Close Kin Dyads Indicate Intergenerational Dispersal and Barriers

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ABSTRACT: The movement of individuals through continuous space is typically constrained by dispersal ability and dispersal barriers. A range of approaches have been developed to investigate these. Kindisperse is a new approach that infers recent intergenerational dispersal ($\sigma$) from close kin dyads and appears particularly useful for investigating taxa that are difficult to observe individually. This study, focusing on the mosquito Aedes aegypti, shows how the same close kin data can also be used for barrier detection. We empirically demonstrate this new extension of the method using genome-wide sequence data from 266 Ae. aegypti. First, we use the spatial distribution of full-sib dyads collected within one generation to infer past movements of ovipositing female mosquitoes. These dyads indicated the relative barrier strengths of two roads and performed favorably against alternative genetic methods for detecting barriers. We then use Kindisperse to quantify recent intergenerational dispersal ($\sigma = 81.5$–197.1 m generation$^{-1}$) from the difference in variance between the sib and the first cousin spatial distributions and, from this, estimate effective population density ($\rho = 883$–4,864 km$^{-2}$). Dispersal estimates showed general agreement with those from mark-release-recapture studies. Barriers, $\sigma$, $\rho$, and neighborhood size (331–526) can inform forthcoming releases of dengue-suppressing Wolbachia bacteria into this mosquito population.

Keywords: dispersal barrier, kinship, RADseq, Wolbachia, neighborhood size, Aedes aegypti.

Introduction

Dispersal is a widely studied process in ecology and evolution that describes how organisms and their progeny come to occupy different locations. Studies have typically investigated dispersal by either observing the specific movement of individuals or gametes (Howard 1960; Berry et al. 2004; Royle and Young 2008) or assessing the intergenerational outcomes of this movement (Wright 1943; Rousset 2000). At the individual level, approaches for investigating dispersal include those that measure movement rates over key life history stages, such as using mark-release-recapture (MRR) methodologies (Royle and Young 2008), and those that assign dispersing seeds to parent plants (Smouse and Sork 2004) or dispersing individuals to their origins (Berry et al. 2004; Schmidt et al. 2019). Approaches that consider dispersal at the population level often aim to estimate the intergenerational dispersal parameter, $\sigma$, the standard deviation of parent-offspring separation distances (Wright 1943; Broquet and Petit 2009). Together with local population density ($\rho$), $\sigma$ defines Wright’s neighborhood size ($N_W = 4\pi\rho\sigma^2$; Wright 1946), the effective number of potential mates or parents within one generations’ dispersal range. While dispersal can be usefully assessed at both individual and population levels, recent studies in spatial population genetics have moved toward resolving this conceptual duality via frameworks that characterize dispersal at both levels (Aguillon et al. 2017; Bradburd and Ralph 2019).

The evolutionary consequences of dispersal can be understood in relation to dispersal barriers and dispersal ability. Barriers that restrict or redirect dispersal can have major effects on the distribution, connectivity, and long-term persistence of wild populations (Ozinga et al. 2009; Berger-Tal and Saltz 2019). Recent and ongoing change in global land use has led to the addition of new barriers that are of particular concern for conservation (Debinski and Holt 2000), and the removal of preexisting barriers can spread biological invasions along new pathways (Hulme et al. 2008). Studies investigating the impact of barriers
that have recently changed or exhibit transient patterns of connectivity require methods capable of detecting their immediate effects (Landguth et al. 2010; Zeigler and Fagan 2014).

Besides barriers, dispersal ability itself works as an isolating force. Conspecific individuals distributed continuously through space are more likely to reproduce with nearby individuals when dispersal ability is limited relative to the spatial extent of the population, resulting in a decline in genetic similarity as distance increases (isolation by distance; Wright 1943). Connectivity within and between populations is strongly influenced by $\sigma$, which determines the spatial scale at which isolation by distance operates (Broquet and Petit 2009). Both distance and barriers affect connectivity within populations, though determining their relative strength is often difficult when barriers at specific geographical positions also subdivide individuals spatially (Cushman et al. 2006). Unrecognized spatial structuring within populations can have strong effects on later inferences (Neel et al. 2013; Battey et al. 2020).

A recently developed genetic approach, Kindisperse (Jasper et al. 2019, 2022), estimates dispersal distance parameters from close kin data. Kindisperse estimates $\sigma$ from the difference in variance between the spatial distributions of two or more kin categories, such as between full sibs and full first cousins. The specific kin categories used depends on the dispersal biology of the species, but individuals must typically be sampled at the same life stage (Jasper et al. 2022). In this regard, Kindisperse aims to summarize the dispersal variance across a single generation of the spatial pedigree (Bradburd and Ralph 2019) and can be considered a close-kin mark-recapture (CKMR) methodology (Bravington et al. 2016). This approach has operational advantages over MRR methods when applied to taxa that are difficult or costly to individually observe or where the marking process is intrusive. Estimates of $\sigma$ derived from close kin dyads have recently been validated in silico for different study designs (Jasper et al. 2022).

These same close kin data may also be useful for testing dispersal barriers. For instance, dyads of first-order kin (parent-offspring or full sib) observed on opposite sides of a geographical barrier indicate traversal of this barrier within the last generation or breeding cycle. As close kin provide information specific to the immediate past, they can assess barrier effects at very fine scales, such as where barriers are crossed in a single generation and individuals do not inhabit the barrier space. This may help evade lag time issues associated with investigating gene flow immediately after a barrier is added or removed (Landguth et al. 2010), which could make close kin methods better suited to detecting recent change than methods that infer barriers from allele frequencies (Bradburd et al. 2013; Botta et al. 2015; Petkova et al. 2016). Several studies have explored kin-based barrier detection methods, but by design either these are limited to assessing absolute barriers (Soanes et al. 2018; Schmidt et al. 2021) or they assess partial barriers but elide the effects of distance (Escoda et al. 2017, 2019); this effectively treats $\sigma$ as being much larger than the distance between sampling points. A more versatile means of barrier investigation would be useful, given that partial barriers are common and $\sigma$ is often relatively small.

Here, we develop a method for using close kin dyads to detect dispersal barriers that accounts for the relative densities and distances between sampling points, and we apply it to a population of Aedes aegypti (yellow fever mosquito) sampled continuously through space in the urban environment of Jeddah, Saudi Arabia. Studies of Ae. aegypti dispersal frequently report the effects of barriers such as roads (Maciel-de-Freitas et al. 2007; Hemme et al. 2010; Schmidt et al. 2018; Regline et al. 2021), but these have not estimated the strengths of specific barriers relative to other barriers and to distance. Here we do precisely that and show how our method based on close kin performs favorably at this scale against methods that consider the genetics of the entire population. The same close kin data are also used to estimate $\sigma$ with Kindisperse (Jasper et al. 2022), which has previously been applied to individuals clustered within apartment buildings (Jasper et al. 2019). We also use isolation by distance patterns to estimate $N_{w}$ (Rousset 2000). Given $N_{w} = 4\pi\rho\sigma^{2}$, we then use $N_{w}$ and $\sigma$ to estimate $\rho$, the effective population density.

Fine-scale information about barriers, $\sigma$, $N_{w}$, and $\rho$ is critically important for this population of Ae. aegypti, as this study site is currently being assessed for mosquito releases aimed at establishing a transinfection of Wolbachia in the local mosquito population following the success of releases with this strain in other areas (Nazni et al. 2019). Wolbachia are intracellular bacteria that inhibit dengue transmission when transinfected into Ae. aegypti (Walker et al. 2011), and Wolbachia can establish and spread through wild mosquito populations when transinfected mosquitoes are released in sufficient abundance (Barton and Turelli 2011; Schmidt et al. 2017). Establishment success can be strongly affected by barriers, which help maintain local infection frequencies above a critical frequency, $\hat{\rho}$, but also reduce the spread of Wolbachia into neighboring regions (Barton and Turelli 2011; Schmidt et al. 2017). Wolbachia release outcomes are also influenced by $\sigma$, which determines the area over which mosquitoes should be released, and $\rho$, which determines how many mosquitoes should be released per unit area (Barton and Turelli 2011; Schmidt et al. 2017). As well as barriers and $\sigma$, this study provides a comparison of $N_{w}$ in this and other Aedes populations, highlighting the utility of this parameter particularly when $\sigma$ can be estimated. Finally, we compare
dispersal estimates for Ae. aegypti derived from MRR studies with those derived from close kin dyads in this and one other study (Jasper et al. 2019).

Material and Methods

**Study Site and Sampling**

*Aedes aegypti* were collected in February 2020 from an ∼0.8 km² urban area in Jeddah, Saudi Arabia (fig. 1A). This area covers part of the Al-Safa 9 region in the Almatar Municipality in Central Jeddah, where *Wolbachia*-based control operations are currently planned, as well as areas to the south and to the west of Al-Safa 9. Al-Safa 9 was separated from the southern area by an ∼60-m-wide road and the western area by an ∼30-m-wide road. Roads within this size range have been previously identified as potential dispersal barriers for *Ae. aegypti* (Russell et al. 2005; Schmidt et al. 2017). Most buildings in Al-Safa 9 are apartments of three to six stories, and pedestrian traffic is frequent throughout the region. *Aedes* mosquitoes are abundant year-round in Jeddah, with a drop in numbers around December (Khan et al. 2018).

Six hundred ovitraps were deployed in the sampling area on February 3, 2020. Traps were individually georeferenced and deployed randomly through the sampling area to collect *Ae. aegypti* across a continuous range of distances and on either side of each road. Each trap used a bucket attached to a bucket containing water and two to three grass pellets to collect eggs from ovipositing *Ae. aegypti* females, which are laid on the felt. On February 11, felts were collected and new felts deployed, which were collected on February 18. Of the 1,200 felt samples taken over the 2-week sampling period, 137 had *Ae. aegypti* eggs, 113 of which were collected from 128 unique locations (fig. 1A). Eggs collected from felts were hatched and reared to adulthood and then stored in 100% ethyl alcohol at −20°C.

**Sequencing and Genotyping**

We generated double-digest restriction site–associated DNA (ddRAD) sequence data from 266 *Ae. aegypti* (text SI in the supplemental PDF), selected to maximize the spatial distribution of individuals. Protocols for DNA library preparation follow previous work (Rašič et al. 2014), but library size was restricted to 20 individuals to decrease variation in coverage within libraries (text SI in the supplemental PDF). Libraries were sequenced using 150 bp paired-end chemistry at BerryGenomics Company (Beijing) on a NovaSeq 6000 (Illumina, San Diego, CA).

We used process_radtags in Stacks version 2.0 (Rochette et al. 2019) to demultiplex sequence reads, trim them to 140 bp, and discard reads with an average Phred score below 20. We used bowtie version 2.0 (Langmead and Salzberg 2012) to align reads to the *Ae. aegypti* genome assembly (Matthews et al. 2018), using very sensitive alignment. Individual single nucleotide polymorphism (SNP) genotypes were called via the Stacks version 2.0 program ref_map. SNPs were retained when genotypes were called in ≥90% individuals and when three or more copies of the minor allele were detected (Linck and Battey 2019). We imputed missing genotypes in Beagle 4.0 (Browning and Browning 2016) and then pruned SNPs by linkage disequilibrium (R package SNPRelate; Zheng et al. 2012), using the snpgdsLDpruning function with arguments method = “r”, slide.max.n = 50, and ld.threshold = 0.005. This reduced the initial set of 81,780 SNPs to a set of 3,058 unlinked SNPs with no missing genotypes.

**Close Kin Identification**

We used the R package PC-Relate (Conomos et al. 2016) to estimate kinship and identity by descent parameters for all 35,245 possible dyads. PC-Relate controls for genetic structure, such as from isolation by distance, by conditioning the data with principal components (PCs). Two PCs were used to condition for genetic structure, as no structure was observed in additional PCs (fig. S1). Parameters included the kinship coefficient (φij) and the probabilities of sharing zero (kij(0)) or two (kij(2)) alleles at a site, and these were used to estimate each dyad’s order of kinship. As all samples were collected within a 2-week period and were from the same generation, we assumed that first-order dyads were full sibs, second-order dyads were half-sibs, and third-order dyads were first cousins. Previous work has found that at fine scales, almost all isolation by distance is caused by such close kin dyads rather than background structure (Agúillon et al. 2017).

Dyads of first-, second-, and third-order kinship have expected φij of 0.25, 0.125, and 0.6625, respectively. Accordingly, dyads with φij > 0.1875 are most likely first-order kin, 0.1875 > φij > 0.0938 are most likely second-order kin, and 0.0938 > φij > 0.0469 are most likely third-order kin. However, more accurate assignments can be obtained using both φij and kij(0) (fig. 1B). Unrelated, first cousin, and half-sib dyads are expected to align along a line intersecting the x-axis at kij(0) = 1 and the y-axis at φij = 0.25 but where full sibs have kij(0) scores ∼0.25 higher (Conomos et al. 2016). Using both parameters to assign dyads resolved several instances of impossible pedigrees that would have arisen if only φij was used (e.g., three individuals containing two full-sib dyads and one half-sib dyad).

Assigning third-order dyads was difficult even when considering φij and kij(0) together (fig. 1B). We reasoned that if unrelated dyads were incorrectly classed as first
Figure 1: Traps, close kin dyads, and spatial genetic structure in Jeddah sample site. A, Map of study site. Gray squares indicate positive traps, red squares indicate traps where full-sib dyads were found at different locations, and lines connect full-sib dyads found across roads. B, Kinship category assignment based on kinship coefficient ($\phi_{ij}$) and probability of sharing zero alleles ($k_{ij}^{(0)}$). C, Density plots of distances separating dyads of each kinship category. D, E, Results from EEMS (D) and sPCA (E), using one individual per trap and with road locations indicated.
cousins, this could bias dispersal estimates upward. This is because distances between cousins represent two generations of dispersal, while distances between unrelated dyads represent additional generations. However, if first cousins were incorrectly classed as unrelated, this would simply reduce the sample size rather than introduce biases, as the Kindisperse method for *Ae. aegypti* considers only sibs and first cousins (Jasper et al. 2022). Considering the uncertainty around estimates, we assigned first cousin dyads conservatively and treated the first cousin category as a composite category containing both full and half first cousins (Jasper et al. 2019). Relatedness parameters and location data for all dyads are in text S1 in the supplemental PDF.

**Road Barrier Testing**

*Frequency of Full-Sib Dyads across Roads.* We tested whether the western or southern roads were functioning as dispersal barriers, using the spatial distribution of trap pairs containing full-sib dyads (fig. 1A). In this study, each individual was sampled as an egg, and thus the distance between any full-sib dyad represents the movement of only a single, unsampled individual—their mother. When two full sibs in a dyad are observed on either side of a putative barrier, this implies that their mother crossed this barrier while moving between ovitraps to oviposit. If a given feature is genuinely a barrier to movement, then fewer full-sib dyads should be observed on opposite sides of the barrier than on the same side relative to expectations from the number of dyads and the distances between traps.

To test for barriers, we first considered three treatments: trap pairs on the same side of the road, trap pairs across the western road, and trap pairs across the southern road. Considering first the trap pairs on the same side of the road, 30 of these contained one or more pairs of full sibs, and these had a maximum separation of 510 m. There were 2,442 trap pairs on the same side of the road within 510 m. We used these values to divide the distance of 0–510 m into 10 distance classes, so that each contained an equal number of trap pairs on the same side of the road (i.e., 244–245; table S1). For each of the 10 distance classes, we calculated how many pairs of traps contained full sibs (*n*full-sib traps). We used the ratio *n*full-sib _traps专门化* to produce expected rates of full-sib detection at each distance class (where *n*traps = 244–245), which we treated as expected rates when barriers are not present. As no full sibs were observed beyond 510 m, we could not calculate ratios for these distances.

We compared these expected rates of detection against rates of detection observed for the western and southern road treatments, which each had a putative barrier. These used the same 10 distance classes, but *n*traps was different for each treatment. For instance, for the first distance class, 0–70.8 m, there were 244 traps on the same side of the road, 14 across the western road, and two across the southern road. For each distance class, we used these *n*traps scores and the expected ratios of full sibs to produce expectations of *n*full-sib _traps专门化* rounding to the nearest integer (table S1). Differences between expected and observed *n*full-sib _traps专门化* at each distance class were compared using Wilcoxon signed-rank tests for paired samples.

We compared the performance of this full-sib approach against three commonly employed methods for detecting barriers: distance-based redundancy analysis in the R package vegan (dbRDA; Legendre and Anderson 1999), spatial principal components analysis (sPCA) in the R package adegenet (Jombart 2008), and estimating effective migration surfaces (EEMS; Petkova et al. 2016). Details of these analyses are in text S2 in the supplemental PDF.

*Separation Distances of Full-Sib Dyads across Roads.* While fewer full-sib dyads are expected across barriers, these dyads are also predicted to be separated by greater distances than when no barrier is operating. This is because longer-range dispersal (e.g., >500 m) in *Ae. aegypti* tends to be anthropogenically associated, such as via transportation in cars (Eritja et al. 2017). These passive movements will not be affected by barriers in the same way as active flight, and thus long-range movement may not be reduced in frequency, despite barriers restricting short-range movement.

To test this prediction, we calculated for each of the three road treatments (same side, across the western road, across the southern road) the ratio of *n*full-sib _traps专门化* found within the ith percentile of trap distances relative to the total *n*full-sib _traps专门化* for that treatment, with *i* = {10%, 20%, …, 90%} (table S2). Thus, *n*full-sib _traps专门化* / *n*full-sib _traps专门化* indicates the proportion of trap pairs containing full sibs that are found within the nearest 40% of trap distances. Differences in ratios between treatments were assessed with ANOVA.

**Dispersal Parameterization**

*Estimating σ from Close Kin Dyads.* We estimated dispersal location kernels (Nathan et al. 2012) using the Kindisperse approach (Jasper et al. 2019, 2022). Kindisperse uses variance addition and subtraction to isolate specific dispersal location kernels from the spatial distributions of close kin dyads. We estimated two kernels. The ovipositional dispersal kernel (σovip) describes the spatial distribution of eggs as a result of females moving between ovitraps to oviposit. This movement of ovipositing females is called skip oviposition when it occurs within one gonotrophic cycle, as in this study (Christophers 1960). The parent-offspring dispersal kernel (σ or σovip)
describes an entire generation of dispersal, life stage to life stage (i.e., egg(−1) to egg(n)). For all analyses, we retained only a single dyad of a given order found in the same trap or trap pair to avoid bias from sequencing unequal numbers of individuals across traps.

The spatial distribution of full sibs was used to estimate \( \sigma_{fs} \). We estimated \( \sigma_{fs} \) with the Kindisperse function axpermute, using a vector of full-sib distances as input and setting composite = 2, as each full-sib dyad represented two draws from this kernel (i.e., \( \sigma_{fs}^2 = 2\sigma_{pm}^2 \)). It is important to clarify that, as our samples were collected as eggs, and as we included full-sib dyads from the same traps, the \( \sigma_{fs} \) kernel is not intended to summarize female movement distances per se. Rather, it represents the distribution of related individuals at a specific life stage (i.e., egg) within a specific generation as a result of female movement (Jasper et al. 2022). The same \( \sigma_{fs} \) kernel can also be estimated from full sibs at the adult life stage that have moved from their locations at the egg stage, though confidence intervals will be broader (Jasper et al. 2022).

The \( \sigma_{po} \) kernel was estimated from the difference in variances between the spatial distributions of sibs and cousins. This analysis considers the recent coancestry of close kin dyads, where sibs coalesce in the parental generation and cousins coalesce in the grandparental generation. For \textit{Ae. aegypti}, if the spatial distribution of a full-sib dyad reflects two draws from the mother’s \( \sigma_{pm} \) kernel, the spatial distribution of a full first cousin dyad will reflect two draws from the grandmother’s \( \sigma_{pm} \) kernel and two draws from the parent’s dispersal kernel from egg through to oviposition (i.e., \( \sigma_{fc}^2 = 2\sigma_{pm}^2 + 2\sigma_{pc}^2 \); Jasper et al. 2022). Using the additive properties of variance, we find that the difference between the full sib and full first cousin dispersal kernels will be equal to two draws from the \( \sigma_{po} \) kernel (i.e., \( \sigma_{fc}^2 - \sigma_{fs}^2 = 2\sigma_{pc}^2 \)). If, as in this data set, the first cousin category contains full and half first cousins, \( \sigma_{po} \) is estimated by compositing the full-sib category with the half-sib category (Jasper et al. 2019, 2022).

We estimated \( \sigma_{po} \) with the axpermute_standard function, using vectors of full-sib and first cousin distances as input and using amixcat = H1C and a vector of half-sib distances to composite the full-sib category (bcompact = HS).

\textbf{Estimating \( N_w \) from Isolation by Distance.} As well as the above close kin–based analyses, we estimated Wright’s neighborhood size (\( N_w \)) using the inverse of the slope of the regression of linear genetic distance among individuals against ln-transformed geographical distance and omitting dyads within \( \sigma_{po} \) (Rousset 2000). We compared these results against \( N_w \) estimates from other \textit{Aedes} populations. These included \textit{Ae. aegypti} populations from urban high-rise apartments in Kuala Lumpur, Malaysia (\( N = 162 \); Jasper et al. 2019), and urban Cairns, Australia (\( N = 171 \); Schmidt et al. 2018), and an \textit{Aedes albopictus} population from islands in northern Australia (\( N = 301 \); Schmidt et al. 2021). All sequence data from the \textit{Ae. aegypti} populations were processed and filtered identically to the Jeddah samples. As the Cairns sample was taken shortly after Wolbachia releases in the area, we estimated \( N_w \) separately for pairs with Wolbachia (\( N = 59 \)) and pairs without Wolbachia (\( N = 112 \)); there was no isolation by distance pattern between pairs of different infection status. The \textit{Ae. albopictus} estimates omitted pairs found on different islands. For the Cairns and \textit{Ae. albopictus} \( N_w \) calculations, we assumed \( \sigma_{po} = 96.5 \) m generation \(^{-1/2} \), the average of the estimates for Al-Safa and Malaysia (46.0 m generation \(^{-1/2} \)).

\textbf{Results}

\textbf{Close Kin Identification}

We identified 190 full-sib dyads, 64 half-sib dyads, and 46 first cousin dyads from the 35,245 dyads (fig. 1B). Most (104) full-sib dyads were from the same trap. All but two full-sib dyads were sampled in the same week, indicating likely movement within a single gonotrophic cycle. There was no relationship between the distance separating full-sib dyads and either \( \varphi_0 (R^2 = 0.005) \) or \( k_{fl0} (R^2 = 0.006) \). Maximum distances among close kin were 1,052 m (full sib), 588 m (half-sib), and 890 m (first cousin; fig. 1C).

\textbf{Road Barrier Testing}

\textbf{Frequency of Full-Sib Dyads across Roads.} There were 44 trap pairs containing full-sib dyads. Thirty were on the same side of the road, while 12 were across the western road and three across the southern road, including a single trap pair across both roads (figs. 1A, 2A; table S1). Within the 10 distance classes that ranged 0–510 m, there were nine trap pairs with full-sib dyads across the western road and zero across the southern road (fig. 2B). These observed values are lower than the expected values for each treatment, with 19 trap pairs with full-sib dyads expected across the western road (Wilcoxon test, \( z = 1.221, P = .111 \)) and eight expected across the southern road (Wilcoxon test, \( z = 2.222, P = .013 \)). The eighth distance class (365–429 m) was omitted from calculations, as it did not contain any full sibs for any treatment, which was likely a stochastic effect.

None of the dbRDAs found either of the road barriers to have a statistically significant effect, regardless of whether analyses considered the whole data set or tested each road individually or whether geographical variables were used to condition the model. However, higher \( F \) values and lower \( P \) values were observed for the southern road barrier.
Separation Distances of Full-Sib Dyads across Roads. Traps with full-sib dyads across the southern road were separated by relatively larger distances than those on the same side or across the western road ($F_{1,235} = 5.62$, $P = .0099$). For the same side, western, and southern road treatments, the 50th percentile of trap distances contained 1,624, 2,115, and 1,643 traps within distances of 296, 499, and 648 m, respectively. The proportions of full sibs within these distances were 90%, 75%, and 33%, respectively (table S2).
Dispersal Parameterization

**Estimating σ from Close Kin Dyads.** Dispersal parameterization used 202 trap pairs: 105 full sibs (\(\bar{x}_{fi} = 105.5\) m), 49 half-sibs (\(\bar{x}_{si} = 133.3\) m), and 41 first cousins (\(\bar{x}_{co} = 274.8\) m). The spatial distribution of full-sib dyads indicated that the ovipositional dispersal location kernel (\(\sigma_{oi}\)) was 108.3 m generation\(^{-1/2}\) (95% confidence interval [CI], 76.4–139.7; table 1). The spatial distributions of the sib and cousin dyads indicated that the parent-offspring dispersal location kernel (\(\sigma_{po}\)) was 146.9 m generation\(^{-1/2}\) (95% CI, 81.5–197.1). As dyads across the southern road barrier had different spatial distributions, we also ran analyses with these omitted, giving \(\sigma_{mi} = 84.1\) m generation\(^{-1/2}\) (95% CI, 61.5–105.4) and \(\sigma_{po} = 142.3\) m generation\(^{-1/2}\) (95% CI, 78.2–193.4). Dispersal estimates are given in meters generation\(^{-1/2}\), as we are modeling dispersal in two dimensions, where \(\sigma\) is an axial standard deviation of a bivariate distribution (Wright 1946).

We compared these *Aedes aegypti* dispersal estimates with estimates derived from MRR studies (fig. 3; table S3). These studies do not comprise an exhaustive review of the MRR literature, as in Guerra et al. (2014); here we focus on more recent research. For each study reporting dispersal estimates from multiple releases, we included only two estimates selected randomly. Estimates are compared against two parameters of study design that vary among dispersal studies: the area over which sampling was conducted (fig. S3A) and the number of specific sampling points per unit area (fig. S3B), both of which were square root transformed to enforce proportionality with dispersal estimates. MRR estimates are compared against close-kin dyad estimates from this study and from Jasper et al. (2019), which have been converted from \(\sigma_{po}\) into mean Euclidean distances (\(r\)) expected under Gaussian assumptions, using \(\sigma^2 = 0.5 \times E[r^2]\) (Crawford 1984; Rousset 2004).

Dispersal studies conducted over larger areas have generally reported larger estimates of dispersal (fig. 3A; \(R^2 = 0.74\)). This is expected, as long-distance movement will be detected only in studies conducted across sufficient area, a pattern noted previously in empirical (Guerra et al. 2014) and simulated (Jasper et al. 2022) investigations. However, studies conducted across large areas tend to also sample from a more dispersed set of points, as it is unfeasible to maintain a high density of traps across large areas. This lower density of trapping correlates with larger estimates of dispersal (fig. 3B; \(R^2 = 0.44\)). As *Ae. aegypti* often disperse over very short distances and stay within a single building their entire life (Harrington et al. 2005; Jasper et al. 2019), study designs with traps spaced far from each other and from release points may fail to record this short-range movement and thus produce inflated estimates.

**Estimating \(N_W\) from Isolation by Distance.** After omitting dyads within the axial dispersal distance of \(\sigma_{po}\) (146.9 m generation\(^{-1/2}\)), neighborhood size (\(N_W\)) in Al-Safa was estimated at 407 (95% CI, 331–526). Using the equation \(N_W = 4\pi \times \sigma_{po}^2 \times \rho\), where \(\rho\) is the effective density of *Ae. aegypti*, we estimate \(\rho = 1,497\) km\(^{-2}\) (95% CI, 833–4,864). Figure 4 shows how the estimates of \(N_W\), \(\sigma_{po}\), and \(\rho\) from Al-Safa compare with estimates from other *Aedes* populations. \(N_W\) was relatively consistent among the *Aedes* populations, considering the approximately two to three orders of magnitude breadth in \(N_W\) recorded among and even within species (Battey et al. 2020). Likewise, estimates were consistent for the *Wolbachia*-infected (\(N_{W,\text{inf}} = 944\)) and uninfected (\(N_{W,\text{uninf}} = 1,016\)) subsamples from Cairns, Australia. While *Ae. aegypti* in Al-Safa had a larger \(N_W\) than those from Kuala Lumpur (407 vs. 124), \(\sigma_{po}\) was also larger at Al-Safa (\(\bar{x} = 146.9\) vs. 46.0), leading to a lower estimated \(\rho\) than in Kuala Lumpur (1.497 vs. 4.663).

**Discussion**

Dispersal shapes the fate of many wild populations and is a frequent focus of ecological and evolutionary research. A conceptual duality in early studies in whether dispersal should be investigated as a life history event (Howard 1960) or an intergenerational process (Wright 1943) has led to a corresponding duality in approach that continues to the present day (Broquet and Petit 2009). Current genetic approaches that can detect dispersal across discrete generations are helping to resolve this duality (Bradburd and Ralph 2019; Jasper et al. 2022). This study has used close-kin dyads sampled from the same life stage and generation to reveal the specific movement of individuals and to estimate average dispersal patterns within the study site over recent generations. The locations of full-sib dyads were used to infer the specific movements of mothers, and these movement patterns revealed fine-scale dispersal barriers with greater sensitivity than methods assessing overall genetic differentiation. The difference in variance between the sib and cousin spatial distributions provided an estimate of \(\sigma\), and spatial genetic differentiation over multiple generations indicated \(N_W\) and \(\rho\). This framework thus uses

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**Table 1: Population parameter estimates for Jeddah *Aedes aegypti***

| Parameter         | 2.5% | 97.5% |
|-------------------|------|-------|
| \(\sigma_{oi}\)   | 76.4 | 139.7 |
| \(\sigma_{po}\)   | 81.5 | 197.1 |
| \(N_W\)           | 331  | 526   |
| \(\rho\)          | 833  | 4,864 |

Note: Dispersal estimates are in meters generation\(^{-1/2}\), and \(\rho\) is in kilometers\(^{-2}\).
a single data set to investigate dispersal as both a life history event and an intergenerational process.

While $j$ is often treated as constant across all populations of a species (Nunney 2016), $j$ may vary when a species like *Aedes aegypti* inhabits a broad range of environments. Our estimate of $j$ for Al-Safa *Ae. aegypti* (146.9 m generation $^{1/2}$) was much higher than that of a population inhabiting Malaysian high-rise apartments (46.0 m generation $^{1/2}$; Jasper et al. 2019), and could reflect differences in behavior or physiology. However, in the Malaysian population, *Ae. aegypti* are clustered within apartment buildings and do not inhabit the spaces between them. Lower estimates of $j$ are thus expected, given that mosquito movement is limited to mostly short distances (within

![Figure 3](image-url)

**Figure 3**: Comparison of Euclidean dispersal distance estimates across studies. Estimates from close kin dyads are a square (this study) and a diamond (Jasper et al. 2019). Data for each estimate are listed in table S3 (Muir and Kay 1998; Ordóñez González et al. 2001; Harrington et al. 2005; Russell et al. 2005; Maciel-de-Freitas et al. 2007a, 2007b; Maciel-de-Freitas and Lourenço-de-Oliveira 2009; Lacroix et al. 2012; Valério et al. 2012; Winskill et al. 2015; Marcantonio et al. 2019; Juarez et al. 2020; Trewin et al. 2021).

![Figure 4](image-url)

**Figure 4**: Neighborhood size ($N_w$), dispersal ($\sigma$), and density ($\rho$) estimates for *Aedes* populations. Units for $\sigma$ are meters generation $^{-1/2}$, and units for $\rho$ are kilometers $^{-2}$. Unplotted 95% CI estimates are as follows: Cairns (Wo$-$) $N_w = 2,374$; Cairns (Wo$+$) $N_w = \infty$; Kuala Lumpur $\rho = 38,550$. 
apartments) with occasional long-distance movement (between apartment buildings) and little intermediate movement. If a continuously distributed population like Al-Safa was sampled in a similarly clustered manner, this absence of intermediate distances would downwardly bias estimates. Nevertheless, the lower σ in the Malaysian high-rise apartment buildings remains an accurate summary of the intergenerational dispersion of alleles, though it may yet be underestimated because of sampling over too small an area (fig. 3A; Guerra et al. 2014; Jasper et al. 2022). Estimates from Malaysia and Al-Safa should thus be cautiously compared.

N_w is known to vary among and even within populations (Shirk and Cashman 2014; Battey et al. 2020). This may reflect variation in local σ as well as density (ρ). The interpretation of N_w is sometimes confused with N_f (effective population size; Nunney 2016); while N_w is limited to describing local spatial structure, it can be usefully applied to continuously distributed populations where σ^2 is much smaller than the area covered by the population (Leblois et al. 2003), whereas in continuous populations, N_f can be subject to strong biases from sampling (Neel et al. 2013). The Aedes N_w estimates reported here (124–1,016) describe variation among populations relating directly to ρ and σ and can be compared with N_w estimates from Anopheline mosquitoes (~150–700; Clarkson et al. 2020) and Drosophila pseudoobscura (~570–1,100; Dobzhansky and Wright 1943). By comparison, N_f estimates in Ae. aegypti alone exhibit much greater variance. Resampling methodologies give estimates of 25–3,000 (Saarman et al. 2017), and coalescent methods give contemporary estimates in postbottleneck invasive range populations from ~5,000 in Mexico (Crawford et al. 2017) to ~1,500,000 across the Caribbean (Sherpa et al. 2018). The difference between these latter estimates may reflect the spatial scales over which individuals were aggregated for analysis, which does not affect N_w in the same way (Neel et al. 2013; cf. Clarkson et al. 2020).

Reconciling individual-based movement observations such as those obtained from MRR with dispersal estimates from molecular data is often difficult (Broquet and Petit 2009). However, here we find that our estimates of Euclidean distance derived from σ accord well with estimates from MRR studies conducted at similar scales (fig. 3). In general, choice of dispersal inference method will depend on the study system. Close kin methods are particularly suitable for short-lived organisms for which dispersal is spatially limited and difficult to observe directly. Close kin can also reveal occasional dispersal over long distances (Escoda et al. 2017; Schmidt et al. 2021). By contrast, MRR methods are particularly effective when applied to larger animals observed at multiple time points, such as through camera traps (Silver et al. 2004; Royle and Young 2008). An additional advantage of close kin methods is that density (ρ) can be estimated from N_w estimates when σ is known (Rousset 2000; Leblois et al. 2003). Running this operation in reverse, in which ρ is used to estimate σ, is also viable (Broquet et al. 2006) but requires density data, which can be difficult to collect.

Fine-scale estimation of barriers, σ, N_w, and ρ can inform management strategies for wild populations, particularly those experiencing recent change. For Ae. aegypti in the Al-Safa 9 region, these will inform Wolbachia releases. The major strategic implication of these findings is that the release site is bordered by barriers, with the southern barrier (60-m width) stronger than the western barrier (30-m width). Accordingly, if the invasion is to either spread outward or retreat inward from Al-Safa (cf. Schmidt et al. 2017), this will more likely occur at the weaker western barrier than at the southern barrier. Other undetected barriers within the study site may also have these effects, but the effects of the two roads are the most critical, as they define the region within which releases will take place. When we consider σ, the much larger estimate of σ = 146.9 m generation^{-1/2} at Al-Safa suggests that dispersal distances are higher than in Malaysia, even if Malaysian estimates are slightly downward biased by small study site dimensions (Jasper et al. 2022). With higher dispersal in Al-Safa, we would expect to observe faster dynamics of spread and reinvasion, and Wolbachia will need to be deployed over a relatively larger area than in Malaysia (Barton and Turelli 2011). Estimated mosquito population densities were much lower at Al-Safa (~1,500 km^{-2}) than in the Malaysian site (~4,500 km^{-2}). Effective densities are also likely lower in Al-Safa than in Cairns. This is because N_w in Al-Safa (407) was much lower than in Cairns (944–1,016), and the rate of Wolbachia spread through Cairns was sufficiently slow such that σ > 100 m generation^{-1/2} is unlikely (Schmidt et al. 2017). Thus, the lower N_w in Al-Safa probably reflects a lower relative density than Cairns. This Cairns sample was taken from around the Parramatta Park region, where trap collections were consistently high for this city and Wolbachia frequencies were relatively stable after establishment (Schmidt et al. 2017). On the other hand, Wolbachia frequencies were more volatile at the lower-density Edge Hill release site in Cairns (Schmidt et al. 2017), which might also occur at Al-Safa, making it important to monitor Wolbachia frequencies carefully.

Conclusions

Ongoing change in global land use brings with it the addition and removal of dispersal barriers, much of which has occurred recently relative to generation time (Zeigler and Fagan 2014). Following previous work showing how close kin dyads can estimate σ (Jasper et al. 2022), this
paper has demonstrated their use in barrier detection. Close kin methodologies can identify how barriers affect different forms of dispersal, such as active flight and passive movement, when these operate over different spatial scales and should be particularly useful for detecting recent changes to barriers down to the scale of a single generation or reproductive cycle. Even so, we have shown that close kin methods can outperform methods that consider the genetics of the entire population in assessing barriers that have existed for hundreds of generations, provided the investigation is conducted at a sufficiently fine scale. This strong signal at fine scales accords with close kin findings in other taxa (Aguillon et al. 2017). Importantly for barrier detection, only data from first-order kin are required, allowing the use of cheaper genetic markers, such as microsatellites, that can capture first-order relationships (Hauser et al. 2021).

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Statement of Authorship

T.L.S., S.E., and A.A.H. designed the study; T.L.S. and S.E. performed fieldwork and egg rearing; M.B.A.F., M.N., and A.A.M. provided research services; L.-J.C., S.-J.W., S.E., and T.L.S. built DNA libraries; T.L.S. and A.A.H. analyzed the data; T.L.S. wrote the paper; and all authors contributed revisions.

Data and Code Availability

Sequence data for the 266 Aedes aegypti have been deposited at the National Center for Biotechnology Information Sequence Read Archive (accession no. PRJNA837703). Other data have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.dfn2z354h; Schmidt 2022). Code is available in Zenodo (https://doi.org/10.5281/zenodo.6609654).

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