under this classification, more than 240 species scattered across the animal kingdom have so far been reported to exhibit a lek mating system (Hoglund & Alatalo 1995).

One of these species is the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae). Although the details of its mating behavior are today of great economic significance, this only came about with the development of the Sterile Insect Technique (SIT) in the 1960s. Numerous studies on medfly mating ensued, but it was not until the first systematic study of sexual behavior under semi-natural conditions was undertaken by Prokopy & Hendrichs (1979) that the existence of lekking as the major component of the mating system was recognized. Since that time, there have been two distinct operational definitions of medfly leks used in the literature. Prokopy & Hendrichs (1979) originally defined medfly leks as "3-6 males grouped within ca. 30 cm of one another, each on a separate leaf". Hendrichs & Hendrichs (1990) more or less followed this classification, as did Field & Yuval (unpublished data), having independently arrived at the same definition based on field observations. However, Whittier et al. (1992), followed by Shelly et al. (1994) and Shelly & Whittier (1995), instead defined a lek as an entire tree, because they usually found only one aggregation formed per tree and males moved readily between leaves, making it difficult to delimit the boundaries of an aggregation.

Before proceeding with a discussion of lek evolution in medflies, it is important to clarify exactly what is meant by the term 'lek' as applied to medflies. We note that both existing definitions have merits and flaws and, in the interests of gaining ecological insight, we advocate the retention of both pending further investigations. We thus propose the recognition of medfly leks at two distinct spatial scales: "small-scale leks" as defined by Prokopy & Hendrichs and "large-scale leks" as defined by Whittier et al. (1992).

With respect to small-scale leks, our own experience has independently supported the original conclusion of Prokopy & Hendrichs (1979) that aggregations of males in the tree canopy within a diameter of ca 30 cm are indeed functional components of the mating system. However, we should note that confirming the objectivity of this working definition will require studies that quantify the spatial distribution of calling males within and among trees, and demonstrate that males are more clustered at this spatial level than would be expected by chance. Nevertheless, a crucial aspect of lek mating systems, and one that makes them so interesting in terms of sexual selection, is that behavioral interactions such as dominance contests, competitive courtship and mate comparisons take place within them, and can heavily influence male reproductive success. Although in medflies communication over longer distances, particularly by chemical means, are likely to be of importance in male mating interactions, much of the behavioral detail that determines the course of sexual selection in lekking species can occur *only* when males are in close proximity. The intensive study of small-scale medfly aggregations is therefore vital to our understanding of sexual selection in medflies and the continued use of this tentative definition is therefore amply justified.

One advantage of the large-scale lek definition is that it is easier to verify quantitatively and indeed is already supported by empirical evidence. Whittier et al. (1992), for example, showed that a small subset of available trees accounted for a large majority of recorded incidences of male calling. Unpublished observations in Israel have suggested the existence of a similar phenomenon (R. K. & B. Y., unpublished data). Such large-scale aggregations differ considerably from, for example, classic avian leks, in which females enter a discrete male aggregation within which both male interactions and relative display efforts are readily observable. Male medflies within a tree, or group of trees, are relatively much more dispersed, separated and obscured from one another and from females by foliage and thus cannot interact or be observed to anywhere near the same extent as males in classic leks. However, it is conceivable that behavioral dynamics could at least resemble a classic lek. Male distribution throughout the tree could be influenced by agonistic interactions, and females could enter a tree and move about it comparing males in an analogous fashion to a female visiting a small group of males on adjacent leaves. This is especially so if, as Whittier et al. (1992) report, males can be somewhat clustered within a single tree canopy at certain times of day. Although the existence and generality of large-scale leks, like their small-scale counterparts, require further quantitative confirmation, present evidence suggests the existence of a distinct pattern of aggregation that must be investigated if we are to achieve a fuller understanding of medfly sexual behavior.

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At present, therefore, we can recognize two distinct spatial scales of medfly aggregation. Our aim in this paper is to investigate the evolutionary causes of both, using existing theoretical models and emerging empirical evidence. We first enumerate the candidate models, then present the relevant evidence from previous and ongoing medfly research. In light of this, we identify critical gaps in our understanding of medfly lek evolution and suggest some practical steps that can be undertaken to fill them. We conclude with the prediction that pursuing the path toward such an understanding may bring many insights of benefit to programs aimed at managing medfly populations.

Candidate Models for Lek Evolution

The main hypotheses that have been put forward to explain lek evolution (see Hoglund & Alatalo 1995) are: i) predation risk; ii) hotspots; iii) hotshots; iv) female preferences. Others, such as the "passive attraction", "information-sharing" and "black-hole" models, are either not applicable to the biology of medflies, or are otherwise of dubious importance, and will not be considered here.

Hotspots. If resources used by females are patchily distributed, or female home-ranges overlap, then by displaying at certain sites (hotspots) in the habitat through which females are constrained to pass when traveling, males may obtain an increased probability of female visitation.

Hotshots. If males differ in quality and certain males are highly attractive to females (hotshots), lower quality males may increase their mating probability by clustering around the hotshots.

Female Preferences. Females may exhibit preferences for mating in male aggregations due to benefits from: a) predator deflection; b) opportunity to compare males; c) increased average quality of males. Alternatively, such a preference could evolve as an arbitrary Fisherian trait (Andersson 1994).

Predation Risk. If males incur a risk of predation due to sexual display, and the *per capita* risk decreases with increasing group size, then selection will favor aggregations.

It should be emphasized that although each of these models generates distinct empirical predictions, they are not mutually exclusive possibilities for the evolution of lekking, and any combination of mechanisms could be operating in a given system. Indeed, some recent attempts at modeling lek evolution have recognized the value of combining elements of several of these models. Below we summarize the main theoretical features of such models and discuss how they can be used to understand lek evolution. As there are no formal mathematical models of the influence of predation on lek evolution, we will concentrate on the hotspot, hotshot and female preference hypotheses.

Before doing so, it is necessary to introduce a critical concept in the theory surrounding lek evolution, *viz*., the mating skew. This parameter can be calculated in many different ways (Kokko & Lindstrom 1997, Kokko et al. 1998), but essentially measures the degree to which matings are non-randomly distributed among males in a lek. The interest in mating skew stems from the common empirical observation that matings in leks are monopolized by one or a few high-ranking males. Given that such differences exist, theoreticians have attempted to explain how leks could evolve, in spite of the fact that low-ranking males seemingly have so little to gain by joining.

Hotspots and Hotshots

Widemo & Owens (1995) proposed that the answer to this question lies in increased levels of aggression and disturbance on the lek as group size increases, and a lesser ability of the high-ranking males to monopolize matings. This lowers the mating skew, and leads to the prediction that low-ranking males will have larger optimal lek sizes than high-ranking males. Thus leks represent the interests of low-ranking rather than high-ranking males, the latter being trapped into staying in the lek due to constraints imposed by habitat limitation or the hotspot effect. Data from the ruff, *Philomachus pugnax*, in which low-ranking males actively increase the lek size by soliciting other males to join, support this conclusion.

However, Hernandez et al. (1999) recently demonstrated that the situation is more complicated than this model suggests. Further to the interaction between lek size and mating skew, it is essential to know how relative competitive differences (RCDs) change as lek size increases. It is not automatic that competitive differences among males will decrease as more males join the lek. It is conceivable that even if the mating skew decreases with increasing lek size as expected, RCDs could actually *increase*, so that the increasing lek size favors the interests of *high*-ranking males rather than low-ranking ones. The analysis of Widemo & Owens therefore represents a special case, which may well be applicable to the ruff, but is unlikely to be general.

Both of these models simultaneously incorporate aspects of the hotspot and hotshot hypotheses. First, they assume that males are constrained in the locations they can choose for display (the essence of the hotspot hypothesis), and hence they do not abandon the lek even if it grows in size beyond what is optimal for them as individuals. Second, they assume that large differences in male quality exist, and, at least for some combinations of RCD, mating skew and lek size, that the lower-ranking males are benefiting from the attractiveness of the high-ranking males (the central idea of the hotshot hypothesis).

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Female Preferences

The evolution of leks by female preferences has been modeled separately, using a game-theoretic approach (Kokko 1997). Here females assess males by comparison both within and between leks, subject to two constraints: within leks, they are not able to assess the best male perfectly; and among leks, travel costs mean they are unable to visit and assess all available aggregations. From the female side, the optimal strategy can be deduced with a straightforward mathematical calculation: when choosing among leks, they should prefer the larger ones, because the average male quality is higher; and within leks, they should choose the male they assess as being top-ranking, no matter what their probability of making an error. However, from the male side, the same problem remains, *viz*. why should low-ranking males join? One obvious answer is the imperfection of female choice, which gives low-ranking males at least a small chance of being chosen by mistake. But female travel costs are also important; if costs are low enough so that females can sample a large number of leks (recall they will prefer the larger ones), then it pays males to join large leks, which will receive the most female visits. Conversely, if travel costs are high, optimal aggregation sizes will remain low and lek evolution is constrained.

Empirical Evidence Concerning Lek Evolution in Medflies

Any narrative for lek evolution in medflies must begin by accounting for why mating does not occur on the host fruit, as it does in many temperate fruit flies. The accepted explanation, propounded by Prokopy (1980) and Burk (1981), invokes several ecological factors (multivoltinism, polyphagy and high predation risk) that in combination make it impossible or at least unprofitable for males to monopolize resources important to females. The enormous host range and multivoltine life cycle of *C. capitata* certainly qualify it to fit this model. Furthermore, the reduction of oviposition to a short time-window in the afternoon, added to the high levels of predation on females observed on fruit (Papaj et al. 1989, Hendrichs et al. 1991, Hendrichs et al. 1994, Hendrichs & Hendrichs 1998), offer strong support for the role of predation. The secondary mating tactic seen in *C. capitata*, of males guarding fruit and attempting to copulate females without courtship, can be seen as an evolutionary relic in a mating system initially resource-based but driven away from resources over evolutionary time by the combined effects of the above-mentioned ecological pressures. Alternatively, it could be an alternative mating strategy used by low-ranking males.

Large-Scale Leks

Having accounted for the evolutionary shift in medflies away from mating on host fruit, it remains to address the question of why sexually active males might aggregate at the first spatial level, that of the tree, or group of trees, within the habitat. The first thing to recognize is that although mating away from the vulnerability of host fruit would have reduced predation risk, it by no means would have eliminated it. Predators such as yellowjacket wasps, *Vespula germanica* (F.) (Hymenoptera: Vespidae), which use a combination of visual and olfactory cues to hunt amongst tree foliage for calling males and resting or copulating flies of both sexes (Hendrichs et al. 1994, Hendrichs & Hendrichs 1998), would continue to pose a substantial risk.

Predation. There are two evolutionary routes by which predation could lead to male aggregation in certain trees. The first is by providing a selective pressure for males to display from the most protected sites available in the habitat, *viz.* trees with a dense canopy structure that would impede the movement of larger predators and provide a variety of refuges and escape routes. This view has been supported by observations made by Hendrichs & Hendrichs (1990) in Egypt, and an analysis by Shelly & Whittier (1995) of lek distribution in Hawaii, showing that leks were clustered in the trees of largest volume, which also seemed (qualitatively) to possess the greatest horizontal foliage density. Nevertheless, it remains for this hypothesis to be explicitly tested. The second route is by males gaining a decreased per-capita risk of mortality by displaying with other males. This can occur either because the per-capita attractiveness to a predator of an aggregation decreases with aggregation size or due to the benefits of group vigilance. As yet there are no data addressing per-capita predator attraction at the large-scale lek level. However, we can deduce that the benefits of vigilance are unlikely to apply on a scale as large as an entire tree. A single wasp attack in one part of the canopy would only alert males in the immediate vicinity and not elsewhere in the tree, unless attacked males produce a specifically designed signal, e.g. an alarm pheromone.

Hotspot. The hotspot hypothesis is also an appealing explanation for the formation of large-scale leks. By choosing to display in fruiting host trees, males could maximize their chances of encountering females, which must visit these sites for feeding and oviposition. Some evidence from the field supports the hotspot interpretation, by showing that male sexual activity is indeed concentrated on fruiting host trees. Hendrichs & Hendrichs (1990, unpublished data cited therein) found most male sexual activity occurred on fruiting citrus. Hendrichs et al. (1991) found that most leks and matings occurred in foliage of the pri-

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mary host (orange), where females went to oviposit after visiting leks. Most recently, Kaspi & Yuval (1999b) have produced several lines of experimental support from a field-cage study. They showed that wild males preferred to display on trees containing real fruit and preferred trees containing a combination of visual and olfactory fruit stimuli over trees with either stimulus alone or no host stimulus. However, although these studies are consistent with the hotspot hypothesis, they are also consistent with the hypothesis that males choose such trees because of their accessibility to food sources. As lekking is energetically costly (Warburg & Yuval 1997, Yuval et al. 1998) this may be an important consideration in male lek site selection.

Evidence inconsistent with the hotspot hypothesis has also been obtained. In a field study in Hawaii, Shelly & Whittier (1995) found lek sites did not correspond with female oviposition or feeding sites, as males settled preferentially on certain persimmon trees that did not have ripe fruit at the time. Similar observations have been made in Israel, where in a mixed orchard, 2 particular pitanga trees have been found to harbor a disproportionate number of calling males. Although the pitanga trees were fruiting at the time, there were also an abundance of suitable citrus, guava (and other pitanga) trees immediately adjacent that harbored few or no males (R. K. & B. Y., unpublished data). These observations strongly suggest that if a hotspot effect is involved, it is by no means the only factor driving male aggregation into large-scale leks.

Many authors have noted the possibility that in addition to offering protection from predation, trees with a dense canopy structure could offer a more suitable microclimate for male calling activity (Arita & Kaneshiro 1985, 1989, Hendrichs & Hendrichs 1990, Whittier et al. 1992, Shelly & Whittier 1995). Although there are as yet no quantitative data on microclimate variations *among* trees of different size and canopy structure, Kaspi & Yuval (1999b) have recently shown that *within* trees, male positioning throughout the day tracks changes in temperature, relative humidity, light intensity and the azimuth of the sun. In particular, males exhibited a marked preference for leaves with microclimate characteristics closely matching those in full shade. Should males actively choose among trees according to such preferences (or be beholden to the decisions of females concerning where to mate), this would provide a complementary explanation to predation avoidance for male clustering in certain trees that have unusually dense canopies.

Hotshot and Female Preferences. With respect to the hotshot and female preference models, we argue that these mechanisms are not viable explanations for clustering at the whole-tree level or at best constitute only weak evolutionary forces. If low-quality males are to gain any benefit from settling near high-quality males, they must be in sufficiently close proximity that visiting females will detect them and possibly mistake them for the high-quality male to which they were initially attracted. Obviously the best position to achieve this is as close to the high-quality male as possible, so the evolutionary effect of the hotshot mechanism would be the formation of groups of males that are small and tightly clustered at a scale well below the level of an entire tree. Similarly, if female preferences for large leks are driving male aggregation, males that settle adjacent to other male(s) will be favored over males that take up position in the same tree, but in a relatively distant part of the canopy. For these reasons we feel the hotshot and female preference hypotheses are more applicable to small-scale male aggregations and delay discussion of them until the following section.

Summary. In overview, a combination of ecological factors appear to have acted to drive medfly mating activity firstly away from host fruit and secondly to become concentrated in certain trees within the habitat. Evidence suggests the action of a composite predation and hotspot effect, modulated by microclimate preferences in habitat selection. There are compelling reasons why hotshot and female preference effects would not be potent evolutionary forces at this spatial level. However, this may not be the case when considering multiple spatially distinct leks within the canopies of particular trees, as we discuss in the next section.

Small-Scale Leks

Predation. As noted above, the need to avoid predation may have driven the mating system away from host fruit, but it is an unlikely explanation for the clustering of males into large-scale leks. However, at the level of small-scale leks, it becomes plausible by the following possible mechanisms. If the number of predator attacks does not increase in proportion to group size, animals in the center of an aggregation are better protected than those on the periphery (Hamilton 1971), and/or efficiency in predator detection is increased by sharing the task of vigilance with conspecifics (Pulliam 1973). If any of these operate, then predation pressure can act as a driving force in lek evolution.

Hendrichs & Hendrichs (1994, 1998) have shown that medfly males lekking at a site in Chios, *Greece* are at substantial risk from yellowjacket wasp attacks, especially when calling, an activity that appears to significantly reduce their vigilance. Most recently they have found strong support for the evolutionary impact of predation by showing that the per-capita number of wasp attacks decreases with lek size, making larger ag-

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gregations safer for calling males (M. & J. Hendrichs, Insect Pest Control Section, IAEA, Vienna, unpublished data). As the experiment was conducted with artificial leks of caged males, there are no data on the number of *successful* attacks as a function of group size. However, accounting for the benefits of group vigilance, we can infer males in large leks would be even better protected than these data imply. It is also relevant to consider the effect of disruption of mate attraction activities by predator attacks. Each time a predator attacks, all males in the lek are forced to disperse and resume searching for a suitable site, temporarily excluding them from mate-attraction activities. The lower per-capita level of predation in larger leks would reduce interruptions and increase the amount of time available for mate attraction. Provided the per-capita rate of female visitation remained comparable with that seen in smaller aggregations (see below), calling in larger groups would result in fitness benefits.

Hotspot. The prospects for hotspot effects to be operating at this spatial level seem remote. A common criticism of the hotspot model is that areas of high female density (driven by resource patchiness) might not be localized enough to account for the tightness of male clustering (Westcott 1994). This would certainly seem to be the case with small-scale medfly leks.

Hotshot. The hotshot hypothesis also deserves attention. It assumes that variations in male quality occur, such that high quality males are able to monopolize matings and less attractive males then benefit by clustering around them. Evidence certainly points to the necessary variation in male quality existing, as laboratory studies have repeatedly found a non-random distribution of matings among males. Although this has not yet been expressed in terms of mating skew (sensu Kokko & Lindstrom 1997), or been verified in a natural setting, it is nevertheless suggestive of variations in male quality that females are able to detect and use as a basis for discrimination during mate choice. However, for the hotshot mechanism to work in medflies, the variations in quality must be apparent to both females and males during long-range mate attraction, i.e. pheromone calling. This is because the majority of small-scale medfly leks disperse without ever receiving a female visit (S.A.F., unpublished data), making it impossible for males to identify hotshots on the basis of the number of matings they achieve, as can occur in other species (see Beehler & Foster 1988). Hotshots could conceivably be identified by the quality of a given male's pheromone, as an indicator of the likelihood that he will attract a female. This could potentially be achieved by first using the presence of pheromone to locate leks and then the relative proportions of certain components in the pheromone blend to discriminate among males of different quality.

However, current evidence on the question of whether males are attracted to the pheromone emissions of other males at all, let alone whether they discriminate among males of different quality, is inconclusive. It had previously been widely assumed that males are attracted to leks by the male pheromone and that the powerful attraction of males to chemicals such as trimedlure was due to its mimicking key components of the male pheromone (Burk & Calkins 1983, Sivinski & Calkins 1986). However, chemical analyses have since refuted this hypothesis (Millar 1995, cited in Eberhard, 1999), leaving the mechanism by which male clustering occurs an open question. Evidence against male attraction to pheromones has come recently from Shelly (UH, Hawaii, unpublished data), who found very low attraction of released males to artificial leks formed in the field using caged calling males. However, positive evidence has also been obtained by Kaspi & Yuval (1999a), who showed that when selecting a calling site in a field cage, males were more likely to settle on a tree from which caged males were emitting pheromone, than on a control tree containing only caged dead males. However, we must take into account differences in methodology. The artificial leks formed by Kaspi & Yuval (1999a) contained 30 males and they released 100 males into a confined space, whereas Shelly (UH, Hawaii, unpublished data) used only 12 males in the leks and released 300 males into the wild. The former experiment thus tipped the balance in favor of detecting an effect, however weak. Nevertheless, the result raises the possibility that males do indeed use the male pheromone as a cue in lek site selection, an issue worthy of further study.

It remains to be directly studied whether males and females are able to distinguish among calling males of different quality using variation in pheromone blends. However, while two studies have indicated that male mating success depends on the quantity of pheromone produced (Whittier et al. 1994, Shelly, UH, Hawaii, unpublished data), there is as yet no evidence favoring an effect of pheromone quality. Shelly found that males with high previous mating success attracted more females than males with low success, but apparently only because they spent more time calling. It also seems clear that the difference in mating success frequently found between sterile and wild flies is not due to females discriminating against them on the basis of pheromone composition; females arrive at leks of both types of males with equal frequency and appear to discriminate only during close-range courtship (Calkins et al. 1994, Shelly et al. 1994, Shelly & Whittier 1996, Shelly 1999. Nevertheless, this could mean simply that the sterilization and/or mass-rearing process affects courtship rather than pheromone quality. The hypothesis that there exist variations in pheromone quality among males remains worthy of investigation.

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A prediction from the hotshot hypothesis would be the presence of "satellite" males, who join leks but engage in little or no calling, but nevertheless attempt to court females that are attracted to the lek by the pheromone emissions of others. Observations by several authors suggest that this may be occurring. Shelly et al. (1994) observed non-calling males in leks in the field. In our observations in the field in Israel, a substantial proportion of males in scan samples of leks were not calling. Further, in a field-cage study (S. A. F. & B. Y., unpublished data), non-calling males in a lek sometimes switched immediately to directed wing-fanning when a female flew past. This may have been simple opportunism but could also represent an evolved strategy. The occurrence of variation in calling activity among males with a uniform rearing history and environment (Shelly, UH, Hawaii, unpublished data) also hints that investigating the possibility of a genetic influence on individual calling strategies may be worthwhile.

Female Preferences. To demonstrate that female preferences are a significant factor in lek evolution, it must be shown that more females arrive per male as lek size increases, causing an increase in per capita male mating success. Three studies have examined this question. Shelly (UH, Hawaii, unpublished data) found the increase in female visitation rate to artificial leks in the field remained in constant proportion to the number of calling males, whether the males had a successful or unsuccessful mating record in the laboratory. Similarly, Kaspi & Yuval (unpublished data) found that the per-capita rate of female visits to artificial leks in a field cage remained constant over the range of lek sizes likely to be encountered in nature (2-8). As such a response can be accounted for by passive attraction of females to a larger olfactory signal, we may be tempted to conclude that there is no evidence for a large lek preference in female medflies. However, the third study, by M. & J. Hendrichs (IPCS, IAEA, Vienna, unpublished data), adds a new twist by simultaneously considering the effect of predation. They found that when wasp predators were allowed to attack leks, the females preferred the smallest of four lek sizes offered. However, when predation was removed, not only did females prefer larger leks, they preferred them out of proportion to the number of males, so that the per-capita rate of female arrival did indeed increase with lek size. This suggests that females in fact do actively prefer large leks, but are constrained in their preference due to the risk of predation. Future studies of female preferences must take into account the possible interaction of this factor with predation.

Summary

To summarize, the evolutionary causes of small-scale leks within trees appear to be distinct from those favoring aggregation into large-scale leks. Hotspot effects, apparently one of the key factors driving large-scale lek formation, is of little relevance for small-scale lek evolution, whereas protection from predation, hotshot effects and female preferences could all be important. Although plausible, no direct empirical evidence is yet available to support the hotspot hypothesis. The evidence is perhaps strongest for the effect of predation acting to increase aggregation size. Evidence also exists for female preference for large aggregations, although this appears to be modulated by predation risk, pointing to an intriguing conflict of interest between the sexes with respect to lek size.

Future Experimental Priorities and Practical Implications

Despite the passage of two decades since the medfly was identified as a lek-mating organism, our understanding of the evolutionary forces driving lek formation in this species remains very rudimentary. It seems this is not due to a lack of research effort into medfly mating behavior but rather because such research has rarely been framed with evolutionary issues specifically in mind or been used to explicitly test evolutionary hypotheses. Understandably, the emphasis has been on experiments designed to bring immediate improvements in the quality of mass-reared males for SIT or to understand the proximate mechanisms determining successful courtships. However, basic and applied research questions are never mutually exclusive, and we believe that attempting to place medfly mating behavior in an explicit evolutionary setting can yield practical benefits, just as practically-oriented research has already begun to benefit our evolutionary understanding, by providing critical empirical data for testing theoretical models. Most importantly, an evolutionary framework can facilitate ongoing critical evaluation of empirical studies, aiding the resolution of experimental ambiguities and contradictions, and speeding the conversion of an otherwise haphazard accumulation of results into an orderly, coherent body of knowledge.

Although the studies cited above have provided a useful start towards understanding medfly lek evolution, many questions and uncertainties remain. Below we identify lines of research that appear to hold promise for teasing apart the influences of various ecological factors and suggest some experiments critical to resolving outstanding issues.

Firstly, most of the tentative conclusions concerning lek evolution drawn above rely on evidence from only one or a few studies. Inevitable variations among studies in the origin, rearing and handling of insects, experimental methodology and analysis make it likely that even the most

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carefully designed and executed studies can produce ambiguous or inconclusive results. In medflies, the potential for discrepancies between studies is perhaps compounded by the fact that this insect has relatively recently colonized a variety of new habitats worldwide, and different populations have possibly undergone (or are undergoing) adaptation to local conditions. It therefore may be necessary to accumulate numerous tests of the same hypothesis under differing ecological conditions before robust conclusions emerge. Ideally, consensus on the evolutionary influence of an ecological factor should be quantitatively assessed after taking multiple similar studies into account (Arnqvist & Wooster 1995). Far from being a redundant exercise, repeating experiments performed by other researchers on different medfly populations may highlight critical ecological factors that influence mating behavior and thus prove essential to the task of understanding its evolution.

At the large-scale lek level, it would be useful to repeat studies like that of Shelly & Whittier (1995), which applied a multivariate analysis to confirm which factors determine the favored sites for male display within the habitat. Ideally, such studies would be longitudinal in nature and would track the location of calling males in relation to seasonal patterns of host availability within seasons and fluctuations in these patterns among seasons. Combined data from different medfly populations, climates, and habitats would provide a rich database with which to identify universal factors determining large-scale lek locations. Should the pattern of males being clumped into large-scale leks be borne out by such studies the next task would be to confirm that this is due to a hotspot effect rather than males simply choosing to lek near nutritional resources. This would require tracking of female distributions (feeding sites, oviposition sites and movements among them) and the demonstration of a correlation between female distribution and the male calling sites.

Concerning specific hypotheses for lek evolution, the effect of predation is one area that has received intense empirical attention recently (Hendrichs et al. 1994, Hendrichs & Hendrichs 1998) and should be pursued further. To clarify whether the formation of large-scale leks in trees with large volumes and dense canopies is in part a response to predation, it would be desirable to measure predation rates in trees of different size and canopy structure. At the level of small-scale leks, the information already obtained on attack rates at different lek sizes could be supplemented by data on the rate of *successful* attacks at different lek sizes, which would indicate whether individuals displaying in larger groups benefit from increased vigilance. As this would entail measurement of predation rates on naturally displaying males, the data would be difficult to obtain but would be well worthwhile as they would clinch the argument for the role of predation in driving male aggregation.

Further investigations of the hotshot hypothesis should focus on testing whether the proximate mechanism by which males aggregate is indeed by cueing on the pheromone emissions of other males, and if so, which are the active components in the blend. A positive result would add credibility to the hypothesis that low-quality males are attracted to leks occupied by hotshot males that can be distinguished by the quality of their pheromone. This hypothesis could then be investigated in an experiment similar to that performed by Shelly (UH, Hawaii, unpublished data), who tested attraction of males and females to calling males of low and high mating ability, with the difference that the calling males should be classified with respect to their ability to attract conspecifics on the basis of their pheromone alone. Classifying them by their mating success leaves open the possibility that the high-mating males were successful not due to quality of their pheromone, but due to the efficacy of their courtship, which is of no evolutionary consequence for lek formation. If both females and males concurred in their choice of males, the pheromone blends of attractive and unattractive males could then be compared and the physiological basis for the hotshot effect identified.

One of the most interesting research directions to pursue is the putative interaction between predation and female preferences for large leks in determining optimal lek size in small-scale leks. While large leks appear to increase male survival by decreasing per-capita attack rate, this may not be true for females, at least judging by the behavior observed by J. & M. Hendrichs (IPCS, IAEA, Vienna, unpublished data). This may be explained by the fact that female vigilance toward predators is at its lowest when receiving courtship, so females may be particularly sensitive to the risk of predation when visiting a lek. This not only brings female interests into conflict with that of males with respect to predation, but also sets up a counterbalance to any preference females might have for mating in larger leks due to the opportunity to compare males. Thus it could be an important selective force acting to set an upper boundary to lek sizes. Further experiments measuring female arrival rates while manipulating lek sizes and predator attack rates would be extremely valuable.

Although the research directions outlined above are primarily directed towards answering a theoretical question in behavioral ecology, there also exist potential avenues whereby such research could make a positive contribution to improving the efficacy of medfly control programs. Tests of the hotspot hypothesis will provide us with detailed knowledge about preferred lek locations in various habitats and climates, enabling

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more judicious selection of sites for monitoring traps and thus improving the ability to detect and respond to infestations. Successful pursuit of the hotshot hypothesis could provide the key to understanding variations in male attractiveness, and be a step forward in improving the quality and mating competitiveness of mass-produced males *vis a vis* their wild counterparts. If specific components of the male pheromone could be identified as responsible for a hotshot effect, they could also be used to manufacture more effective chemical baits and lures. It is our hope that the future will see more interaction between applied empirical research on medfly mating behavior and theoretical modeling of lek evolution, to mutual profit.

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