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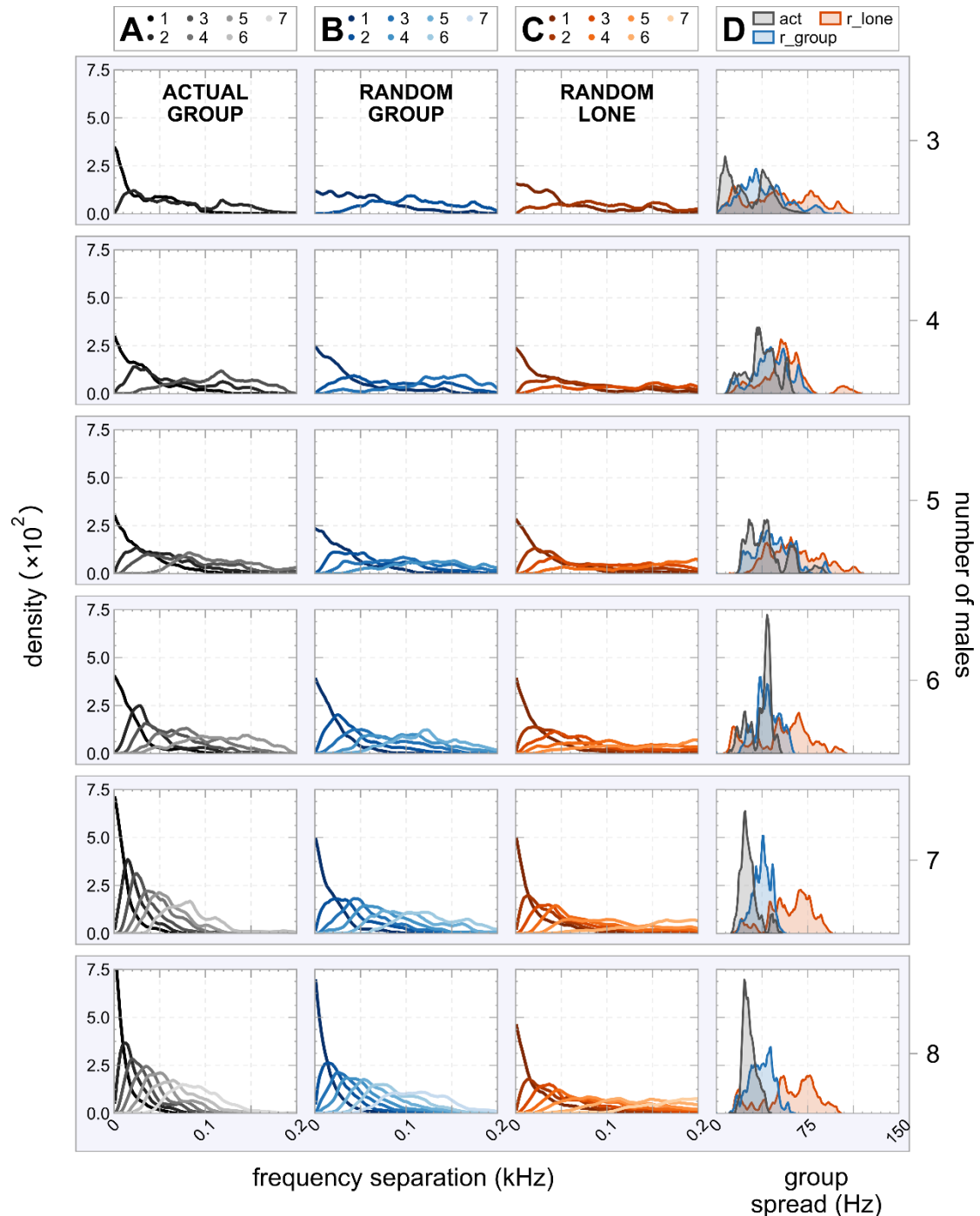
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Supplemental Information: Emergent acoustic order in arrays of mosquitoes

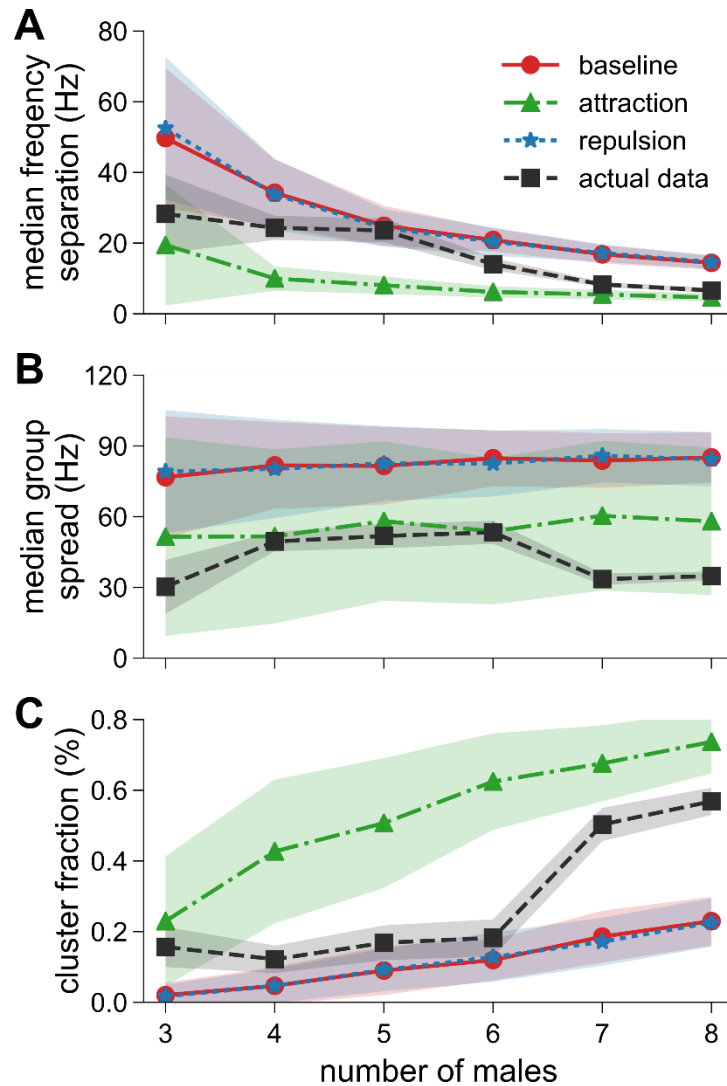
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Figure S1: Probability distributions of k^{th} -nearest neighbour frequency separation and group-wide flight tone spread for live recordings and randomised arrays



(A)-(C) Normalised distributions showing absolute pairwise wing beat frequency differences between a male and his closest (1), second closest (2), third closest (3), etc., flight tone match aggregated over every mosquito in a given array size. For all individuals, separation magnitudes are ranked at each instant in time (see Data Analysis in Supplemental Experimental Procedures). Data shown are for (A) actual recordings, (B) random groups, and (C) random lone permutations. (D) Normalised distributions of the instantaneous group-wide flight tone spread, aggregated across all arrays at a given size for live recordings (“act”), random group (“r_group”), and random lone (“r_lone”) data. For the randomised groups, distributions shown are from a single permutation of the sampling procedure. All distributions are computed at 2Hz intervals.

Figure S2: Results of computational simulations showing summary statistics of modelled groups compared to those of actual recorded groups



Behavioural model results showing summary statistics (equivalent to those presented in Figure 1D-F) of differently-sized groups simulated under different interaction regimes contrasted against data obtained from actual experimental recordings. (A) Median frequency separation between a male and his closest instantaneously sorted wing beat frequency match. (B) Median instantaneous group spread. (C) Mean cluster fraction, or the fraction of recording/simulation time for which a given male has at least two others within 20Hz of his own flight tone. For models, results are the mean (\pm standard deviation) from 200 replicate simulations at each group size. For actual data, the shaded region is the standard deviation obtained over 1000 permutations whereby R groups of size N are randomly sampled with replacement (specific combinations of N and R given in Figure 1 caption).

Supplemental Experimental Procedures

Mosquito husbandry

Aedes aegypti eggs obtained from the London School of Hygiene and Tropical Medicine (original field material West Africa) were hatched by submerging in containers filled with deoxygenated distilled water. Larvae were fed on a diet of four crushed pellets of dried cat food, given every 3 days. Upon emergence, pupae were placed individually into 15ml Falcon tubes, covered at the top with cotton wool. Adult males were released into flight cages (net-covered wire frames of size 40×20×20cm) and offered a 20% glucose solution. All juveniles and adults were held on a D16:N8 circadian cycle inside a temperature (26°C) and humidity (60-80%RH) controlled laboratory.

Behavioural assays

Individual virgin male mosquitoes between 2 and 7 days old were extracted at random from flight cages using an insect aspirator. We typically extracted $2N$ males — N being the size of the largest array we desired to record in any single experiment during that particular session, ranging from $N = 3 - 8$ individuals. Whilst sedated by exposure to cold (induced by placing the insects on ice for 60 seconds), individuals were affixed to the rounded end of an insect pin on the dorsal surface of the thorax using liquid latex (according to established methodology in [S1–S4]). After allowing the insects sufficient time to recover (adjudged to be the point at which regular flight could be successfully stimulated, typically less than 10 minutes), they were introduced to the recording array. Only males that demonstrated consistent uninterrupted flight were selected for live recordings.

The recording arena itself comprised of several components, depicted schematically in Figure 1A. First, a mounting platform with a linear array of small holes drilled at 30mm intervals, similar to the separation distances used in previous studies of local acoustic interactions between mosquito pairs [S1–S4] and thought to be the approximate range over which pursuit behaviours are triggered [S5]. Tethering pins were loaded into this with plastic adhesive Blu-Tack (Bostik Ltd, Leicester, UK, a small <5mm sphere was used for each pin), which also acted as a damping material to reduce the potential for transmission of mechanical vibrations between flying individuals through the platform. Beneath each tethered mosquito, at a distance of around 10mm (beyond the range of physical contact), was placed an electret condenser microphone (FG-23329-C05, Knowles Electronics, Itasca, IL, USA), which enabled the recording of every individual in the array on a separate unique channel (as performed with pairs in [S4]). This apparatus was placed inside a soundproofed box with a removable front access panel. The microphones were passed through a custom-built integrating multi-channel sound amplifier [S6] and logged digitally at a sample rate of 10kHz using a National Instruments USB data acquisition device (National Instruments, Austin, TX, USA).

Individuals were placed in the arena facing the darkened back wall to minimize any potential visual disturbances. Recordings were initiated by inducing flight in all test subjects, which was achieved by gently blowing across the array or through tarsal contact. The males were “startled” into flight before relaxing to normal wing beat activity [S3]. Recordings lasted 30 seconds (after the initial startle period). Between trials, the positions and identities of males were randomly shuffled, utilising as many individuals from the collected pool as possible. All experiments were performed between 1200h-1600h on the mosquito diurnal cycle (i.e. towards the beginning of the evening) in a temperature-regulated laboratory (range: 24-28°C).

Signal processing and extraction of wing beat frequencies

The mosquito wing beat produces an acoustic signal consisting of a high-energy fundamental frequency stacked with progressively weaker harmonic overtones at integer multiples of the main pitch [S7,S8]. In several mosquito species – including *Aedes aegypti* – there is a high degree of sexual dimorphism, with males and females producing fundamental wing beat tones that are essentially non-overlapping [S8]. Thus, opposite-sex acoustic signalling is known to involve the sensing and interaction of (overlapping) harmonic sound components [S1–S4]. In this regard, male-male acoustic interactions likely take place at the fundamental, where there is substantial frequency overlap between individuals [S1,S3,S4,S9]. We therefore extracted the fundamental flight tone component of individual males, which was performed using previously developed signal processing tools [S8]. Briefly, this involves automated detection of frequency “peaks” on each digital channel, adaptive signal filtering, and subsequent extraction of time-evolving instantaneous wing beat frequencies (as a set of 1-dimensional time series) via Hilbert spectral analysis [S8,S10,S11]. Time-frequency spectra for all arrays were screened prior to further analysis; only those in which all mosquitoes exhibited consistent simultaneous flight for at least 20s were used.

Data analysis

To quantify acoustic effects in recorded groups of mosquitoes we derived a set of measures to capture both individual and group behaviours. The calculation of these metrics is described below.

Frequency separation to k^{th} -nearest neighbour

The difference between the fundamental flight tones of two mosquitoes has previously been demonstrated to be a useful means to quantify their interaction [S4]. In a group of size N , every individual has $N - 1$ partners with whom an interaction can potentially take place (the auditory sensitivity of the male mosquito being such that detection of more than just nearest spatial neighbours on the array is possible [S5,S12]) and – at each sampled time point – is acoustically separated from them by some amount in the frequency domain. By sorting these pairwise differences according to their magnitude, we are able to determine the separation between a given male and his k^{th} -nearest wing beat frequency neighbour ($k = 1, \dots, N - 1$; $k = 1$ being the smallest frequency differential) at any moment in time. The aggregated distributions of this measure through time and across all individuals for a given array size are shown in Figure S1A, while the median for $k = 1$ is plotted in Figure 1D.

Group-wide flight tone spread

To measure group-level acoustic characteristics in our recordings we calculate the standard deviation across the wing beat frequencies of males at each instant in time. Aggregating this metric over all arrays for a given number of mosquitoes yields the distributions shown in Figure S1D (black line). The median value of these distributions is plotted in Figure 1E.

Cluster fraction

Clustering in wing beat frequency space is measured as the proportion of time for a given recording that a particular male has at least two neighbours within 20Hz of his own flight tone. That is, the magnitude of the separation between a male and his 2nd-nearest frequency neighbour is less than or equal to 20Hz. Figure 1F shows the mean cluster fraction aggregated over all males as a function of group size.

Permutation sampling

Mosquito wing beat frequencies are constrained by the physiological limits at which flight can be sustained. It is thus possible that observations on the effect of group size on the acoustic characteristics of individuals are an artefact caused by saturation of the available frequency space as more males are introduced to the swarm. We used permutation (or randomisation) testing [S13,S14], whereby experimental data are randomly reshuffled and reassigned into new groups, to determine the significance of our results through the calculation of various test statistics (specifically, the median frequency separation to the closest neighbour, the median group spread, and the mean cluster fraction, as described above). By repeating the randomisation many times (thus generating a large number of permutations), we can compare the distribution of possible outcomes for a particular test statistic to that of the actual data, giving us a probability that the value of the test statistic from the observed data appeared by chance [S14]. In animal behaviour studies, which often yield data that are not amenable to standard parametric testing, this may prove a more effective means to evaluate proposed hypotheses [S15]. There are many examples of the use of this technique in the behavioural ecology literature, for examples see [S16–S19].

The generation of artificial arrays of male mosquitoes here follows a simple randomisation algorithm. The artificial arrays are constructed using either flight recordings of males flying in groups (data collection described above, “random group”), or of those flying alone (data from [S8], “random lone”). Suppose then that we have R different recordings of male insects in an array of size N and wish to create an artificial array, of size N , from these samples. To fill each position i (where $i = 1, \dots, N$) we choose, at random, the frequency time series of a mosquito at location i from one of the R recordings. We then discard that particular trial from the remainder of the process, so that no artificial group contains more than one signal from the same live recording (note that $\forall N: R > N$). This routine is repeated until all positions in the array are occupied. When creating an artificial group from lone recordings, the condition of positional preservation does not apply and is simply dropped. We repeat this procedure 1000 times, thus generating 1000 random samples of R arrays containing N individuals. The specific combinations of N and R used are as follows: $N = 3: R = 14$; $N = 4: R = 17$; $N = 5: R = 17$; $N = 6: R = 13$; $N = 7: R = 14$; $N = 8: R = 15$.

Modelling interaction behaviours

To test hypotheses about the possible mechanisms underlying mosquitoes’ flight tone dynamics, we develop simple individual-based models for male mosquito behaviour in frequency space. Our models are conceptually similar to those in which individuals respond to the spatial movement of others [S20], but instead of considering spatial positions and movement, we model interactions in the frequency domain mediated by individual flight

tones. We contrast three models and associated hypotheses for how mosquitoes interact. First, we consider a “baseline model” in which individuals do not interact. Second, we implement a “repulsion model” inspired by observations that males avoid the flight tones of others [S1,S3,S21]. Third, in the “attraction model” we hypothesise that males seek to match the flight tones of other nearby males, which although commonly associated with opposite-sex interactions [S1–S3,S22], has also been readily observed among male pairs [S4]. A full description of these models, and how they are fit to the experimental data, is presented below.

We model the flight tone time series of individual male mosquitoes, $\omega_i(t)$ (where $i = 1, \dots, N$) at a temporal resolution of $\Delta t = 0.01s$ (i.e. a sampling frequency of 100Hz). Based on our experimental observations, all models assume that male flight tones are limited by preference or physiology to a frequency band between 500Hz and 800Hz. Our baseline model assumes that males do not interact and that they perform an unbiased random walk. The flight tone of each individual is thus updated according to $\omega_i(t) \sim N_T(\omega_i(t - \Delta t), \sigma)$, where N_T denotes the truncated normal distribution with upper and lower limits defined by the assumed frequency band and the standard deviation σ is a model parameter.

The remaining models are similar in structure to the baseline model, but suppose that interactions with conspecifics introduce a bias in the flight tone of males. We assume that males respond to the flight tones of all other individuals within a fixed radius r in frequency space. If no individuals are within this radius of a focal male, it reverts to the baseline model behaviour. In the repulsion model, flight tones update at each time step so that each male is repelled (in the manner of a biased random walk) from the average of all other males within the radius r . That is, $\omega_i(t) \sim N_T(\omega_i^{rep}(t), \sigma)$, where $\omega_i^{rep}(t) = \omega_i(t - \Delta t) + \alpha x^{rep}$. The model parameter $\alpha \geq 0$ governs the strength of repulsion, while x^{rep} gives the direction pointing away from the average frequency of all other males within r , determined as $x^{rep} = \text{sign}[\omega_i(t - \Delta t) - \sum_j \omega_j(t - \Delta t)/N_j]$. Here, the sum over all j is such that $j \neq i$ and $\text{abs}[\omega_i(t - \Delta t) - \omega_j(t - \Delta t)] \leq r$. N_j is the number of males within a distance r from i . Similarly, for the attraction model we use $\omega_i(t) \sim N_T(\omega_i^{att}(t), \sigma)$, where $\omega_i^{att}(t) = (1 - \beta)\omega_i(t - \Delta t) + \beta[\sum_k \omega_k(t - \Delta t)/N_k]$. Here $\beta \in [0,1]$ is a model parameter which determines the strength of attraction, and the index k runs over all individuals such that $|\omega_i(t - \Delta t) - \omega_k(t - \Delta t)| \leq r$, with N_k being the number of males within r from i (including i). Both the repulsion and attraction models are thus able to capture weak and strong interactions between individuals (low and high values of α and β , respectively).

We compare these models to our experimental data by computing the same summary statistics shown in Figure 1D-F for the modelled flight tone dynamics. Model simulations run for 1,000 update steps (i.e. 10s) and we initialise the flight tones of individuals by placing them randomly inside the permitted frequency range. The model parameter σ is determined directly from the data by computing the standard deviation of the distribution $\omega_i(t) - \omega_i(t - \Delta t)$ across all time points and individuals. The additional parameters r , α and β for the repulsion and attraction models are determined using a broad parameter scan. We run 50 replicate simulations for all possible combinations of parameters in the sets $r \in \{1, 3, 5, \dots, 49\}Hz$, $\alpha \in \{0.01, 0.11, 0.21, \dots, 0.81\}$ and $\beta \in \{0.018, 0.047, 0.12, 0.27, 0.50, 0.73, 0.88, 0.95, 0.98\}$ and determine the parameter combination for which the squared error between simulated and experimental summary statistics across group sizes is minimised. We normalise the experimental summary statistics across group sizes by subtracting the minimal value and dividing by the range of values, and apply the same normalisation to the summary statistics obtained from simulations. Using this procedure, we find the following parameter values and use them to generate the results shown in Figure S2: baseline model: $\sigma = 4.43Hz$; repulsion model: $\sigma = 4.43Hz, r = 3Hz, \alpha = 0.11$; attraction model: $\sigma = 4.43Hz, r = 49Hz, \beta = 0.047$.

Supplemental Discussion

Time-frequency observations

The mean wing beat frequency of all males recorded was 681.1 Hz, consistent with analyses of lone (684.4 Hz [S8]) and paired (691.1 Hz [S4]) male *Ae. aegypti* (one-way ANOVA; $df = 2$, $F = 0.36$, $p = 0.70$). Larger groups display an increasingly uniform flight tone density over the range of frequencies that are biologically plausible (Figure 1B). In addition, group size had a significant effect on the average variability of an individual male’s wing beat frequency (one-way ANOVA; $df = 5$, $F = 6.16$, $p < 0.001$). As the number of males in the array increases, both the between- and within-male flight tone variance decrease.

Visual inspection of time-frequency plots (samples in Figure 1B) indicates that groups exhibit a diverse set of dynamic frequency-based behaviours. These include pairwise convergence of flight tones — associated with male-female courtship [S1–S3,S23–S25] but also identified [S1] and quantified [S4] in same-sex pairs — “hunting” of one another’s wing beat signal (characterised by rapid modulation and/or transient excursion of flight

tones) [S1,S4], and frequency divergence [S1,S3,S4]. Such behaviours appear to varying degrees within swarms, over a range of timescales, often in combination with one another, and may involve more than two males. Flight tone modulation is at times then co-ordinated across multiple individuals into subgroups that remain in close frequency proximity for some duration of time, displaying within them some or all of these qualitative acoustic properties. It is important to note that such observations are thought to be the result of acoustic interactions between the individuals, as opposed to other physical phenomena (such as mechanical coupling through airborne or tethered vibrations) [S4]. Acoustic sensing of conspecifics is a highly important of mosquito biology [S26] and deafened individuals have been shown to not attempt to acoustically engage with others [S1,S2]. It is thus unlikely that explanations of interactions based on non-acoustic responses are sufficient to account for our observations among groups.

The qualitative description provided above, while useful in informing initial investigations and hypotheses, is inherently limited by its subjectivity. This motivated us to develop more quantitative means to study emergent acoustic properties in our experimental swarms. There are several advantages to the approach we have taken. Firstly, it enables us to aggregate and summarise frequency-based interactions and phenomena across many individuals using a set of simple descriptive statistics (outlined previously), and facilitates direct comparison between groups of different size. Secondly, and following on from the first point, it invites the use of permutation sampling for significance testing (described below), and can be easily used to interpret the results from a large number of interaction model simulations (Figure S2).

Permutation sampling

We permuted across two data repositories to generate non-interactive arrays of mosquitoes: in the first instance, we sampled from recordings of male mosquitoes flying in groups (i.e. data collected in this study, “random group” arrays), and in the second instance from recordings of individuals flying alone (data from [S8], “random lone” arrays). The reasoning behind using these two different recording types was to investigate whether group context had any effect on male frequency characteristics, even when direct interactions in the group were absent (i.e. do males in groups behave fundamentally different to those recorded alone?).

In both non-interactive array types, the average minimum inter-individual frequency separation decreases with increasing group size, much as it does for the live experimental recordings (Figure S1A-C). In addition, as in the live arrays, an increased structuring of all ranked flight tone differences is observed in the non-interactive groups, with the distributions of frequency differences becoming increasingly peaked for $N \geq 6$ (Figure S1A-C). At the group level, the distributions of flight tone dispersal show much overlap for actual and non-interactive groups when $N \leq 5$ (Figure S1D), and a broad range of flight tone configurations are found. For $N \geq 6$ however, as in the live recordings, we observe the appearance of a prominent peak in the “random group” distributions which is not seen in the “random lone” arrays (Figure S1D). While this effect does not occur to the same degree as in our actual data, it does serve to highlight the clear differences between mosquitoes sampled from grouped and lone recordings. Mosquitoes recorded in a collective environment exhibit demonstrably different acoustic characteristics from those recorded in isolation. The effect of the collective can be seen even in random combinations of non-interacting mosquitoes taken from grouped recordings, which are themselves quite different to ensembles constructed of individuals flying alone.

On average, both the minimum frequency separation and spread of group flight tones were always lowest in the live recordings – rather than non-interactive groups – for all group sizes tested (Figure 1D,E). We can investigate the statistical significance of this effect by comparing summary measures from a large number of permutations of the non-interactive arrays to those of the live recordings. Specifically, we generated 1000 samples (of size R : see methodological details above) of both the “random group” and “random lone” group types at each array size. For each of these permutations, we computed the median minimum flight tone separation (across all individuals), median flight tone dispersal, and mean cluster fraction. By counting the number of times each statistic was smaller than the corresponding measure in live arrays we effectively generate a “p-value”, allowing us to test the null hypothesis that our measurements from mosquitoes recorded together occurred by chance. We used a threshold requirement that $p < 0.05$, i.e. that the statistic for the non-interactive array could only be smaller than that of a live group in 5% of cases, to test significance. Under this framework, rejection of the null hypothesis consistently occurs only in the largest group sizes recorded ($N = 7,8$). In smaller arrays, we cannot rule out the possibility that random process (i.e. epiphenomena) are responsible for the observations described. These results indicate a detectable shift from potentially passive (arising without the need for interaction) to actively modulated (requiring a dynamic behavioural response) acoustic characteristics as the number of individuals in the group is increased.

Comparing male-male interactions in pairs and groups: observations and modelling

In previous studies of tethered *Toxorhynchites* [S1] and *Culex* [S3] mosquitoes, paired-male sound interactions were reported to involve brief bouts of convergence and hunting, yet always culminated in fixed divergence, with the individuals stabilising at dissonant wing beat frequencies. It was suggested that, in free-flight, this would lead to an increase in the physical separation between the mosquitoes [S1,S21]. Acoustic interactions between pairs of male *Ae. aegypti* mosquitoes are diverse, but do not consistently result in divergence [S4]. Rather, their nature may be determined by the initial proximity of the males in frequency space; smaller differences in fundamental flight tones increase the likelihood that convergence and/or hunting behaviours will occur [S4]. Such processes are also likely to act among larger groups, too, where a regime of strict flight tone avoidance would appear contrary to the cohesive acoustic properties of swarms we report here.

This assertion is supported by the results of simulations that modelled the flight tones of mosquito swarms under different interaction regimes. Models based on frequency avoidance yielded results essentially equivalent to those in which interactions were entirely absent, while only those incorporating attraction were able to qualitatively reproduce our observations of live swarms (Figure S2). We do not purport that these models capture entirely the dynamics of acoustic interactions taking place within groups of male mosquitoes, and there is clearly much scope to increase their complexity. Rather, their intended use is in testing of simple behavioural and mechanistic hypotheses that are often submitted based on experimental observation. To that end, we can conclude from this that (a) male mosquitoes in groups certainly interact with one another in an acoustic sense, and (b) this interaction involves a combination of both wing beat frequency attraction and repulsion. Acoustic interactions between mosquitoes likely act over various spatial, temporal, and frequency scales. To understand how these behaviours manifest, it will be necessary consider them in relation to other aspects of the mosquito ecology that may be influenced by such interaction (such as locomotion).

Collective behaviour in free-flying swarms

Studies of free-flying aggregations of mosquitoes and midges further substantiate a developing framework of swarm behaviour. Localised movement coordination, inter-individual coupling, and the density-dependent formation of velocity-matched subgroups have all been detected within natural groups of dipterans [S27–S32], and are characteristic of many collective animal systems [S20,S33]. Such traits are consistent with relationships that go beyond simple collision-avoidance, and indeed only those models which incorporate explicit local interaction terms adequately capture internal swarm dynamics [S29,S34]. However, the sensory basis of this interaction has arguably been under-explored. Several investigations have alluded to an “attractive force” operating at the level of the swarm that maintains its cohesion [S27,S28,S31,S32]. A range of mosquito species – including *Ae. aegypti* – are known to be stimulated into swarming by both visual, olfactory, and potentially auditory cues [S26,S35–S39], yet the influence of inter-individual interactions on swarm characteristics have not been sufficiently considered. More recent work (on midges) suggests that long-range acoustic sensing may be used to help model and quantitatively explain swarm behaviour [S34].

The emergent organisation of subgroups in the frequency domain that we report here also suggests further corroboration between observations in the acoustic and locomotive fields. Could flight tone clustering and motion alignment simultaneously be used by males to reduce local acoustic disturbances and thus best prime males to detect and respond to the sound of an incoming female? Conservative estimates of the mosquito hearing suggest that acoustic detection of conspecifics is possible at distances of up to 9-10cm [S12]. In the linear test arrangement we have used here, it is thus possible that any given male can hear others up to 3 positions away. Analysis of the structural composition of frequency clusters indicates that while on average they are always formed between individuals who are within this detection range, there is no inherent clustering bias for males that are particularly spatially close to one another (figure not shown due to spatial constraints; raw data available online, see [S40] for more information). Nevertheless, it is interesting to consider that the collective acoustic characteristics of groups that we have observed may well be the result of local sound interactions between individuals within one another’s field of sensory perception. In swarms of *Anopheles gambiae*, the average nearest-neighbour distance between males has been reported to be around 13cm [S28], yet this is known to decrease (to <5mm) with increasing density in other swarming insects [S41]. While detailed knowledge of how *Ae. aegypti* swarms are organised in space is currently lacking, the separation distance of 30mm used in this study is probably representative of “close encounters” between individuals engaged in interaction [S5,S42]. Swarming likely relies on the integration of varied sensory modalities operating at different temporal phases and spatial scales. In that respect, acoustics offer insight into the effect of local interactions on this dynamic behaviour that are not easily accessible in other domains.

Our analyses of the wing beat frequency properties of grouped mosquitoes indicate that increasing the number of males interacting with one another results in a transition in flight tone behaviours, which – through comparison with equivalently-sized non-interactive arrays constructed through a permutation paradigm – we propose is driven

by acoustic interactions between the individuals. Size-dependent, non-smooth transitions are common among aggregate systems (see, e.g., [S43–S45]). For *Ae. aegypti* mosquitoes, in the acoustic field, it takes place between $N = 6$ and $N = 7$, and is characterised by homogenisation of flight tone properties, a significant increase in within-group clustering, a reduced average inter-individual flight tone separation, and an overall tighter binding of each individual to the acoustic “centre” of the array. Qualitatively similar asymptotic behavioural limits have also been found in the spatial and kinematic properties of comparably sized swarms of free flying *Chironomus riparius* midges [S41]. Comparisons of our data to randomly generated artificial arrays lead us to reject the notion that these processes are epiphenomena driven solely by increased density in the frequency domain. The observed acoustic effects occur most strongly when individuals actively engage in frequency communication, and are less pronounced, or even absent, among non-interactive groups.

Studies of natural mating swarms of *Ae. aegypti* are relatively sparse [S46]. However, they are reported to be fairly small in size, containing an estimate of 12-30 individuals, the majority of which are male [S47]. It is thought that males are stimulated into swarming behaviour by the presence of others [S39]. The transition in acoustic behaviours of groups of males identified in this study (between $N = 6$ and $N = 7$) may thus reflect a lower-limit on what may be considered an interactive “swarm”, as opposed to a collection of non-interacting individuals aggregated within the same physical volume of space. At the very least, it is only at this scale at which acoustically-mediated individual communication becomes a prominent feature of the group’s internal dynamics.

Author Contributions

Conceptualization, A.A., D.R., A.C. and M.H. Methodology, A.A., N.B. and D.R. Software, Formal Analysis, and Investigation, A.A. and N.B. Funding acquisition, Resources, and Supervision, D.R., A.C. and M.H. Writing – Original Draft, A.A. Writing – Review and Editing, A.A., D.R., N.B., A.C. and M.H.

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