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Hilara sp. (Diptera: Empididae; Empidinae): Mating System, Swarm Movements, and Inbreeding Avoidance

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Abstract In a study spanning parts of nine years, an undescribed species of *Hilara* Meigen was observed to form mating swarms displaying complex behaviors. Typically, swarms were shaped like a flattened torus rotating rapidly about a horizontal axis. Many swarms also moved up and down and turned slowly back-and-forth about a vertical axis. Both up-and-down and turning movements were random in extent and direction, suggesting that they might arise as random, asymmetric density fluctuations within the swarms themselves. A rotating secondary swarm appeared intermittently inside one end of some primary swarms. Swarm membership changed continually as flies left one swarm to join another and as entire swarms coalesced. At one site the set of all swarms displayed properties not found in the swarms individually: spatial extension, daily dissipation and reconstitution over a period of weeks or months, reproductive potential, and gene flow. Such emergent properties qualify the set as a multicomponent swarm, an object heretofore known only in computer models. *Hilara* sp. appears to be protandrous, univoltine, and promiscuous. Generally, males paired preferentially with somewhat smaller females, but some small and medium-sized males paired with much larger females. Although males of nearly all known *Hilara* species present nuptial gifts of prey or other items to females, nuptial gifts were not observed at any time during the present study. Many characteristics of swarms of *Hilara* sp. can be understood as adaptations that reduce inbreeding.

Keywords *Hilara* · rotating · swarms · multicomponent

Animal swarms have attracted much scientific attention in recent decades. The literature mentions many kinds of swarming insects, including flies (Neems et al. 1992) and

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swarms of other animals such as crustaceans, fish, birds, and mammals. Kirby and Spence (1823) reported observations of rotating swarms of dagger flies in the United Kingdom: “In May and June. .. you may observe. .. the motions of a countless host of little black flies of the genus *Empis*. .. which. .. assemble to wheel in aëry circles over stagnant waters.” No further reports of rotating swarms have been published for almost two centuries. This lacuna is particularly remarkable considering the importance of swarm-forming empid flies in research on insect mating systems (Cumming 1994, Forrest 1985, Svensson 1997, Svensson and Petersson 1987).

Mating swarms of an undescribed species of *Hilara* along streams in the coastal forest of Central California rotate rapidly about a horizontal axis. The present paper explores basic characteristics of these swarms. Some swarms simultaneously turn slowly back and forth about a vertical axis and engage in vertical translational movements with no apparent loss in swarm organization. Swarms display a distinct structure that appears to enhance mating opportunities.

Previously, dual- or multicomponent swarms have been known only as mathematical objects as described by Deguet et al. (2006) and You et al. (2009). A swarm qualifies as dual- or multicomponent if it manifests emergent properties, which are "behaviour[s] of the system, taken as whole, that [are] not expressed by any one of the lower-scale components that comprise it” (Cohen and Harel 2007). *Hilara* sp. appears to accord with this definition and thus provide the first reported example of a biological multicomponent swarm.

Assortative mating has been reported in animal groups as diverse as flies (Hegde and Krishna 1997), snails (Kimura et al. 2014), salamanders (Acord et al. 2013), and birds (Harris and Siefferman 2014). The size-assortative mating system of *Hilara* sp. appears to incorporate a novel strategy by which small males mate not only with small, presumably low-fertility females but also with exceptionally large, high-fertility females.

The possible role of predators as a selective force in the origination of swarming behavior was investigated by Olson et al. (2013) in a computer model. The model prey gathered into swarms that confused the model predators. In a literature survey of predator systems that included a swarm-forming prey, Jeschke and Tollrian (2007) found that predators became confused in 16 of 25 systems.

The primary goal of this study is to elucidate the nature of the swarms in *Hilara* sp. and to determine the selective forces that might maintain them.

Materials and Methods

More than 200 swarms of *Hilara* sp. were observed on more than 100 occasions from June to mid-August in 2010–2013, and from May to July in 2014–2017 at Dutch Bill Creek and two sites near Salmon Creek near the unincorporated town of Occidental in western Sonoma County, California (38.39° N, 122.97° W; elev. 310 m). The dominant vegetation in this area is Douglas fir, *Pseudotsuga menziesii* (Mirb.); redwood, *Sequoia sempervirens* (Lamb); and California live oak, *Quercus agrifolia* Nee.

Wing length, an index of overall body size (Norry et al. 1997), was measured to the nearest 0.03 mm in 46 male-female pairs collected just after they had ascended out of swarms and in 65 males and 65 females collected within swarms.

Distances between 11 swarms along 260 m of Dutch Bill Creek and 13 swarms along 267 m of a creek at Westwood Lane were measured on 5 July 2016. The number of flies in each swarm was roughly estimated in four categories: 10–19, 20–39, 40–59, and 60–79.

Observations of pairs of flies rising from swarms were generally opportunistic and qualitative due to the flies' small size (2.5–3.0 mm), fast flying speeds (up to 90 cm/s), and height above the ground (up to 7 m). Sharp contrasts of light and shadow in the background vegetation usually limited observation to at most a few seconds. However, a cabin at Salmon Creek served as a uniformly-colored backdrop for swarms that produced many rising pairs. There, flies were tracked for as long as six or seven seconds.

Samples taken from swarms for the purpose of determining sex ratio were examined with a dissecting microscope. In 2015, when swarms were sampled frequently, sample sizes were kept small ($\overline{X} = 15.4$) to avoid depleting the population.

Compass headings of a rotating swarm were determined by aiming a handheld nautical compass along the swarm's long axis as the top stream of flies traveled away from the observer. Up-and-down movements were tracked with a pole-mounted digital level (Digi-Pas™ DWL-80E). The number of flies in one large swarm at Salmon Creek observed on 19 June 2014 was estimated as follows: (1) The swarm was video-recorded (Panasonic® HDC HS700, Two Riverfront Plaza, Newark, NJ 07102) against the uniform background of a painted wooden wall. (2) In playback, the video was stopped at a single frame, and the positions of the flies were marked in ink on a transparent sheet of plastic covering the computer monitor. (3) After all visible fly images had been marked, the video was advanced by a single frame, bringing more flies into view. (4) All fly images were again marked. (5) Steps 3 and 4 were repeated until no new flies came into view. (6) The number of image strings, each string representing the path of a single fly, was counted.

Flight paths of three pairs of flies were recorded with the camcorder at a shutter speed of 1/60 s and played back frame-by-frame. To facilitate an understanding of the relative positions of a male-female pair, a three-dimensional physical model of their paths was constructed from two 30 cm-long sections of stiff wire joined at one end. The model was constructed with the aid of a reference figure prepared by tracing the sequence of video frames onto a glass pane covering the computer screen. The reference figure and the pair of wires were then mounted on separate camera tripods and positioned so that the reference figure appeared superimposed on the wires as the wires were viewed through the pane. Finally, the wires were bent repeatedly until their shapes matched those of the superimposed figure.

Voucher specimens were deposited in the insect collection of the Canadian National Collection of Insects, Ottawa, Canada, and the Natural History Museum of Los Angeles County, California.

Results

Expanded basitarsi Males of *Hilara* sp. possess greatly expanded forebasitarsi, as do males of most other species in the tribe Hilarini. However, at no time were flies observed to exchange nuptial gifts such as prey items or silk balloons; neither were such gifts ever discovered in nets containing captured flies.

Swarm Characteristics and Behaviors Swarms appeared each year in the same patches of sunlight shining through the forest canopy. Degree of swarm organization and swarm duration varied greatly. Most swarms were shaped like a flattened torus with a length of 0.5–2.0 m. In a large majority the top stream of flies was separated from the bottom stream by only a few centimeters, but in some swarms the separation was larger (Fig. 1). Swarms located within about 1.5 m of the east bank of a creek generally rotated clockwise as seen from the north, This orientation placed the pair-forming arena in the open space above the creek and away from any overhanging vegetation on the bank.

Upon approaching either end of a swarm, most flies followed a smoothly curving path either upwards or downwards; however, some, both males and females, continued well past the main body of the swarm before abruptly reversing course and rejoining it (Fig. 1). Transient cycling shortcuts formed inside the east end of some large, clockwise-rotating swarms, connecting flies directly with the pair-forming arena (Fig. 1).

Slow, back-and-forth turning movements about a vertical axis (Fig. 1) were observed at Dutch Bill Creek. Compass headings of a swarm turning slowly back and forth about a vertical axis are shown in Fig. 2 (average heading 3° south of the sun's azimuth). Both the amount and direction of turning during 33 paired observations were normally distributed (Fig. 3). Many swarms were observed to move up and down as they continued to rotate about a horizontal axis (Fig. 4). As in the case of turning movements, the amount and direction of up-and-down movements during 43 paired observations were normally distributed (Fig. 5).

On several occasions, adjacent pairs of clockwise-rotating swarms at Dutch Bill Creek were observed to turn slowly back and forth synchronously about a vertical axis.

Other swarm behaviors were: (1) *Translational movements along vertical axis.* (2) *Translational movements along north-south axis*, i.e., parallel to the creek bed. (3) *Dissipation*. Entire swarms often dissipated over periods varying from several seconds to several minutes. Even breezes <1 m/s often caused rapid dissipation.

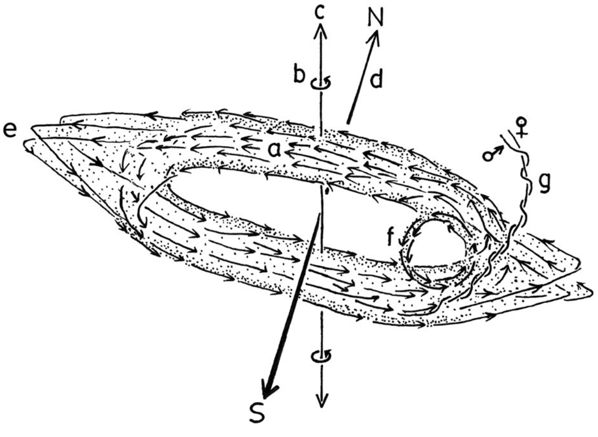

Fig. 1 Schematic diagram of swarm. a, rotation about horizontal axis; b, back-and-forth motion about vertical axis; c, translational movement along vertical axis; d, translational movement along north-south axis; e, extended terminal path; f, transient cycle; g, ascending male-female pair

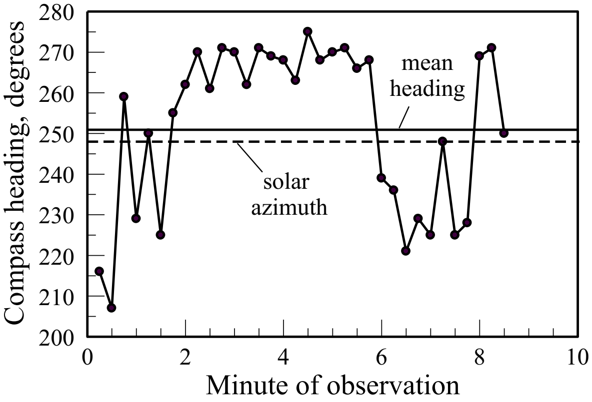

Fig. 2 Compass headings of a turning swarm at 15-s intervals

Slower dissipation sometimes resulted from the shrinking of a sunny patch as the sun sank closer to the horizon. In many cases the cause of dissipation was not apparent. (4) *Coalescence* of two swarms. (5) *Member exchanges*. Flies traveled between the tops of two adjacent, clockwise-rotating swarms. Swarm behaviors varied greatly depending upon the number of flies in the swarm, the site, the precise location of the swarm within a given site, time of day, the degree of overcast, the period within the swarming season, and presumably upon other, unknown, factors.

Non-toroidal swarms were interpenetrating, with flies streaming in opposite directions in the same air space. In some small, interpenetrating swarms, individuals concentrated in pulses that persisted through several trips from one end of the swarm to the other. Interpenetrating swarms often developed into rotating swarms over the course of several minutes.

Size and Separation of Swarms Swarm separation: Dutch Bill Creek, $\overline{X}$ 26.1 m, SD 8.40, range 2.2–38.0 m, $n = 10$; creek at Westwood Lane, $\overline{X}$ 18.7 m, SD 15.50, range 0.5–49.7 m, $n = 13$. Estimated total numbers of flies: Dutch Bill Creek, 200–360; creek at Westwood Lane, 240–600.

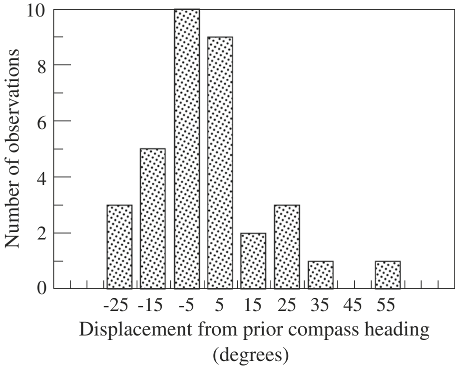

Fig. 3 Frequency distribution of amounts and direction of swarm turning during paired observation periods

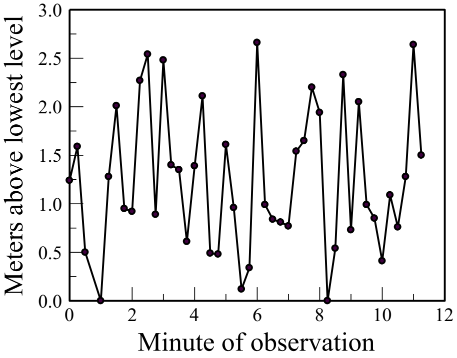

Fig. 4 Up-and-down swarm movements at 15-s intervals

Mate Recognition and Pairing Dynamics The paths of a male and a female fly are depicted in Fig. 6. Each cell represents movement over a period of about 17 ms. In frame #1, the male is situated about 40° above the female and several cm to her right. Over the next 170 ms (times rounded to the nearest 10 ms) the male descends to a position about 5° above the female, still to her right. At some time during the next 30 ms (the absence of the male's image in two frames precludes greater precision), the male turns left abruptly. Upon interception, the male spirals about the female at the rate of 2.3 revolutions/s. The female appears to respond about 50–70 ms later (female not visible in two frames) by starting to ascend out of the swarm.

In Fig. 7A two flies are shown approaching the videocorder. One fly, presumably male, appears to the left of the presumed female and about level with her at a distance of several cm. The male then alters his course to intercept the female, passes behind her, and completes about 3/4 of a spiral around her by the end of the video segment. Figure 7B depicts the flight paths of two flies, both of which were presumably males because the paths spiral around each other.

Production of Male-Female Pairs Pairs arose only from the swarm end in which flies reverse course by traveling in an upward direction, i.e., the east end of clockwise-rotating swarms and the west end of counter-clockwise rotating swarms. In many cases the male's path closely paralleled that of the female, but in other cases the male spiraled about the

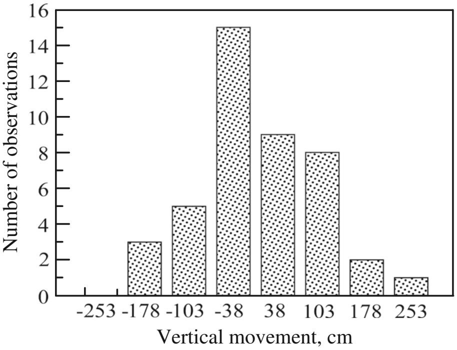

Fig. 5 Frequency distribution of amounts and direction of up-and-down swarm movements during paired observation periods

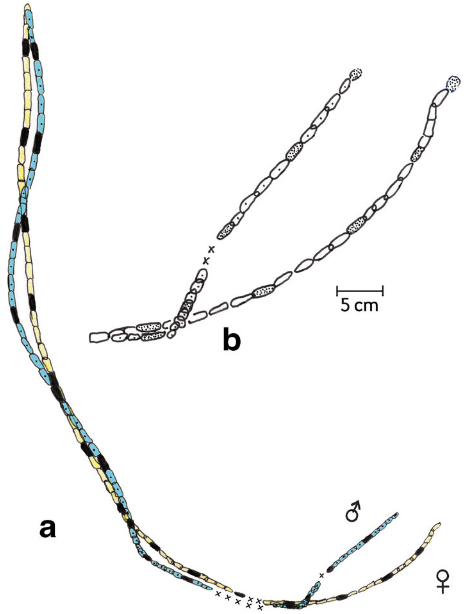

Fig. 6 Flight paths of rising male-female pair obliquely approaching the video camera, 17 ms per cell. Filled and stippled cells indicate relative positions at 83-ms intervals. x, fly not visible in frame. a. 1.22-s period. b. Initial 380 ms of flight paths in a enlarged 2.3×

female as she rose from the swarm (Fig. 1g). Pairs that included a spiraling male slowed their flight speed and sometimes even hovered in place for several seconds.

Rates of pair production over the course of ten minutes varied from zero in the case of many small swarms to 3/s. One swarm of 80 individuals observed at Salmon Creek on 18 June 2014 (sex ratio 0.18) produced 4 pairs per male per min. During several minutes on 18 May 2014, a swarm of about 50 individuals at the creek at Westwood Lane produced pairs at the estimated rate of 3/s.

Several swarms numbering about ten to 40 individuals each were observed above Dutch Bill Creek at 14:30 h on 23 May 2015. Although the swarms were unstable, repeatedly dissipating and reforming over a period of about 20 min, their compass headings remained close to 345°. No rising pairs were observed. At 1510 h the swarms repositioned themselves closer to the west bank of the creek, changed their compass heading to about 280°, and began producing rising pairs.

Intrasexual Competition On rare occasions a trio of flies rose together from a swarm. While one fly, presumably female, flew a straight or gradually curving path, the other two, presumably both male, spiraled about her and intermittently contacted each other in an apparent display of aggression. No competition was ever observed between flies inside a swarm.

Promiscuous Mating Throughout the study, the large majority of rising pairs were quickly lost to view against the confusing forest background of contrasting light and shade; however, members of pairs that did remain visible were seen to separate from each other and return to the swarm.

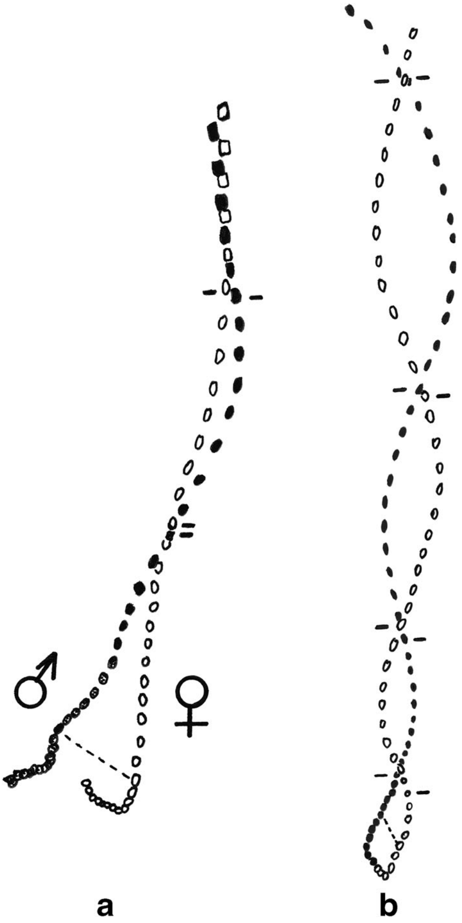

Fig. 7 Flight paths of rising pairs, 17 ms per cell. Dashes and dotted lines indicate relative positions at 83-ms intervals. a. male-female pair, 650-ms period. b. Probably two males, 730-ms period

Protandry and Univoltinism Early-season swarms (23–28 May 2015) were heavily male-biased (Fig. 8). By mid-June the sex ratio declined to less than 0.4. Probably, this trend is due to protandry, i.e., earlier eclosion of males. The absence of a second period of male bias strongly suggests that *Hilara* sp. is univoltine.

Size-Assortative Mating Each of the 46 data points in Fig. 9 represents the wing lengths of both sexes in a rising pair. The slope (b = 0.509) of the lower regression line and its position well below the dashed line denoting male-female size equality indicates sex-assortative mating. Females along this regression line averaged 87.6% the size of their male counterparts (range 79.3%-101.0%). Most small males (WL < 2.90 mm) paired with small females (WL $\overline{X}$=2.65 mm), but as shown at the upper left, five small males paired with females averaging 11.5% larger (range 5.6% to 17%, b = 0.177). The smallest 6% of males (WL < 2.65 mm) in the general population did not appear in samples of males in ascending male-female pairs.

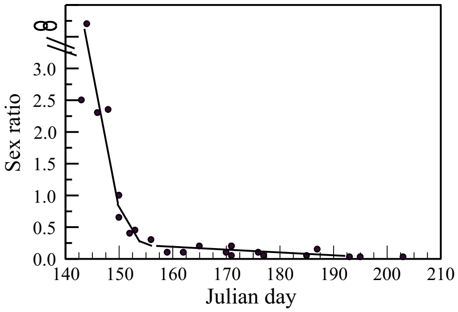

Fig. 8 Changing sex ratio, May–July (data from more than one year)

Stacking Defense On the afternoon of 23 June 2015 large numbers of predatory robber flies (*Leptogaster* sp.) were seen attacking all swarms of *Hilara* sp. along a stretch of the creek at Westwood Lane several hundred meters long. Only one pair of large, stacked, clockwise-rotating swarms remained intact. In this pair of swarms, only a few centimeters separated the eastbound stream of the bottom of the upper swarm from the westbound stream of the top of the lower swarm.

Discussion and Conclusions

Absence of Nuptial Gifts The absence of nuptial gifts in mating swarms of *Hilara* sp. is highly unusual; male Empidinae typically transfer such gifts to females prior to copulation (Cumming 1994). Possibly, long diel duration of swarm activity may explain, at least in part, this absence. Forrest (1985) observed the transfer of balloons in swarms of a *Hilara* species that persisted for only about 20 min per evening. In contrast, swarms of *Hilara* sp. in the present study sometimes persisted for hours. Sadowski et al. (1999) remarked that a nuptial gift carried in flight would cause aerodynamic drag. *Hilara* sp. might not be able to tolerate this drag over long hours of flight activity. A related consideration is angle of approach. Males of gift-bearing

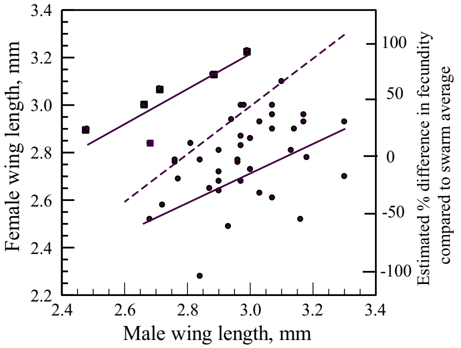

Fig. 9 Size-assortative pairing: WLs in 46 male-female pairs rising from swarms. Dashed line, WL equal in males and females; squares, pairs in which female WL > 6% of male WL; dots, female WL/male WL < 1 or only marginally (<1%) greater; horizontal line, mean wing length based on sample of 65 females in general swarm population. Right-hand ordinate, relative fecundity of different-sized *Hilara* females, estimates based on studies of various insects by Carron (2007) and Honěk (1993)

Hilara species may approach females from various angles, whereas males of *Hilara* sp. must keep pace with females within the rotating swarm before they even have the opportunity to approach.

Expanded Basitarsi As already noted, males of *Hilara* sp. possess expanded forebasitarsi. If, as it appears, these basitarsi neither produce silk nor hold prey items as they do in the large majority of *Hilara* species, what might be their function? The expansions may serve as sexual recognition tokens. As Fig. 4B suggests, there are occasions of sexual confusion, and males may demonstrate their sexual identity by displaying their expanded basitarsi either to either females or other males. Grootaert (2004) came to a similar conclusion in his study of a Malaysian species (*Hilara isaanensis* Grootaert & Kiatsoonthorn) in which some males were asymmetric, possessing expanded basitarsi on either the right or left foreleg. Likewise, Daugeron et al. (2010) proposed the explanation of sexual recognition in their study of an asymmetric Japanese species (*Empis jaschhoforum* Daugeron). Males of *Crabro cribrellifer* (Packard) offer an interesting parallel in that they cover a female's compound eyes with elongate foretibial plates during mating (Low and Wcislo 1992).

Avoidance of Inbreeding Depression Many of the observed swarm behaviors stem ultimately from the habit of swarming in patches of sunlight and the habit of assembling in the same patches year after year. These habits hold populations at low numbers and tend to isolate populations from each other. In May of 2016 the average interswarm distance along Dutch Bill Creek was 26.1 m; along the creek at Westwood Lane the average separation was 18.7 m. A fly leaving one patch of sunlight would be unlikely to encounter a swarm in a nearby patch because patches outnumber swarms. Furthermore, since a nearest neighboring swarm might be quite small (e.g., <20 individuals), joining it might offer relatively little benefit. In such conditions, inbreeding depression is a recurrent threat (Fox and Scheibly 2006). To counteract this threat, *Hilara* sp. appears to have evolved a variety of behaviors that maximize heterozygosity.

Promiscuity The genetic benefits of promiscuous mating can include increased heterozygosity (Jennions and Petrie 2000). Incontrovertible evidence of promiscuity in *Hilara* sp. is lacking because of the extreme difficulty of distinguishing between actual copulation and close but non-copulatory interactions. However, the mere existence of swarms over a period of months in a univoltine species such as *Hilara* sp. strongly argues for the existence of promiscuity in both sexes. If males and females mated only once, they would leave their swarms after mating and the swarms would soon disappear for the remainder of the year. If only one sex mated promiscuously, individuals of the opposite, monogamous sex would soon be left without potential mates. In a meta-analysis of 122 experimental studies Arnqvist and Nilsson (2000) confirmed that polyandry in female insects leads to increased production of offspring. Polyandry developed in a laboratory population of the red flour beetle, *Tribolium castaneum* (Herbst), in response to inbreeding with males carrying genetically incompatible haplotypes (Michalczyk et al. 2011). The same mechanism may explain the development of polyandry in *Hilara* sp. In some insects this benefit is augmented by cryptic female choice. Bretman et al. (2009) state that "promiscuous females avoid inbreeding by controlling sperm storage."

Sexual Selection Many rising pairs of *Hilara* sp. were observed to interact either by actually contacting each other or by approaching each other closely while remaining separated. Although details of these interactions could not be observed, it is clear that they must involve sexual selection. If male *Hilara* deplete their seminal fluid at the same rate as bed bugs, i.e., 19% per copulation (Reinhardt et al. 2011), *Hilara* males would be able to mate with only five females before their seminal vesicles would have to be recharged. Given a pairing rate of 257/h and a successful copulation rate of 5/h, the pairing failure rate would be 98% over a one-hour period. This high failure rate implies stringent sexual selection by females in rising pairs.

Swarm Recruitment Both turning movements and up-and-down translational movements are presumed to make swarms more visible to potential recruits, and increased recruitment equates to more mating opportunities and less inbreeding. Large swarms of *Empis borealis* (L.) attract more males than small swarms and support higher mating rates of both sexes.

Back-and-Forth Turning and Up-and-Down Movements Both turning and up-and-down movements may result from random, asymmetric density fluctuations within the swarm itself. If any section of a swarm were to become asymmetrical with respect to density, e.g., if the density of flies on one side of a swarm's long axis were to decrease momentarily for any reason, flies returning from the terminal extensions (Fig. 1e) to the main body of the swarm might join the opposing, denser, more visible concentration to preserve a constant distance from their neighbors. The expected consequence would be a turning of the swarm in the direction of the denser side. Essentially the same analysis would apply to up-and-down movements which presumably are caused by vertical asymmetries. Both types of swarm movement would result from flies' following the three rules of swarming behavior advanced by Reynolds (1987): "Move in the same direction as your neighbours, remain close to your neighbours, and avoid collisions with your neighbours." The bar graphs of Figs. 3 and 5 approximate random, normal distributions, thereby supporting the argument that the swarm movements are caused by random density fluctuations. This analysis, if correct, leads to a surprising conclusion: Although the movements are beneficial in that they enhance swarm recruitment, they have no genetic underpinnings. Rather, the movements are emergent properties that arise entirely from random statistical fluctuations.

Protandry Bulmer (1983) remarks that protandry "is common in insects in which females mate once only soon after emergence" and that in such insects early-emerging males have more opportunities to mate than late-emerging males.

Swarm mixing Intra-swarm mixing occurs when flies follow long paths in terminal swarm extensions (Fig. 1) or return to a swarm after pairing outside it. Intra-swarm mixing also occurs after flies join an interior cycle. The sporadic nature of interior cycles implies that the benefit of rapid reintroduction to the pair-forming arena is relatively small. Males may typically require more time to locate potential mates than the short-cut interior cycle affords.

Although continuous, within-swarm mixing would increase heterozygosity, it would not maximize heterozygosity throughout the entire population present at any given site.

Inter-swarm mixing occurs when flies travel from one swarm to another and when two swarms coalesce. Swarm dissipation may also be such an adaptation, since flies leaving one component swarm would be expected to join another.

The rate at which males within a component swarm reduce their pairing opportunities can be expressed as a power of the sex ratio. For example, in a component swarm consisting of one male and 20 females, the probability that a male will encounter a female which he has not previously encountered is $.95^{n-1}$ where n is the male's total number of encounters with females. After four encounters, the probability that his fifth encounter will be with a previously unencountered female is $.95^4$ or .814.

Cooperation between Swarms Two stacked *Hilara* swarms at the creek at Westwood Lane remained intact even while being heavily attacked by dozens of *Leptogaster sp.* Nearby unpaired swarms were severely disrupted. Apparently, the predators were less successful in coping with a binary swarm in which two of the four traffic streams were close together and moving in opposite directions (one east-to-west, the other west-to-east). Olson et al. (2013) demonstrated the formation of particle swarms in response to predator attack and showed that predator confusion was the underlying mechanism. Predator confusion might also underlie the evolution of swarm cooperation in *Hilara* sp. Another type of swarm interaction that could be considered cooperative was the synchronized rotation about a vertical axis of adjacent pairs of *Hilara* swarms at Dutch Bill Creek. Synchronization allowed swarms to remain near enough to each other to exchange members, thereby increasing heterozygosity and diminishing the threat of inbreeding depression. This may be the first example of cooperation between independent animal swarms.

Size-assortative Mating Assortative mating is asserted to have important evolutionary consequences such as increased homozygosity (Lynch and Walsh 1998). Sperm competition is believed to be the driving force behind sex-assortative mating (McDonald and Pizzari 2016).

Female fertility is proportional to body size in many insects (Honěk 1993). The same relationship would be expected to hold true in *Hilara* sp. *Hilara* males of all sizes might therefore be expected to pair preferentially with the largest available females, yet, as Fig. 9 indicates, this was not the case. Rather, each male tended to pair with females somewhat smaller than his own size. Small males that pair with females smaller than the size required to minimize sperm competition sacrifice a portion of their reproductive potential. A similar trade-off operates in damselflies (Waage 1979). Assortative mating in *Hilara* sp. therefore appears to be maintained by a balance of the opposing selective pressures of sperm competition from larger males and reduced reproductive potential associated with mating with small, low-fertility females. The exact balance point between these two selective pressures depends upon male size.

Although the present study did not include relationships among wing length, dry body weight, and fecundity, these relationships are of interest for the light they might shed on the selective factors underpinning size-assortative mating in *Hilara* sp. Dry weight in the mosquito *Ochlernotatus caspius* (Pallas) increases 50% in linear relationship with wing length as wing length increases 10% from a low of 2.45 mm (Carron 2007). Assuming a similar proportional increase in *Hilara*, dry weight would increase 210% as wing length increased 42% from a measured low of 2.28 mm. How would this increase in dry weight be expected to affect fecundity? Honěk (1993) calculated a common regression for 57 species of various insect orders, finding a 0.95% increase in median fecundity for each 1% increase in dry body weight. Therefore, median fecundity in *Hilara* sp. can be inferred to increase by 199.5% from the smallest to the largest female specimen collected. This scale is shown in modified form on the right-hand ordinate of Fig. 9.

Figure 9 indicates that small-to-medium-sized males have two distinct preferences: either females that are slightly smaller than themselves or females that are much larger than themselves. This novel mating system can be termed "dual-preference size-assortative mating." The six square data points at the upper left of the figure represent small-to-medium-sized males (WL 2.48–3.04 mm) paired with larger-than-average females (WL 2.84–3.23 mm). Males that mate with much larger females gain a reproductive advantage varying from 35 to 85%. Furthermore, in these unequal matings, sperm competition from large males (WL ≥ 3.05 mm) is moderate because, as Fig. 9 indicates, large males generally prefer females smaller than themselves.

Within-swarm Natural Selection Within-swarm natural selection against individuals impaired by inbreeding depression can be presumed to be intense. Any individuals unable to keep pace with the rapid streaming of their fully-functional counterparts would be at a severe disadvantage in finding mates. The need to keep pace with flies in the mainstream of the swarm would establish a strict fitness threshold. Thus, swarm rotation is, in effect, a sieve that filters out deleterious genes and contributes substantially to the ability of small, local populations of *Hilara* sp. to persist in relative isolation from each other.

Multicomponent Swarms A multicomponent swarm is defined by its possession of emergent properties. The set of all *Hilara* swarms present at a particular site appears to meet the test of emergent properties. In *Hilara* the emergent properties include: (1) *Spatial extension*. A multicomponent swarm extends over a substantial area precisely defined by the boundaries of its resource, i.e., the sunlit patch in which it occurs, whereas subcomponent swarms in a large sunlit patch may drift from one part of the patch to another. (2) *Continuity*. A multicomponent swarm dissipates at the end of each day and reconstitutes itself on the following day from the same population of adult flies; only the configurations and memberships of its component swarms change. (3*) Reproductive potential*. Unlike ephemeral subcomponent swarms, a multicomponent swarm has a theoretically quantifiable reproductive potential. (4) *Population stability*. Numbers of flies in subcomponent swarms vary on time scales too short (sometimes only seconds) for the components to qualify as biological populations. By contrast, the number of flies in a multicomponent swarm can remain more-or-less stable over a period of weeks. (5) *Gene flow*. Although in standard usage this term usually refers to exchanges of genes between populations, the parallel between separate populations and individual swarms in a multi-component swarm seems close enough to warrant its use in the present context.

Unanswered Questions Perhaps the most striking unexplained characteristic of swarms of *Hilara* sp. is their variability. Closely adjacent swarms at Dutch Bill Creek turned synchronously, but adjacent swarms did not appear in all years at that location and not at all at the other two study locations. How do swarms synchronize their turning if, as evidence suggests, an isolated swarm turns as a result of random, asymmetric fluctuations in swarm density? A secondary, interior cycle formed in some swarms at Dutch Bill Creek, but such a cycle did not appear at either of the two other study sites. How does turning behavior arise and evolve in a population given that any swarm composed of both turning and non-turning members would be highly unstable? In addition to these fundamental questions of swarm behavior, there are more particular questions of mating behavior and development. Does a male recognize a target fly as female before he intercepts her within a swarm? Are females autogenous (i.e., having fully-developed eggs from the moment of adult eclosion) as the absence of nuptial gifts suggests? Further research might provide answers.

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Compliance with ethical standards

Conflicts of interest The author declares that he has no conflicts of interest.

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