Review

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All About Lekking: A Comprehensive Examination of Lekking and the Lek Mating System in the Black Soldier Fly, *Hermetia illucens* (Diptera: Stratiomyidae)

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Short Summary: Using Bradbury's expanded criteria for lekking species, the basis of the lek mating system is assessed in both free-living and captive black soldier fly populations.

Abstract: The black soldier fly, *Hermetia illucens* (Diptera: Stratiomyidae), is an economically important fly that is now mass-reared globally to produce livestock protein and frass that can serve as sustainable alternatives to conventional fishmeal and synthetic fertilizer. The species' mating system has repeatedly been described as lekking, though there have been doubts raised as to the appropriateness of this terminology, especially for captive populations. Hence, the purpose of this review is to formally evaluate the mating system of the black soldier fly using Bradbury's expanded criteria for lekking species to better understand what indeed the natural mating system and behavior of the black soldier fly is. From an applied perspective, accurately describing the mating system is important for understanding whether the industrial breeding system is inducing (unintentional) phenotypic changes. However, it is also important to point out that because the black soldier fly are not being mass-reared for release into the wild, as would be the case for those reared for Sterile Insect Technique (SIT), unless a particular mating system can be linked to an increase in fertile egg production, then there is a very limited reason why that mating system should be preserved in favor of the more productive one, other than perhaps the discovery of correlated genetic erosion or through the desire to promote insect-welfare, which places an emphasis on emulating a natural environment, maintaining natural behaviors, and reducing stress of confined animals.

Keywords: reproduction; behavior; plasticity

Lekking

The lek is a mating system and as first described in1867 in grouses, a group of nesting ground birds Lloyd 1867); after which it attracted the attention of Darwin (1871), who used observations of lekking in birds to develop his ideas of sexual selection (Höglund 1988). Despite this, criteria for lekking were not formally defined until the 1970's (Wiley 1974, Bradbury 1977). Lekking is generally typified by a highly skewed operational sex ratio and the inability of males to economically defend a resource site (food, water, shelter, nest) where females aggregate (Emlen & Oring 1977). Additionally, because males are emancipated from parental care, they are then free to establish themselves at a lekking site where they advertise and jostle for position within a dominance hierarchy. Females visit the lek[1] strictly to mate and select dominant males on the basis of their courtship displays (Höglund and Alatalo 1995). Decreased male involvement also preadapts males to respond to slight environmental changes in potential for polygamy (as in, when there are deviations in instantaneous

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[1] Lek – used to describe both the physical site where lekking occurs, and the aggregation of males at that location

operational sex ratio), allowing them to be opportunistically or facultatively polygamous (Emlen & Oring 1977).

Tomberlin & Sheppard (2001) reported on a naturalized population in which females aggregated in the substrate beneath a CAFO at 91.3% operational sex ratio, OSR, (n = 123) and males aggregated in kudzu nearby at 91.9% OSR (n = 109), which agrees with the aforestated definition, but since then, there have been no additional published reports investigating lekking (per say) in the species (but see: Lemke et al. 2023, in which a conceptual model was proposed). Still, research has continued to ascribe this term (and mating system) to a largely captive-living fly, which has experienced a drastic shift in not only its living conditions via domestication and industrialization (Price 2002, Sheppard et al. 2002), but also a shift in the selective pressures that give rise and perpetuate the lek mating system in free-living species, raising the question of whether or not the black soldier fly continues to lek in captivity. Certainly, in other species such as the Queensland fruit fly (Diptera: Tephritidae) it is the case that lekking quickly disappears in captive populations (Personal communication, O. Edwards). Complicating the matter, the term 'lek' has not always been used appropriately (Hoffmann & Blows 1992, Shelly & Whittier 1997)[2][3], and the lek mating system can also be plastic (Emlen & Oring 1977), and exists on a continuum with other mating systems.

This is because the ability of males to monopolize matings (in this case with the females that periodically enter and leave the lek site) is primarily affected by how spatiotemporal patterns of resource dispersion trade off with predation pressure, meaning if resources are dispersed, animals must spend more energy traveling between them. But if those resources are too dispersed, then the environment itself may preclude resource/mate monopolization, and thus any form of mate monopolization from evolving as a viable reproductive strategy (Brown 1964). Yet another layer to consider is that even if resource patches are clumped, there may be physiological limitations that prevent the organism from utilizing them effectively (Emlen & Oring 1977). In the case of black soldier flies, an important consideration is how polyphagy enables flies to exploit multiple types of resources, which might make them more patchy throughout the environment, and indeed polyphagy is typically associated with lekking, although some species of monophagic Tephtridis still lek in the wild (Dodson 1986).

Once evolved, the lek system tends to perpetuate itself through the demonstrated preferential success of the dominant males within a lek, as they have the optimal balance of genetic factors to influence norms of the population (Brown 1964). This then gives rise to the paradoxes in which (a) non-dominant males help maintain aggregations despite not necessarily gaining any fitness benefits from doing so, and (b) genetic diversity across the population is somehow maintained even though mating is restricted to a few individuals (Borgia 1979, Rowe and Houle 1996). Despite continued studies throughout the years (e,g,, Taylor and Williams 1982, Rowe and Houle 1996, Dugand et al. 2019) this paradox has yet to be fully resolved.

The occurrence of lekking is now recognized across the Animalia (though it is not ubiquitous in its occurrence), and has been described in crustaceans (Croll & McClintock 2000), insects (Alcock 1987), fish (Windle & Rose 2007), anurans (Kindermann & Hero 2016), reptiles (Wikelski et al. 1996), birds (Höglund and Lundberg 1987), bats (Bradbury 1977), ungulates (Isvaran 2021), pinnipeds (Boness et al. 2006), and humans (Lycett & Dunbar 2000).

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[2] *Protopiophila litigata* Bonduriansky 1995 (Diptera: Piophilidae) are listed as a lekking species by Shelley at Whittier (1997). While (Bonduriansky & Brooks 1999) describe these flies as aggregating and establishing territories on ungulate antlers; their behavior does not strictly fit the definition for lekking, because the females also oviposit either in the meat of the corpse or the cracks in the antlers, making the mating system more closely resemble resource-defense polygyny.

[3] Hoffmann & Blows (1992) conducted a study whose results suggest that *Drosophila mycetophaga* are not true lekking species because females were found to oviposit in the exudate of bracket fungi, where males also aggregate.

The criteria for lekking species established by (Bradbury 1977) have since widely been used and are paraphrased as follows:

(1) the complete absence of male parental care; males contribute nothing but gametes to the female
(2) the existence of a mating arena where males establish territories, within which they display to prospective mates[4]
(3) male territories that contain no resources vital to females and are used only for mating
(4) the opportunity for females to freely select mates

Evolutionarily, this also implies that in addition to no male parental care prerequisites for lekking also include the following (Höglund & Alatalo 1995):

(i) internal fertilization by females, due to the need to visit lek sites without ovipositing there
(ii) high mobility which reduces the cost of searching by females for mates and predation risk against both sexes
(iii) the lack of ability of males to monopolize available resources
(iv) some degree of discriminatory behavior of females to prevent random mating/panmixia

In considering insect mating systems, Bradbury's original criteria would later be revised such that each (except parental care) exists along an axis, akin to G. E. Hutchinson's (1957) concept of *niche* which he postulated is formed by an n-dimensional hypervolume. Like that hypervolume, any particular insect's mating system can lie within a multidimensional space formed from the interaction of separate axis, which may individually adhere more strictly or loosely to the criteria for lekking. This conceptualization thus gives rise to the term "lek-like" to describe those species which do not completely adhere to Bradbury's classical criteria but do so more closely than any other given mating system. Envisioning a lek as a topology led to some mating systems being described as, for example, exploded leks or resource-based leks in which the size of the territories substantially expands or there is a loose association with some resource, which would otherwise violate a strict definition. This of course arises from the need to fit discrepancies found in real world data to an idealized definition, a process that often becomes imprecise and idiosyncratic (Shelly & Whittier 1997). Unfortunately, in many cases taking on a more fluid definition has led many to ascribe the term lek to mating systems that deviate drastically from what it should describe, simply on the basis of mating swarms being present. Still, rather than treat this as merely an issue of semantics or categorization, what is most pertinent is using the definition to enhance understanding the (applied) behavioral ecology of the species (Alcock 1987). And so, it is not just as important to ask whether black soldier flies exhibit lekking, but what ecological basis leads to the evolution of their mating system, as well as similar flies, and whether an artificial environment significantly disrupts these forces. Therefore, for our purposes, it is best to first explore whether black soldier flies have the preadpations for lekking species, before applying Bradbury's criteria.

Preadaptations

Lack of parental care. Although it has been suggested that black soldier flies may give nuptial gifts to extend female longevity (Harjoko et al. 2023), there is no direct evidence for this, and actually the hypothesis that nuptial gifts serve as a paternal investment has been questioned due to a lack of correlation between male investment and improved fertility across empirical studies (Vahed 1998). Other insects can exhibit biparental division of labor or offspring provisioning (Gilbert & Manica 2010); but in black soldier flies, currently it appears male do not provide females anything other than gametes. Even in the case that future research should validate the presence of nuptial gifts given by male black soldier flies to females, this should not necessarily conflict with lekking since providing a nuptial gift that originates from resources collected as a larvae would not preclude adult males from spending the entirety of their time engaged at lekking sites, whereas the direct care of offspring would.

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[4] Alcock (1987) separates this criterion into two separate criteria.

Internal fertilization. Like most insects, black soldier flies have internal fertilization. After copulation, male sperm is temporarily stored in spermethecae (Munsch-Masset et al. 2023) prior to fertilizing eggs (Malawey et al. 2020), which would allow females to visit a lek site, mate, return to the oviposition site, and then lay fertilized eggs (Lemke et al. 2023).

Mobility. While captive black soldier flies are somewhat lethargic, they can still have a reported 2.55 km/h minimum flight speed (derived from Giunti et al. 2018), which is ~35-times their body length per second. Naturalized and native populations are even more mobile, and can travel great distances (Lemke et al. 2023, Lemke 2024b); though a conflicting review states their range as being restricted to <100 m (Meneguz et al. 2023). To date, all accounts of black soldier fly mating give no mention of sex pheromones (Mayer 2019), and cuticular hydrocarbons appear to be sexually monomorphic (Lemke et al. 2023), similar to the Screwworm fly *Cochliomyia hominivorox* (Diptera: Calliphoridae) (Pomonis 1989). In other species sex pheromones can be responsible for lek formation, such that artificial attractants (viz. Trimedlure for Tephritidae) can be used to induce lek formation (Shelly et al. 1993). For black soldier flies the recognition of olfactory cues by females must be important for their dispersal away from leks, and is potentially explained by sexual dimorphism and allometry in various structures of the antenna, for which females generally have more the more developed organs (Birrell 2018). This is contrasted with the more developed neural ganglia for males (Barrett et al. 2022), which are postulated to be important for mate recognition during nuptial flights (Lemke et al. 2023), and potentially the recognition of wing interference patterns (Butterworth et al. 2021, Meneguz et al. 2023).

Inability to defend resource. Because of the costs/demands of flight (Lemke 2024a), and so much of the energy they utilize as adults is acquired during their larval life stage rendering adults effectively energy-limited (Harjoko et al. 2023), there are likely additional limitations that prevent black soldier flies from attaining the energy that would be necessary to monopolize all the females in a given area. The hypothetical constant draw on a male's energy reserves to maintain a territory would require intense foraging to replenish any spent reserves and draw males away from where females are emerging. Females also have larger, more powerful wings and flight muscles (Birrell 2018), making prolonged attempts to monopolize even small numbers of females fairly costly. Such limitations could be compounded if either the resources females utilize, or the resources adult males use to attain energy were patchy (thus increasing the total space that needed to be patrolled, which could have the knock-on effect of increased predation pressure). To put it another way, while some biological traits are plastic, such as the size of larvae (West-Eberhard 1989), organisms cannot be infinitely plastic, because of life-history trade-offs and selective pressures (DeWitt et al. 1998). While it is difficult to *prove* that black soldier flies cannot adequately defend resources (females, oviposition site, water, food), game theory provides that a short-lived and energy-limited species cannot play infinite games.

Female choice. Sexual choice by females of lekking species exists at two levels, the first being a selection between multiple leks, and the second being choice among males within the lek (See § on hotspots and hotshots). While it was previously through that female insects could not exert choice (and thus were rendered a special case sometimes referred to as occupying swarms (Shelly & Whittier 1997))[5]; however, since the 1980s, these axiomatic views have increasingly been shown to be false

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[5] In their review of lekking behavior in insects, Shelly & Whittier (1997) make an additional division between aerial maters and substrate-based maters and propose that aerial maters, generally lack territoriality and courtship, which are necessary for lekking. They state that roughly 80% of substrate-based swarms could be considered lekking, whereas only 44% of aerial swarms could be, however this dichotomy is unnecessarily reductionist in its approach and obscures patterns that become evident at a phylogenetic scale, particularly for species that do not fit easily into the two categories. For example, Yuval (2006) showed that across the Diptera, lekking is a transition between the aerial and substrate-based systems; and further states that reproductive success is universally correlated with foraging (Yuval *et al.* 1998).

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(Shuker & Simmons 2014), and motivated by politics of the era, which a historical treatment shows is rooted in scientific sexism dating back to Darwin (Richardson 2014) and the cultural motivations to restrict sexual liberties in women by ignoring the same in other animals. Since then, this increased understanding that females, and specifically female insects can express a wide range of choice can be viewed by reviewing successive editions of (Thornhill & Alcock 1983, 2013) and the revisions embraced by the lattermost. Research in lekking and hilltopping insects has shown that choice by females can range along 'grades' from: (I) being captured by males while passing through an area and having little-to-no ability to resist copulations, (II) actively selecting an area to mate with the dominant male there, but still being able to be intercepted by subordinate males; (III) selecting a male based on position within the territory, but not being able to be intercepted by another male; and (IV) direct inspection of all or many males within the lek prior to choosing which to copulate with (Alcock 1987). Because of this, often there is a spatial component to female mate choice and that the males which receive the most matings may for example be those that are centrally located within the lek or occupy the highest or lowest strata (See also § on hotspots and hotshots).

Returning to the discussion of lekking in the black solider fly, while empirical evidence demonstrating explicit female sexual choice in black soldier flies is still sparse, the research that does exist has suggested several precopulatory mechanisms by which females can exert choice. For instance, females may discern the quality of males through wing-interference patterns (Eichorn et al. 2017, Butterworth et al. 2021), duration of wing-buzzing (Giunti et al. 2018) which is correlated with size, and tapping or gentilic stridulation "songs" (Eberhard & Gelhaus 2009, Lemke et al. 2023). In addition to precopulatory choice, recent work has begun to elucidate the role that sexual conflict (i.e., sperm competition and cryptic female choice) can play (Manas et al. 2023) that arise from real or perceived competition (Jones & Tomberlin 2019, 2021). Furthermore, (Hoffmann 2021) showed that clutches can have multiple paternity, owing to fact that sperm from multiple donors can be stored within the spermathecae (Malawey et al. 2020, Munsch-Masset et al. 2023) and thus compete within the genital tract of the fly.

Wild

To date, the fieldwork conducted by Tomberlin and Sheppard (2001) provides the only account of either "a mating arena" or "male territories, free of female resources" in wild population. The most important information they provide is that the distance between the male aggregation site (Kudzu and morning glory lining the edge of a hardwood forest) and the oviposition site is ~100 meters (the edge of chicken houses) which are spatially disjunct by virtue of a pond. Together these partially satisfy the criteria for lekking species under the assumption that females are not traveling to the wood's edge to forage for resources that are explicitly required for reproduction. This aligns with knowledge of behavior in captive flies, considering in captivity soldier flies are capital breeders (Stephens et al. 2009) and, while adults benefit from feeding (Klüber et al. 2023), do not necessarily need to be supplemented with food or water for successful breeding (Lemke et al. 2023). The behavioral response Tomberlin and Sheppard (2001) describe of perching males to intruders also seems to be a territorial bout (Brown 1964), because "resting males return to the same perch" after fighting off males and copulate with visiting females.

Because one the main factor limiting the study of lekking in the wild is the infrequency of mating observations (Alcock 1987), instead an alternative view of lekking can be taken that is agnostic of the lekking site, which instead would only need to consider the complete absence of lekking behavior at any observed female resources. Undertaking this shift in perspective, then allows additional evidence to be considered. For instance, Tomberlin & Sheppard (2001) also report no chasing or mating observed within the layer house (where the oviposition site was), which likewise suggests that wild males cannot economically defend resources that females aggregate around and instead have evolved an alternative method for securing matings (i.e., lekking). Evolutionarily speaking, the benefits

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conferred by lekking at a site away from where young flies emerge are potentially the diversion of predators to an area away from where larval densities are highest, as well as the ability for slightly older males to mate with females prior to the arrival of younger, better-conditioned males that would supplant them in the dominance hierarchy (Emlen & Oring 1977).

Sexual Selection in the Wild

Thus far the first three criteria for wild[6] black soldier flies as a lekking species seem reasonably well supported. The final criterion for lekking species of free female choice has historically been difficult to demonstrate in insects, particularly in field studies. Höglund and Alatalo (1995) point out that the previous three criteria were typically enough to allow insects to be considered lekking species. That said, females in the wild should exhibit precopulatory choice (whether implicit or explicit) (Thornhill & Alcock 1983) at multiple levels. The first is that they need to select between leks. This is because as males jostle for position within the lek, it eventually becomes more advantageous to establish a satellite lek due to reduced competition. This then leads to the debate over whether females are attracted to 'hotspots' (i.e., locations) or 'hotshot' (i.e., individuals), which state that females may be attracted because of an increased chance of securing mattings or an increased chance of acquiring 'good genes'. Within the lek that females select, they then must select mates (as discussed previously).

Hotspots. While this aspect of female choice has yet to be investigated in black soldier flies, (Weldon 2007) showed that in *Bactrocera tryoni* (Froggartt) (Diptera: Tephritidae), females visited the largest aggregations more frequently than lone males, but only if those larger aggregations had more calling males, due to a limited ability by the female to perceive differences in aggregation size. Conversely, a study by Barry et al. (2003) that examined the behavior of *Ceratitits capitata* (Wiedemann) (Diptera: Tephritidae) under different operational sex ratios (OSRs) suggested that a male-bias is necessary for effective female discrimination of mates, whereas an equal OSR slowed down neural processing, and a female-biased OSR intensifies female competition reducing reproductive success. For fruit flies, which lay their eggs in intact fruit and nuts, the ecology of the lekking site is also a factor, since the size of these lek distributions have been shown to be affected by tree species, tree size, foliage density, and distance to nearest neighbor. Specifically, research has shown that *C. capitata* establishes the most leks clustered on the underside of persimmon tree leaves (compared to other fruit tree species) and their two nearest neighbors, while avoiding the smallest trees (but not preferring the largest trees) (Shelly & Whittier 1993b). Precise position within these leks has been shown to affect mating success rate as well, with the most attractive males being those that occupy the highest position (Niyazi et al. 2008).

Hotshots. Alcock (1990) wrote that large male *Hermetia comstockii* (Diptera: Stratiomyidae) had a competitive advantage in defending territories and securing mates. This is generally intuitive, as large males have more energy reserves (Yuval et al. 1998), as well as more powerful wings and flight muscles (Kaufmann et al. 2013), that also enable them to buzz their wings and advertise to females for longer durations, which is correlated with increased reproductive success in black soldier flies (Giunti et al. 2018), as well as fruit flies (Burk & Webb 1983). The effects of adult body size in structuring reproductive success was also suggested by the results of an experiment by Jones and Tomberlin (2021) who paired populations of flies of different sizes, showing that large males

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[6] The use of 'wild' is merely meant to discern flies living in captivity form those that are not, rather than convey the sense that these flies exist within pristine and unmolested wilderness. Black soldier flies are typically found in close association with organic waste of anthropogenic origin and have yet to be observed in old growth tropical forests. This is theorized to be due to a high opportunity cost faced by flies not utilizing such an abundant resource. Moreover, changes in global land use have made primary growth forests disjunct and are likely increasing such an opportunity cost, because as forests become patchier, the distance from any geographic point to a anthropogenic resource patch potentially able to be exploited is reduced.

generally perform similar or better than small males, especially when paired with large females. In heterogenous populations, this is because females may select large males even if small males are present, as was shown in *C. capitata* (de Aquino & Joachim-Bravo 2014), but this is not always the case as it depends on the specific reproductive ecology of the species. Tejeda et al. (2020) showed that increased male size affected reproductive success in the *Anastrepha obliqua* (Maquardt) (Diptera: Tephritidae) but not *Anastrepha ludens* (Loew). The researchers explain that this may because the latter have males that often call individually, and so female discrimination between different size males may be counterselected. Likewise, a more recent experiment by (Sánchez-Rosario et al. 2022 found that mating in these same two species is entirely size independent, and rather females discriminate based on strain. Research comparing the mating propensity between black soldier flies of different haplo-, or ecotypes is wanting, but it stands to reason that the populations can intermix freely due to reports that black soldier flies revert to the wild phenotype when escaped from captivity (personal communication, C. Sandrock).

Industrial System

The black soldier fly mating system currently aims to achieve high volumes of egg production by placing flies of both sexes at densities from ~3800 flies/m^3 (assuming a maximum of 10,000 / 2.88 m^3 cage), but potentially as high as ~6000 flies/m3 or higher (personal communication, S. Salari, InsectoCycle), as well an oviposition attractant, and potentially food, all within the confines of mating cages. Because of this, ascribing the lek mating system to flies in captivity is questionable, for the somewhat obvious reason that mating aggregations are not occurring in a space independent from the resources which females need for reproduction (viz. the oviposition site). This can potentially be circumvented in situations when food is not provided to flies, and the oviposition substrate is provided after peak mating (to effectively simulate asynchrony and the duration females would travel to a distant oviposition site in the wild) (Lemke, Li, et al. 2024); and hypothetically if the cage is large enough then this may also provide the means for females to oviposit in an area that is free from interference by flies occupied in lekking. The results of (Lemke, Rollison, et al. 2024) in which marked black soldier flies were observed in cages supplied with artificial plants suggests that this may be occurring in larger-scale cages, because even within the confines of a 0.93 m3 cage, males typically occupied aerial swarms near ultraviolet breeding lamps (especially in mid-morning to mid-afternoon), whereas females spent most of their time perching.

Besides this report, currently, there is little evidence that territoriality is preserved in captive or domesticated populations It is the case that aggression can actually increases in captivity, which is the case for the Mediterranean fruit fly (Diptera: Tephritidae) (Briceño et al. 1999, Benelli et al. 2014). For such species, territoriality may be preserved simply since these flies are comparatively much smaller and might have enough space within cages to establish territories. However, the black soldier fly is a relatively large fly species (average 16 mm long), that are at least five times the size of other mass-reared species like mosquitoes and fruit flies. Moreover, while it is certainly the case that black soldier flies in cages continue to engage in aerial duels (Tomberlin & Sheppard 2001, Lemke et al. 2023) and courtship rituals, it is unclear as to whether the current dimension of cages allow enough space for these without injury (e.g., broken wings), and whether these duels persist due to territorial disputes associated with a particular location within the cage environment or another reason, such as an evolutionary holdover from a previous (lekking) phenotype that is no longer advantageous. Certainly, there is an interest within the community of examining whether increased vertical space promotes fertile egg production (personal communication).

To verify, future research would need to track the motion of flies in cages via computer vision (James et al. 2024), as well as validate whether the presence of perches contribute affects behavior (Briceño et al. 1999) or reproductive success ((Lemke 2024b), since theoretically the additional surface area should allow the equivalent number of flies to spatially segregate to a greater degree, or provide a substrate that can promote acoustic signals potentially required during courtship.

In *Capititits sp.* fruit flies (Diptera: Tephritidae), the addition of horizontal slats within mating cages was hypothesized to create a lekking site by segregating aggressive males (Briceño et al. 1996, 1999, Benelli et al. 2014) from females, and effectively increasing mating success (though, it should be noted that (a) *C. capitata* adults are only 3-5 mm in length, and are often kept in field cages that are large enough to enclose entire trees (Shelly et al. 2012). However, it is important to note that a direct comparison cannot be drawn since the metrics for quality control are different under a biological control framework than would be for black soldier flies that are not released into the wild. As such, pursuing a similar result in black soldier flies, may not necessarily promote industrial objectives to increase production at minimum operational and material cost (Boller 1972)

Maintenance of the Mating System in Confinement

Female choice and sexual selection are the most important drivers behind the evolution of lekking behavior because it is females that assess the displays of males (whether those be visual, acoustic, or another modality). This can be contrasted with other mating systems in which the opportunity for precopulatory female choice is severely limited, due to the high degree of mate monopolization (consider, for example, the male digger wasp that waits at the entrance of a burrow for a female to emerge). For black soldier flies, being confined to a hyperinflated population density at equal sex ratio presents issues for black soldier flies preserving this aspect of lekking because of the shifts in selective pressures that are necessary for lekking to evolve and be maintained.

In the wild, although the instantaneous operational sex ratio can vary over time due to immigration, emigration, and mortality; lek sites should still maintain a highly male-skewed operational sex ratio. As mentioned previously, the consequences of an equal- or female-biased sex ratio were explored (albeit at densities <10 flies) in experiments on *C. capitata*, showing that male-skews are essential for females to effectively discriminate amongst potential mates (Barry et al. 2003), and lower male densities can retard neural processing. Indeed in black soldier flies it has been shown that the perceived level of competition between males affects reproductive biology, albeit in the level of sperm competition (Manas et al. 2023). Since sex ratio for optimal production is likely female biased (Hoc et al. 2019), since female black soldier flies only need to mate with one male at minimum to fertilize their eggs and males continue to produce sperm throughout their lives (personal communication, C. Bressac), this likely means there is a trade-off in terms of production between maintaining lekking and optimizing production.

In the wild setting, the plethora of males for females to choose from normally places huge precopulatory selection pressure by females on male traits (de Aquino & Joachim-Bravo 2014, Sánchez-Rosario et al. 2022). However, if that ratio suddenly is relaxed, as in the case of standard industrial operating procedure which utilizes sex ratios close to 50:50, then so too would selection pressure. Moreover, as males die off throughout, the instantaneous OSR actually becomes female biased, meaning that postcopulatory selection is likely becomes increasingly favored. Indeed parameters related to physiological condition (Aluja et al. 2009), sperm quality, age (Malawey et al. 2020, Addeo et al. 2022, Dickerson 2023), experience (Shelly & Whittier 1993a), and nutrition (Aluja et al. 2001) are important in structuring reproductive success due to the increased prevalence of sperm competition (Malawey et al. 2020) and related mechanisms such as cryptic male choice (Barbosa 2015, Godwin et al. 2017, Manas et al. 2023) and mate-guarding (Manas et al. 2023).

Plasticity

Like many experimental organisms, the context by which the vast majority of research conducted on the black soldier fly is in captivity. One apparent consequence of this is that there appears to be a disagreement between lekking behavior that appears to fit well amongst wild populations, and the behavior that actually occurs in this new confined context. One explanation could be that the mating system is plastic, and the behaviors that they exhibit in a confined habitat are merely a consequence of being in that habitat. Indeed, lek mating has been shown to be plastic

(Emlen & Oring 1977). For example, under reduced population densities animals such as dragonflies, bullfrogs, turkeys, puku, topi, and Ukanda kob, that previously engaged in lekking shifted towards mate- or resource-guarding systems (Emlen & Oring 1977). Conversely, those such as Tephritid fruit flies that were placed under increased population densities instead shifted towards scramble competition polygyny (Dodson 1986, Herberstein et al. 2017). The former strategies are more optimal because the prevalence of females is too low for advertising to be effective; while scamble competition polygyny is theoretically favored due to the high opportunity cost of wasting time advertising when the cage is saturated with available mates.

Indeed, causal observation of escaped flies from a colony maintained in a greenhouse at Texas A&M University, revealed that males will readily migrate towards and defend nearby plants (Cotton, peas) within the greenhouse (Lemke 2024b), which conceptually aligns with the results of (Lemke, Rollison, et al. 2024). If verified, this could entail that any shift in behavior between wild and captive populations may not have a strong genetic basis (West-Eberhard 1989).

Theory has long predicted (Emlen & Oring 1977) that shifts in mating systems are modulated by concomitant changes in ecological factors that, in addition to population density, include the immediate operational sex ratio and spatiotemporal constraints of their local environment that together act to alter the intensity of intrasexual competition as well as opportunity costs and risk during foraging and reproduction. Shifts in these ecological factors hence affect the traits which are necessary for individuals to succeed at passing on their genes and produce viable offspring, which of course then has long-term evolutionary consequences, as they ultimately affect the level of alleles across populations. Perturbations that change population densities or environmental conditions can ultimately give rise to shifts in mating systems and is predicted to be the case of domesticated species whose population density can be increased by several orders of magnitude within cages.

Conclusion

In conclusion, the opinion rendered here is that black soldier flies exhibit lekking in the wild, but within the industrial setting, shift towards a mating system that is more akin to scramble competition polygyny. This shift, however, probably does not have a strong genetic basis, because when accidentally released, black soldier flies have been observed to revert to their wild phenotypes (personal communication, C. Sandrock) and display lek-like behaviors (personal observation). Because of this, even using term such as 'facultative lekking' belies the fact that under most normal eco-evolutionary circumstances, the black soldier fly species appears to lek. Because of their position within the middle of the fly phylogeny (i.e., being basal Brachycera), this means that future studies to model lekking in black soldier flies can be especially important for understanding large-scale evolutionary transitions across the Diptera. For example, blood feeding flies have transitioned from aerial swarms to leks to resource based polygyny as they have become more derived (Yuval 2006). Likewise, since at smaller ecological time scales shifts in selection pressure can drive a species that normally leks to instead adopt a new mating system, modeling the factors that drive such changes is also important for understanding mating system dynamics in mass-reared or cultured insects.

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References

Addeo, N. F., C. Li, T. W. Rusch, A. J. Dickerson, A. M. Tarone, F. Bovera, and J. K. Tomberlin. 2022. Impact of age, size, and sex on adult black soldier fly *Hermetia illucens* L. (Diptera: Stratiomyidae) thermal preference. Journal of Insects as Food and Feed 8: 129–139.

Alcock, J. 1987. Leks and hilltopping in insects. Journal of Natural History 21: 319–328.

ALCOCK, J. 1990. A large male competitive advantage in a lekking fly, *Hermetia comstocki* Williston (Diptera: Stratiomyidae). Psyche: A Journal of Entomology 97: 267–279.

ALUJA, M., I. JÁCOME, and R. MACÍAS-ORDÓÑEZ. 2001. Effect of adult nutrition on male sexual performance in four Neotropical fruit fly species of the genus *Anastrepha* (Diptera: Tephritidae). Journal of Insect Behavior 14: 759–775.

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. Journal of Insect Physiology 55: 1091–1098.

DE AQUINO, J. C., and I. S. JOACHIM-BRAVO. 2014. Relevance of male size to female mate choice in *Ceratitis capitata* (Diptera: Tephritidae): Investigations with wild and laboratory-reared flies. J Insect Behav 27: 162–176.

BARBOSA, F. 2015. An integrative view of postcopulatory sexual selection in a soldier fly: Interplay between cryptic male choice and sperm competition. *In* A. V. Peretti and A. Aisenberg (Eds.) Cryptic Female Choice in Arthropods: Patterns, Mechanisms and Prospects. pp. 385–401, Springer International Publishing, Cham. Available at: https://doi.org/10.1007/978-3-319-17894-3_14 [Accessed September 30, 2021].

BARRETT, M., R. K. GODFREY, E. J. STERNER, and E. A. WADDELL. 2022. Impacts of development and adult sex on brain cell numbers in the black soldier fly, *Hermetia illucens* L. (Diptera: Stratiomyidae). Arthropod Structure & Development 70: 101174. Available at: https://www.sciencedirect.com/science/article/pii/S1467803922000354 [Accessed October 19, 2022].

BARRY, J. D., L. C. K. TRAN, and J. G. MORSE. 2003. Mating propensities from different ratios of male and female Mediterranean fruit flies (Diptera: Tephritidae). flen 86: 225–226.

BENELLI, G., E. DONATI, D. ROMANO, C. STEFANINI, R. H. MESSING, and A. CANALE. 2014. Lateralisation of aggressive displays in a tephritid fly. Sci Nat 102: 1.

BIRRELL, N. 2018. Sensory morphology, investment and plasticity in the black soldier fly (*Hermetia illucens*). Thesis. ResearchSpace@Auckland. Available at: https://researchspace.auckland.ac.nz/handle/2292/37256 [Accessed September 19, 2022].

BOLLER, E. 1972. Behavioral aspects of mass-rearing of insects. Entomophaga 17: 9–25.

BONDURIANSKY, R., and R. J. BROOKS. 1999. Why do male antler flies (*Protopiophila litigata*) fight? The role of male combat in the structure of mating aggregations on moose antlers. Ethology Ecology & Evolution 11: 287–301.

BONESS, D. J., W. D. BOWEN, B. M. BUHLEIER, and G. J. MARSHALL. 2006. Mating tactics and mating system of an aquatic-mating pinniped: the harbor seal, Phoca vitulina. Behav Ecol Sociobiol 61: 119–130.

BRADBURY, J. W. 1977. Lek mating behavior in the hammer-headed bat. Zeitschrift für Tierpsychologie 45: 225–255.

BRICEÑO, R. D., D. RAMOS, and W. G. EBERHARD. 1996. Courtship behavior of male *Ceratitis capitata* (Diptera: Tephritidae) in captivity. The Florida Entomologist 79: 130–143.

BRICEÑO, R. D., D. RAMOS, and W. G. EBERHARD. 1999. Aggressive behavior in Medflies (*Ceratitis capitata*) and its modification by mass rearing (Diptera: Tephritidae). Journal of the Kansas Entomological Society 72: 17–27.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. The Wilson Bulletin 76: 160–169.

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)1. Annals of the Entomological Society of America 76: 678–682.

BUTTERWORTH, N. J., T. E. WHITE, P. G. BYRNE, and J. F. WALLMAN. 2021. Love at first flight: Wing interference patterns are species-specific and sexually dimorphic in blow flies (Diptera: Calliphoridae). Journal of Evolutionary Biology 34: 558–570.

CROLL, G. A., and J. B. MCCLINTOCK. 2000. An evaluation of lekking behavior in the fiddler crab Uca spp. Journal of Experimental Marine Biology and Ecology 254: 109–121.

DEWITT, T. J., A. SIH, and D. S. WILSON. 1998. Costs and limits of phenotypic plasticity. Trends in Ecology & Evolution 13: 77–81.

DICKERSON, A. J. 2023. Impact of adult age on the reproductive output of the black soldier fly, *Hermetia illucens* (L.) (Diptera: Stratiomyidae). Texas A&M University, College Station.

DODSON, G. 1986. Lek mating system and large male aggressive advantage in a gall-forming tephritid fly (Diptera: Tephritidae). Ethology 72: 99–108.

DUGAND, R. J., J. L. TOMKINS, and W. J. KENNINGTON. 2019. Molecular evidence supports a genic capture resolution of the lek paradox. Nat Commun 10: 1359.

EBERHARD, W. G., and J. K. GELHAUS. 2009. Genitalic stridulation during copulation in a species of crane fly, Tipula (Bellardina) sp. (Diptera: Tipulidae). Rev. Biol. Trop. 57: 6.

EICHORN, C., M. HRABAR, E. C. VAN RYN, B. S. BRODIE, A. J. BLAKE, and G. GRIES. 2017. How flies are flirting on the fly. BMC Biology 15: 1–9.

EMLEN, S. T., and L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215–223.

GILBERT, J. D. J., and A. MANICA. 2010. Parental care trade-offs and life-history relationships in insects. The American Naturalist 176: 212–226.

GIUNTI, G., O. CAMPOLO, F. LAUDANI, and V. PALMERI. 2018. Male courtship behaviour and potential for female mate choice in the black soldier fly *Hermetia illucens* L. (Diptera: Stratiomyidae). Entomologia Generalis 38: 29–46.

GODWIN, J. L., R. VASUDEVA, Ł. MICHALCZYK, O. Y. MARTIN, A. J. LUMLEY, T. CHAPMAN, and M. J. G. GAGE. 2017. Experimental evolution reveals that sperm competition intensity selects for longer, more costly sperm. Evol Lett 1: 102–113.

H6GLUND, J., and A. LUNDBERG. 1987. Sexual selection in a monomorphic lek-breeeding bird: Correlates of male mating success in the great snipe Gallinago media. Behav Ecol Sociobiol 21: 211–216.

HARJOKO, D. N., Q. Q. H. HUA, E. M. C. TOH, C. Y. J. GOH, and N. PUNIAMOORTHY. 2023. A window into fly sex: mating increases female but reduces male longevity in black soldier flies. Animal Behaviour 200: 25–36.

HERBERSTEIN, M. E., C. J. PAINTING, and G. I. HOLWELL. 2017. Scramble competition polygyny in terrestrial arthropods. *In* M. Naguib, J. Podos, L. W. Simmons, L. Barrett, S. D. Healy, and M. Zuk (Eds.) Advances in the study of behavior. Advances in the study of behavior. pp. 237–295, Elsevier, Cambridge, Massachusetts. Available at: http://www.scopus.com/inward/record.url?scp=85011627891&partnerID=8YFLogxK [Accessed August 16, 2023].

HOC, B., G. NOËL, J. CARPENTIER, F. FRANCIS, and R. C. MEGIDO. 2019. Optimization of black soldier fly (*Hermetia illucens*) artificial reproduction. PLOS ONE 14: 1–13.

HOFFMANN, A. A., and M. W. BLOWS. 1992. Evidence that *Drosophila mycetophaga* Malloch (Diptera: Drosophilidae) is not a true "lekking" species. Australian Journal of Entomology 31: 219–221.

HOFFMANN, L. 2021. Genetic diversity and mating systems in a mass-reared black soldier fly (*Hermetia illucens*) population. Stellenbosch University, Stellenbosch, Western Cape, South Africa.

HÖGLUND, J. 1988. Size and plumage dimorphism in lek-breeding birds: A comparative analysis. The American Naturalist 134: 72–87.

HÖGLUND, J., and R. V. ALATALO. 1995. Leks.

HUTCHINSON, G. E. 1957. A treatise on limnology. (No Title). Available at: https://cir.nii.ac.jp/crid/1370022219400970113 [Accessed August 20, 2023].

ISVARAN, K. 2021. Lek territory size and the evolution of leks: A model and a test using an Ungulate with a flexible mating system. Front. Ecol. Evol. 8. Available at: https://www.frontiersin.org/journals/ecology-and-evolution/articles/10.3389/fevo.2020.539061/full [Accessed August 2, 2024].

JAMES, A., A. SETH, A. MARCIREAU, S. MUKHOPADHYAY, T. HU, and R. ATAYDE. 2024. FlyCount: High-speed counting of black soldier flies using neuromorphic sensors. IEEE Sensors Journal 1–1.

JONES, B. M., and J. K. TOMBERLIN. 2019. Impact of larval competition on life-history traits of the black soldier fly (Diptera: Straiomyidae) V. Stull (Ed.). Annals of the Entomological Society of America 112: 505–510.

JONES, B. M., and J. K. TOMBERLIN. 2021. Effects of adult body size on mating success of the black soldier fly, *Hermetia illucens* (L.) (Diptera: Stratiomyidae). Journal of Insects as Food and Feed 7: 5–20.

KAUFMANN, C., C. REIM, and W. U. BLANCKENHORN. 2013. Size-dependent insect flight energetics at different sugar supplies. Biological Journal of the Linnean Society 108: 565–578.

KAYA, C. ET AL. 2021. Global population genetic structure and demographic trajectories of the black soldier fly, *Hermetia illucens*. BMC Biol 19: 94.

KINDERMANN, C., and J.-M. HERO. 2016. Rapid dynamic colour change is an intrasexual signal in a lek breeding frog (Litoria wilcoxii). Behav Ecol Sociobiol 70: 1995–2003.

KLÜBER, P., E. AROUS, H. ZORN, and M. RÜHL. 2023. Protein- and carbohydrate-rich supplements in feeding adult black soldier flies (*Hermetia illucens*) affect life history traits and egg productivity. Life 13: 355.

LEMKE, N. 2024a. Spatiotemporal effects modulate reproductive success in the black soldier fly, *Hermetia illucens* (L.) (Diptera: Stratiomyidae). Dissertation. Texas A&M University, College Station.

LEMKE, N. B. 2024b. Artificial plant perches reveal sex-specific behavior in the black soldier fly, Hermetia illucens.

LEMKE, N. B., A. J. DICKERSON, and J. K. TOMBERLIN. 2023. No neonates without adults: A review of adult black soldier fly biology, *Hermetia illucens* (Diptera: Stratiomyidae). BioEssays 45: 2200162. Available at: https://onlinelibrary.wiley.com/doi/10.1002/bies.202200162 [Accessed July 10, 2023].

LEMKE, N. B., C. LI, A. J. DICKERSON, D. A. SALIZAR, L. N. ROLLINSON, J. E. MENDOZA, C. D. MIRANDA, S. CRAWFORD, and J. K. TOMBERLIN. 2024. Heterogeny in cages: Age-structure and timing of attractant availability impacts fertile egg production in the black soldier fly, Hermetia illucens. 2024.08.13.607807. Available at: https://www.biorxiv.org/content/10.1101/2024.08.13.607807v1 [Accessed October 29, 2024].

LEMKE, N. B., L. N. ROLLISON, and J. K. TOMBERLIN. 2024. Sex-specific perching: Monitoring of artificial plants reveals dynamic female-biased perching behavior in the black soldier fly, *Hermetia illucens* (Diptera: Stratiomyidae). Insects 15: 770.

LLOYD, L. 1867. The game birds and wild fowl of Sweden and Norway: With an account of the seals and salt-water fishes of those countries. F. Warne and Company.

LYCETT, J. E., and R. I. M. DUNBAR. 2000. Mobile phones as lekking devices among human males. Hum Nat 11: 93–104.

MALAWEY, A., A. TARONE, J. TOMBERLIN, and E. WALSH. 2020. Interaction of age and temperature on heat shock protein expression, sperm count, and sperm viability of the adult black soldier fly (Diptera: Stratiomyidae). Journal of Insects as Food and Feed 7.

MANAS, F., C. LABROUSSE, and C. BRESSAC. 2023. Sperm production and allocation respond to perceived risk of sperm competition in the black soldier fly *Hermetia illucens*. 2023.06.20.544772. Available at: https://www.biorxiv.org/content/10.1101/2023.06.20.544772v1 [Accessed July 10, 2023].

MARSHALL, S. A., N. E. WOODLEY, and M. HAUSLER. 2015. The historical spread of the black soldier fly, *Hermetia illucens* (L.) (Diptera, Stratiomyidae, Hermetiinae), and its establishment in Canada. JESO 146.

MAYER, M. S. 2019. Handbook of insect pheromones and sex attractants. CRC Press.

MENEGUZ, M., C. D. MIRANDA, J. A. CAMMACK, and J. K. TOMBERLIN. 2023. Adult behaviour as the next frontier for optimising industrial production of the black soldier fly *Hermetia illucens* (L.) (Diptera: Stratiomyidae). Journal of Insects as Food and Feed 9: 399–414.

MUNSCH-MASSET, P., C. LABROUSSE, L. BEAUGEARD, and C. BRESSAC. 2023. The reproductive tract of the black soldier fly (*Hermetia illucens*) is highly differentiated and suggests adaptations to sexual selection. Entomologia Experimentalis et Applicata n/a. Available at: https://onlinelibrary.wiley.com/doi/abs/10.1111/eea.13358 [Accessed August 15, 2023].

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). Biological Journal of the Linnean Society 95: 479–487.

POMONIS, J. G. 1989. Cuticular hydrocarbons of the screwworm, *Cochliomyia hominivorox* (Diptera: Calliphoridae). J Chem Ecol 15: 2301–2317.

PRICE, E. O. 2002. Animal domestication and behavior. CABI Pub, Wallingford, Oxon, UK ; New York.

RICHARDSON, S. S. 2014. Darwin and the women. Nature 509: 424–424.

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

SÁNCHEZ-ROSARIO, M., D. PÉREZ-STAPLES, J. VALLE-MORA, D. SÁNCHEZ-GUILLÉN, L. RUIZ-MONTOYA, and P. LIEDO. 2022. Does body size influence mating success? A morphometric study of two *Anastrepha* (Diptera: Tephritidae) fruit fly species. Bulletin of Entomological Research 112: 298–310.

SHELLY, T. E., and T. S. WHITTIER. 1993a. Effect of sexual experience on the mating success of males of the Mediterranean Fruit Fly, *Ceratitis capitata* Wiedemann (Diptera: Tephritidae). 32.

SHELLY, T. E., and T. S. WHITTIER. 1993b. Lek distribution in the Mediterranean fruit fly (Diptera: Tephritidae): Influence of tree size, foliage density, and neighborhood. Proceedings of the Hawaiian Entomological Society 32: 113–121.

SHELLY, T. E., and T. S. WHITTIER. 1997. Lek behavior of insects. *In* B. J. Crespi and J. C. Choe (Eds.) The Evolution of Mating Systems in Insects and Arachnids. pp. 273–293, Cambridge University Press, Cambridge. Available at: https://www.cambridge.org/core/books/evolution-of-mating-systems-in-insects-and-arachnids/lek-behavior-of-insects/DFFF3C2DB9D350A02F7DACD99FFE4ABA [Accessed August 20, 2023].

SHELLY, T. E., T. S. WHITTIER, and K. Y. KANESHIRO. 1993. Behavioral responses of Mediterranean fruit flies (Diptera: Tephritidae) to trimedlure baits: Can leks be created artificially? Annals of the Entomological Society of America 86: 341–351.

SHELLY, T., J. EDU, and E. PAHIO. 2012. Mate choice by lekking males: Evidence from the Mediterranean fruit fly from field cage trials (Diptera: Tephritidae). Annals of the Entomological Society of America 105: 368–376.

SHEPPARD, C., J. TOMBERLIN, J. JOYCE, B. KISER, and S. SUMNER. 2002. Rearing methods for the black soldier fly (Diptera: Stratiomyidae). Journal of Medical Entomology 39: 695–698.

SHUKER, D. M., and L. W. SIMMONS eds. 2014. The evolution of insect mating systems. Oxford University Press, University of Oxford.

STÅHLS, G., R. MEIER, C. SANDROCK, M. HAUSER, L. ŠAŠIĆ ZORIĆ, E. LAIHO, A. ARACIL, J. DODEROVIĆ, R. BADENHORST, P. UNADIREKKUL, N. A. B. MOHD ADOM, L. WEIN, C. RICHARDS, J. K. TOMBERLIN, S. ROJO, S. VESELIĆ, and T. PARVIAINEN. 2020. The puzzling mitochondrial phylogeography of the black soldier fly (*Hermetia illucens*), the commercially most important insect protein species. BMC Evol Biol 20: 60.

STEPHENS, P. A., I. L. BOYD, J. M. MCNAMARA, and A. I. HOUSTON. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90: 2057–2067.

TAYLOR, P. D., and G. C. WILLIAMS. 1982. The lek paradox is not resolved. Theoretical Population Biology 22: 392–409.

TEJEDA, M. T., J. ARREDONDO, F. DÍAZ-FLEISCHER, and D. PÉREZ-STAPLES. 2020. Does size matter? Mate choice in two lekking flies. Journal of Insect Science 20. Available at: https://doi.org/10.1093/jisesa/ieaa019 [Accessed June 28, 2021].

THORNHILL, R., and J. ALCOCK. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Massachusetts.

THORNHILL, R., and J. ALCOCK. 2013. The evolution of insect mating systems. *In* The Evolution of Insect Mating Systems. Harvard University Press. Available at: https://www.degruyter.com/document/doi/10.4159/harvard.9780674433960/html [Accessed July 13, 2023].

TOMBERLIN, J. K., and D. C. SHEPPARD. 2001. Lekking behavior of the black soldier fly (Diptera: Stratiomyidae). Florida Entomologist 84: 729–730.

VAHED, K. 1998. The function of nuptial feeding in insects: a review of empirical studies. Biological Reviews 73: 43–78.

WELDON, C. W. 2007. Influence of male aggregation size on female visitation in *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). Australian Journal of Entomology 46: 29–34.

WEST-EBERHARD, M. J. 1989. Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics 20: 249–278.

WIKELSKI, M., C. CARBONE, and F. TRILLMICH. 1996. Lekking in marine iguanas: female grouping and male reproductive strategies. Animal Behaviour 52: 581–596.

WILEY, R. H. 1974. Evolution of social organization and life-history patterns among grouse. The Quarterly Review of Biology 49: 201–227.

WINDLE, M. J. S., and G. A. ROSE. 2007. Do cod form spawning leks? Evidence from a Newfoundland spawning ground. Mar Biol 150: 671–680.

YUVAL, B. 2006. Mating systems of blood-feeding flies. Annual Review of Entomology 51: 413–440.

YUVAL, B., R. KASPI, S. SHLOUSH, and M. S. WARBURG. 1998. Nutritional reserves regulate male participation in Mediterranean fruit fly leks. Ecological Entomology 23: 211–215.