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Abstract

1. Models of host-pathogen interactions help to explain infection dynamics in wildlife populations and to predict and mitigate the risk of zoonotic spillover. Insights from models inherently depend on the way contacts between hosts are modelled, and crucially, how transmission scales with animal density.
2. Bats are important reservoirs of zoonotic disease and are among the most gregarious of all mammals. Their population structures can be highly heterogenous, underpinned by ecological processes across different scales, complicating assumptions regarding the nature of density-transmission scaling. Although models commonly parameterise transmission using metrics of total abundance, whether this is an ecologically representative approximation of host-pathogen interactions is not routinely evaluated.
3. We collected a 13-month dataset of roosting *Pteropus* spp. from 2,522 spatially referenced trees across eight roosts to compare density estimates across scales (roost-level, subplot-level, tree-level). We then focus on tree-level measures of abundance and density, the scale most likely to be relevant for virus transmission between tree-roosting *Pteropus* , and evaluate whether roost features at different scales are predictive of local dynamics.
4. Our density estimates varied greatly by scale. Mean density of*Pteropus* at the roost level was 13-fold lower than at a subplot-level that accounted for heterogenous distributions of bats (0.38 bats/m^2 vs 5.13 bats/m^2). Additionally, roost-level measures (roost abundance and roost area) did not represent tree-level abundance or tree-level density, with models explaining minimal variation in tree-level measures.
5. This indicates that basic measures, such as roost-level population counts, may not provide adequate approximations for population dynamics at scales relevant for transmission, and that alternative measures are needed to compare transmission potential between roosts. From the best candidate models, the best predictor of local population structure was tree density within roosts, where roosts with low tree density had a higher abundance but lower density of bats (more spacing between bats) per tree.
6. Together, these data highlight unpredictable and counterintuitive relationships between abundance and density, and between measures at different scales. More nuanced modelling of transmission, spread and spillover from bats likely requires alternative approaches to integrating contact structure in host-pathogen models, rather than simply modifying the transmission function.

Keywords: Contact rate; density-dependent transmission; frequency-dependent transmission; heterogeneity; mass action; nonlinearities; pseudo-mass action

Introduction

A central aim of disease ecology is to understand how pathogens spread within host populations (Brandell *et al.* 2020). Implicit to this is the elucidation of a pathogen's transmission dynamics (Smith *et al.* 2009). For directly transmitted pathogens, transmission is effectively the product of the contact rate between hosts, the proportion of contacts that are between susceptible and infectious hosts, and the proportion of effective contacts that result in infection (McCallum, Barlow & Hone 2001). In models of infectious diseases, transmission mechanisms are typically combined into a single term, the transmission coefficient (β), and

modelled with one of two simplified functions that describe how infectious contacts scale with population size: that scaling is linear ('density-dependent') or independent ('frequency-dependent') (McCallum, Barlow & Hone 2001; Begon *et al.* 2002; McCallum *et al.* 2017). Selecting a function that provides a useful approximation for modelling transmission has been debated extensively (e.g. McCallum, Barlow & Hone 2001; Begon*et al.* 2002; Lloyd-Smith *et al.* 2005; Cross *et al.*2013), although in practice, the model is often based on the transmission route of the pathogen: density-dependent for direct transmission, and frequency-dependent for vector-borne or sexual transmission. While this approach may accurately reflect transmission at the local scale where contacts happen (though see Ryder *et al.*2005), there is growing evidence to suggest this may not scale correctly to describe transmission in the population as a whole (the 'global' scale) (Smith *et al.* 2009; Ferrari *et al.* 2011; Cross, Caillaud & Heisey 2013). For example, transmission may be density-dependent at the local scale, but appear more consistent with frequency-dependent transmission at the global scale (Ferrari *et al.* 2011; Cross, Caillaud & Heisey 2013). Two interrelated questions arising from this paradox need to be answered to more thoroughly consider the nature of transmission in wildlife populations: how should density in natural populations be defined and measured, and what spatial scales are appropriate for understanding transmission in particular host pathogen systems (De Jong 1995; McCallum, Barlow & Hone 2001; De Jong 2002). Understanding how transmission scales with density is especially important for wildlife populations, in comparison with human infections, where population size may change by orders of magnitude over relatively short periods.

Quantifying animal density can be complex, however. Animal behaviour and heterogeneity in the environment can create aggregate distributions of animals that are not adequately represented in estimates when divided by total inhabited area (Krebs 1999). Defining and measuring density is additionally complicated if animals are distributed in three dimensions (i.e. across horizontal and vertical space). Finally, aggregative distributions of animals may also deviate from the random-mixing assumption that underlies density-dependent and frequency-dependent transmission models, if contacts between neighbours are more frequent than contacts between distantly spread animals (McCallum, Barlow & Hone 2001). An imperative question, therefore, lies in determining the appropriate 'local' scale at which transmission occurs, and where contacts may be more homogenous (McCallum, Barlow & Hone 2001). In addition, for highly aggregative species, where local groups form within the global population, processes that drive transmission within groups may not match processes that drive transmission between groups. In such species, transmission within groups may be driven by local group size, while transmission between groups by the structure of the population and the connectivity between local groups (Jong, Diekmann & Heesterbeek 1995; Ferrari *et al.* 2011).

These issues are prevalent across most wildlife disease systems. Indeed, it has been suggested that seal colonies are one of the few natural situations where transmission can be adequately modelled with population abundance rather than animal density (possibly owing to uniform distancing between individuals) (De Koeijer, Diekmann & Reijnders 1998; McCallum *et al.* 2017). Issues surrounding the definition and estimation of density are particularly problematic in models of zoonotic pathogens that have bat reservoirs. Bats are among the most gregarious of all mammals – a high proportion of species are social, with some forming the largest aggregations of resting mammals known (Kerth 2008). Bats typically gather together during inactive periods of the diurnal cycle, either in natural habitat (e.g. tree foliage, tree hollows and caves) or anthropogenic structures (e.g buildings, mines and bat boxes) (Kerth 2008). Some species switch roosts frequently (e.g. Rhodes 2007) while others regularly return to the same roost space, or even to specific locations within the roost (Nelson 1965; Lewis 1995; Markus & Blackshaw 2002). This can also be variable among individuals within species (e.g. Welbergen 2005; Welbergen *et al.* 2020). Spatio-temporal changes to roost structure and organisation are often observed in response to ecological factors like season, mating and gestation, food availability, thermoregulation, parasite accumulation, or site disturbance (Lewis 1995; Kerth 2008). By altering rates of contact, spatial and temporal changes in bat aggregations can contribute to spatio-temporal dynamics of transmission, infection, and risk of disease spillover (Altizer *et al.* 2006). Framing transmission in ecologically relevant contexts will therefore be important for accurate infection modelling in these species, where population size often changes dramatically.

In models of bat viral transmission where contact rate is assumed to be density-dependent, and where

pathogen transmission occurs within the roost (generally the case if individuals forage independently), the transmission coefficient is often parameterised with total roost abundance (George *et al.* 2011; Plowright *et al.* 2011; Wang*et al.* 2013; Hayman 2015; Jeong *et al.* 2017; Colombi*et al.* 2019; Epstein *et al.* 2020). Likewise in statistical models, population size is often fit with total abundance (Serra-Cobo*et al.* 2013; Giles *et al.* 2016; Páez *et al.* 2017). If the population size is modelled to be constant (e.g., Plowright*et al.* 2011; Wang *et al.* 2013) it is irrelevant how transmission scales with population size. If population size is variable however, parameterisation with total abundance implicitly assumes that the area occupied remains constant with increasing population size (so that roost abundance scales linearly with bat density), and that this is consistent across scales. Whether this occurs in reality is not routinely evaluated. Indeed, changes to density may be multifaceted and hard to predict. In tree-roosting *Pteropus* , for example, new individuals arriving into the roost could be accommodated by an expansion of the total roost area, by increasing the number of trees occupied within the roost perimeter, or by crowding more animals into occupied individual trees. These processes may all occur simultaneously.

Over what spatial scale transmission can reasonably be expected to occur within roosts is also a critical question, and one that will define the scale at which density is ecologically relevant to infection dynamics. This is likely to depend on: (i) the mode of pathogen transmission, (ii) animal behaviour and (iii) the structural heterogeneity in the roost environment. First, the mode of transmission will determine the distance over which transmission can occur and will frame the scale relevant for population measures – transmission via aerosols or droplets, or indirect contact with infectious excretions has a greater potential for spread over large distances compared with transmission via direct contact, meaning that a larger scale of density estimation may be warranted. Second, animal behaviour, specifically range of movement, site fidelity, and tendency to aggregate, will influence the spatial extent of contact throughout populations, and so also the scale relevant for population measures. Animals that constantly move through their environment will be likely to contact other animals over a greater area than animals that are more sedentary, for example. Finally, environmental heterogeneity can influence the probability and rate of movement between groups in highly aggregative populations, and so influence the rate and extent of spread over space. Currently, there is little empirical evidence available to understand how viral transmission depends on density in bat populations, or the spatial scale on which density might be relevant. Moreover, there is little empirical support for traditional density-dependent viral transmission in bats, which may reflect complexity in transmission underpinned by ecological processes across different scales (Plowright *et al.* 2015; McCallum *et al.* 2017).

Here, we investigate the roosting characteristics of Australian*Pteropus* bats. Australian Pteropodid bats are the reservoir hosts for Hendra virus (HeV), an emerged paramyxovirus in the genus*Henipavirus* that causes lethal disease in horses and humans in eastern Australia (Plowright *et al.* 2015). We present a 13-month dataset of roosting *Pteropus* spp. from 2,522 spatially referenced trees across eight roost sites, to compare estimates of density across scales (roost-level, subplot-level, and tree-level). We focus on tree-level measures of abundance and density to then evaluate whether roost features at the different scales relate to these local dynamics. We focus our analyses on tree-level measures of abundance and density, as this is the scale at which the majority of contacts are likely to occur, given the nature of viral transmission between bats, and aspects of bat behaviour – i.e. while vertical transmission of Hendra virus has been documented (Halpin *et al.* 2000), transmission between bats is assumed to be primarily horizontal through contact with infectious urine, either through close contacts with individuals, contacts through the vertical tree column (e.g. with excretion from bats roosting above), or exposure to clouds of aerosolised urine over small distances (Field*et al.* 2001; Plowright *et al.* 2015). In addition, flying-fox activity within roosts is limited - bats rarely move from their roosting position after they return at dawn, and diurnal activities primarily consist of roosting, sleeping and grooming (Markus & Blackshaw 2002). Moreover the roosting positions of individuals can be highly consistent, with animals often returning to the same branch of a tree over many weeks or months (Markus 2002; Welbergen 2005). Considered together, it is plausible that tree-level measures of abundance or density will be the most relevant for understanding transmission in these species. Through these analyses we aim to provide data on ecologically relevant estimates of density for these species and highlight predictors of the local density most important for transmission of Hendra virus. Understanding gained on the nature

of animal density will be important to give more realistic predictions of pathogen invasion and persistence within bat populations. To this end, we also propose a framework to help guide incorporation of heterogenous contact structures into bat infectious disease models more generally.

Methods

Data collection

We collected data on roosting structure of three species (black flying-fox: *P. alecto* , grey-headed flying-fox: *P. poliocephalus* and little red flying-fox:*P. scapulatus*) from eight roost sites in south-east Queensland and north-east New South Wales, Australia (Fig. 1).*P. alecto* are believed to be the primary reservoir for Hendra virus in this study region (Goldspink *et al.* 2015), however a newly-identified Hendra virus variant has been detected in *P. poliocephalus* and *P. scapulatus* tissues (Veterinary Practitioners Board of New South Wales 2021). All sites were previously documented as having continuous occupation by at least one species of flying-fox (National Flying-Fox Monitoring Program 2017). Roosting surveys were repeated once a month for 13 months (August 2018 - August 2019).

Methodological details are described in Lunn *et al.* (2021). Briefly, we mapped the spatial arrangement of all overstory, canopy and midstory trees in a grid network of 10 stratified random subplots (20 x 20 meters each) using an ultrasound distance instrument (Vertex Hypsometer, Haglöf Sweden). Trees were mapped and tagged using tree survey methods described in the "Ausplots Forest Monitoring Network, Large Tree Survey Protocol" (Wood *et al.* 2015). This approach allowed for precise spatial mapping of trees, with locations of trees within subplots accurate to 10-30 cm. Tagged trees were revisited monthly, and the number of bats per tree was visually estimated and recorded per species using a quasi-logarithmic index: 0: no bats, 1: 1-5 bats, 2: 6-10 bats, 3: 11-20 bats, 4: 21-50 bats, 5: 51-100 bats, 6:101-199 bats and 7: 200+ bats. In total 2,522 trees were mapped across the eight sites. For a subset of trees (60 per site, consistent through time) absolute counts, minimum roosting height, and maximum roosting height of each species were recorded. The roost perimeter boundary (defined as the outermost perimeter delimitating occupied space, as per Clancy and Einoder (2004)) was mapped with GPS (accurate to 10 meters) immediately after the tree survey by walking directly underneath roosting flying-foxes. This track was used to calculate perimeter length and occupied roost area (QGIS 3.1). Total abundance at each roost was estimated with a census count of bats where feasible (i.e. where total abundance was predicted to be <5,000 individuals), or by counting bats as they emerge in the evening from their roosts ("fly-out"), as per Westcott *et al.*(2011). If these counts could not be conducted, population counts from local councils (conducted within ˜a week of the bat surveys) were used, as total abundance of roosts are generally stable over short timeframes (Nelson 1965). Because roost estimates become more unreliable with increasing abundance, we converted the total estimated abundance into an index estimate, as per values used by the National Flying-Fox Monitoring Program (2017). Index categories were as follows: 1: 1-499 bats; 2: 500-2,499 bats; 3: 2,500-4,999 bats; 4: 5,000-9,999 bats; 5: 10,000-15,999 bats; 6: 16,000-49,999 bats; and 7: 50,000+ bats.

All observations were made from a distance to minimise potential disturbance to bats during the survey. In general, bats showed minimal response to the observers during the surveys, providing observers remained quiet, did not move quickly, and kept an appropriate distance, consistent with other studies on flying-foxes (Markus & Blackshaw 2002; Klose *et al.* 2009).

Abundance and density estimates

Information collected during the bat roosting surveys were used to calculate measures of bat density and abundance at three scales: roost-level, subplot-level and tree-level. For a visual summary of metrics see Fig. 1.

Roost-level density was calculated as the total roost abundance divided by the total roost area (Fig. 1A). Measures of subplot-level density were estimated with two methods: either as a total count per subplot

divided by the total subplot area ("subplot-level density", Fig. 1B), or as the average of fixed-bandwidth weighted kernel estimates, estimated using the *spatstat* package in R (Diggle 1985) ("subplot-level kernel density", Fig. 1C). Kernel values were estimated using tree locations weighted by tree-level bat abundance with Gaussian kernel smoothing and a smoothing bandwidth of 0.6 (Baddeley 2010). Bandwidth was selected by comparing projected kernel density values to expected density values based on within tree abundance and canopy area. Kernel averages were calculated per subplot, and averages included only occupied pixels in the subplot (pixel size = 0.156 x 0.156 meters). This latter approach has the advantage of explicitly incorporating the distribution of trees into the density estimate, as well as the number of bats per tree, and can therefore distinguish between degree of tree-level aggregation. Note that neither roost nor subplot-based density measures consider the vertical distribution of bats.

Measures of tree-level density were estimated in either two-dimension (2-D; for comparison with other two-dimensional estimates) or three-dimension (3-D). Tree-level 2-D density was estimated from within tree abundance and canopy area (Fig. 1D). Tree-level 3-D density was estimated for the tree subset, as the absolute count of bats divided by the volume of tree space occupied (i.e. per cubic metre rather than square metre, Fig. 1E). Volume of tree space was calculated from the height range occupied (maximum height minus minimum height) and the approximate crown area of trees. To estimate crown area of tagged trees for both measures, we computed the area of Dirichlet-Voronoi tessellations from tree distribution maps of canopy trees per subplot, with the *spatstat* package in R (Baddeley 2010). To control for edge effects we imposed a maximum crown area of 199 m^2(radius ˜8 m) based on mean values reported across species of eucalypts in New South Wales (Verma *et al.* 2014). Overstory trees and trees outside of the canopy were also assigned this mean value. Crown area of midstory trees was assigned as the first quartile of canopy tree crown area (5.8 m^2), to reflect observations that trees beneath the canopy were typically smaller than trees within the canopy. Mean calculated crown area was 30.4 m^2 (crown radius ˜ 3.1 m). To investigate whether the choice of maximum crown area impacted results, we also repeated analyses for additional values of maximum crown area (140 m^2, 170 m^2 and 230 m^2) chosen to cover the range in smallest to largest mean values reported for individual eucalypt species in Verma *et al.* (2014).

Statistical analyses

To evaluate how roost features at different scales influence tree-level abundance and 3-D density of bats, the measures most likely to be relevant for transmission of virus between tree-roosting*Pteropus* , we fitted generalized additive models (GAMs) with restricted (residual) maximum likelihood (REML) estimation, Poisson distribution with a log link, and random effects of roost site, subplot and survey session with the *mgcv* package in R (Wood 2017). Roost site and subplot were fitted with random effects smoothers to account for high variability within and between roost sites, and survey session with a cyclic cubic regression spline to allow for seasonal variation. We accounted for nesting of subplots within roosts by including an autoregressive model for errors in the model (Yang *et al.* 2012; Laurinec 2017). We constructed a candidate set of GAMs comprising of a null model of random site, subplot and survey session effects only, alongside models with roost features hypothesised to impact tree-level measures: number of trees tagged within subplots, total roost abundance, total roost area, total subplot abundance, tree preference (whether the tree was regularly occupied: occupied in at least 80% of surveys; or irregularly occupied: occupied in less than 80% of surveys, as referred in Lunn *et al.* (2021)), and proportion of trees occupied per subplot, fit with the same set of random model effects relevant to that scale. We compared GAMs with the Akaike information criterion (AIC) and considered models within 2 ΔAIC units to be competitive (Burnham & Anderson 2002). We performed checks of standardised residuals to evaluate model fit, as per Wood (2017).

Results

The dataset includes tree-level abundance and tree-level 2-D density estimates from 2,522 spatially referenced trees, and tree-level 3-D density estimates from 480 of these trees. Measures were repeated monthly

for 13 months; however, 52 tagged trees were cut or had fallen during the survey period, giving a final dataset of 32,206 tree-level abundance and 2-D density estimates, and 6,240 tree-level 3-D density estimates. Mean tree-level abundance was 3.75 bats per tree across all trees (interquartile range: 0.00-3.00 bats) and 13.35 bats per tree across all occupied trees (3.00-15.50). A full set of summary data are available at: < https://github.com/TamikaLunn/FF-roost-structure >.

Comparison of density estimates across scales

Density estimates varied substantially by scale, both in magnitude and pattern over time (Fig. 2). The highest mean estimate was generated for subplot-level kernel density: 5.13 bats/m^2(interquartile range: 2.71-6.09), then tree-level 2-D density: 0.71 bats/m^2 (0.10-0.76, subplot-level density: 0.46 bats/m^2 (0.16-0.57), roost-level density: 0.38 bats/m^2 (0.21-0.47), and tree-level 3-D density 0.34 bats/m^3 (0.03-0.32) (means across roost sites and time). Estimates per species were comparable, though temporal patterns were variable between species over time (Appendix S1).

Drivers of tree-level 3-D density and abundance

Among subplot-level models, the most parsimonious predictors of tree-level 3-D density were (i) the total abundance within the subplot; (ii) proportion of trees occupied within the subplot; and (iii) the density of trees within the subplot (Table 1). Density of trees had a large and highly significant positive effect on tree-level 3-D density (regression coefficient: 9.664 ± 1.492, p <0.0001), as did the proportion of trees occupied (regression coefficient: 1.067 ± 0.301, p <0.0001) (Table 2). Subplot-level abundance was only a significant contributor when interacting with the proportion of trees occupied, but the effect was small (0.001 ± 0.001, p=0.0492) (Table 2).

Results were comparable when modelled with tree-level abundance, for all variables except density of trees (Table 2). Density of trees had a substantial and significant negative impact on the abundance of bats per tree (regression coefficient: -5.053 ± 0.105, p <0.0001) (Table 2), suggesting that abundance per tree is higher when fewer trees are available for bats to roost in. Bats occupy more of the tree's vertical space when more bats are present (a pattern consistent across tree crown classes, Appendix S2). The difference between tree-level 3-D density and tree-level abundance indicates that bats change the height range they occupy as total tree abundance increases.

At the roost level, density of trees was a relatively poor predictor of tree-level 3-D density and abundance and was not in the top-ranking model sets (Table 1). All fixed terms in the roost-level model had negligible effects on tree-level 3-D density (roost abundance: -0.084 ± 0.06, p=0.159; roost area: <0.0001, p=0.014; and the interaction term: <0.0001, p=0.021) and tree-level abundance (roost abundance: 0.447 ± 0.005, p=<0.0001; roost area: <0.0001, p<0.0001; and the interaction term: <0.0001, p<0.0001).

Roost-level predictors explained minimal variation in tree-level 3-D density, with the overall most parsimonious GAM only explaining 3.8% of variation (Table 1). Models with subplot-level and tree-level predictors explained slightly more variation (subplot-level: 11.7% of variation; tree-level: 13.6% of variation). The explanatory power of roost-level models with tree-level 3-D density was comparable when species were modelled separately (Appendix S3 in the Supporting Information). Explanatory power and rankings were comparable for models with tree-level abundance as the response variable (7.8% - 11.6% between top ranking models) (Appendix S4 in the Supporting Information).

Neither estimated tree-level 3-D density, nor model outputs, varied substantially under different values realistic for eucalyptus species (Appendix S5). Full model outputs for both response variables are given in Appendix S3 and Appendix S4 in the Supporting Information.

Discussion

We evaluated animal abundance and density at multiple scales to determine what information is relevant for understanding transmission. We used an extensive empirical dataset of roosting *Pteropus* spp. collected over 13 months and including 2,522 spatially referenced trees across eight roost sites. Measures most commonly used to parameterise models of bat-pathogen interactions (roost-level abundance and area) did not reflect the density of bats at scales where transmission is likely to take place (the abundance or density of bats within trees). Roost-level models explained a little of the variation in these tree-level measures. Density of trees was a better predictor of the likely conditions for transmission than was the population size of bats at the roost, where roosts with low tree density typically had a higher abundance but lower density of bats per individual tree. These results have implications for the structuring of infectious disease models for these species, particularly for pathogens transmitted over small local scales (e.g. within roosting trees), as discussed below.

An important consideration for bat-pathogen interactions should be whether local abundance or density is the more pertinent measure for transmission-relevant contact structure. In subplot-level models the best predictor of tree-level measures (abundance and density) was density of trees within roosts, and this had opposing effects on tree-level bat abundance and tree-level 3-D bat density. Roosts with a lower density of trees typically had more bats per tree, but a lower 3-D density of bats within these trees. This suggests that, while abundance per tree is higher when fewer trees are available for bats to roost in, bats are able to decrease their local density by expanding their occupied tree area (i.e. by spacing themselves out across the tree). Roosts with a sparse tree structure may have larger crown areas or have more foliage height available for roosting. For pathogens transmitted by direct contact, density is likely to be the relevant measure (as per standard mass action principles). If pathogens are transmitted indirectly through contact with liquid urine falling downward, or via contact with aerosolised urine particles, then total abundance within trees may be the more pertinent measure. To help illustrate this point, we provide a visual in Appendix S6 in the Supporting Information. Distinction between these measures will be key to framing ecologically relevant contact structures.

At the roost level, the associations between tree density, and bat density and abundance were diminished, as density of trees was a relatively poor predictor of tree-level abundance and 3-D density. This is likely an artefact of scale, and heterogeneity of tree density across larger areas (see similar issues of spatial heterogeneity and scale originally discussed in Krebs (1999)). Individual roosts in our dataset varied substantially in their density of trees across space. As a result, the mean density of trees (as used in these roost-level models) may not be a meaningful measure of density in roosts with a heterogenous tree structure. In other words, the variation in tree density is important at localised scales (i.e. patches within the roost), but not if averaged over the roost.

Measures of density also varied greatly by scale. This reflects the highly aggregative nature of bat distribution which is captured to different extents across the scales. Estimated mean density of*Pteropus* at the roost level was 13-fold lower than the subplot-level mean estimate that accounted for heterogenous distributions of bats (0.38 bats/m^2 with an interquartile range of 0.21-0.47, vs 5.13 bats/m^2 with an interquartile range of 2.71-6.09). At the roost-level, the total roost area can encapsulate substantial unoccupied space, if trees are sparsely distributed or not occupied, as the perimeter of the roost boundary captures the maximum extent of inhabited roosting habitat, but not trees that are occupied and unoccupied within this boundary. This contrasts with other scales of density estimate in this study, like subplot-level kernel density, which more effectively delineate unoccupied and occupied space, and so generate higher estimates of density. The latter estimates were more consistent with previous estimates of *Pteropus* density, which have ranged between 0-8.7 bats/m^2 (average 2.1 bats/m^2) for tree-level visual approximations (Welbergen 2005). The finding that spatial distributions are a function of scale is not new (e.g. see discussions of spatial distribution and scale in Krebs (1999)), but highlights the need to consider which scale (or scales) are ecologically relevant when considering the nature of density-transmission scaling in host-pathogen interactions.

Mean estimated tree-level 3-D density was 0.34 bats/m^3(0.03-0.32). The low level of variation explained by roost-level and subplot-level models (minimum 3.8% and maximum 13.6% of variation across top ranking models) likely reflects the highly heterogenous spatial structuring of *Pteropus* bats, and indicates that neither roost-level measures nor subplot-level measures adequately capture heterogeneity in these finer, tree-level estimates. In *Pteropus*bats, ecological processes operate in complex ways to influence animal density across different scales - at the roost level, a population can expand in area in response to increasing total abundance (and so remain constant in density), or remain stable in area occupied (and increase in density). If a roost does not expand its roost area in response to increasing total abundance (e.g. due to restrictions on space), bats may either fill more trees within the perimeter of the roost (and increase the density of bats at an intermediate subplot level by increasing the proportion of trees occupied but not the density within individual trees), or fill already occupied trees (and so increase both intermediate subplot density and local tree-level abundance). Whether tree-level 3-D density increases will be determined by how much bats increase their utilisation of tree space, which will be driven by the height and crown area available for roosting. The implication is that the relationship between total roost abundance and density at any scale may be unpredictable, and critically, that roost and subplot measures may not provide adequate approximations for population density at scales relevant for transmission. Tree density within roosts may provide a better standard of comparison across roosts when reflecting the conditions for transmission, but only when considered in local scales, and in context of whether local abundance or density is the more pertinent measure for transmission-relevant contact structure.

We would note here that our estimates of tree-level 3-D density and 2-D density were based on overall estimated crown area, not occupied crown area, and so may be underestimates of true density. This is an acknowledged limitation of our approximation of crown area by Dirichlet-Voronoi tessellation. True estimates of tree-level density would require empirical estimation of occupied crown area in the field. However, crown area can be difficult to measure accurately (Verma*et al.* 2014) and measurement of occupied area may not be practical. Our Dirichlet-Voronoi tessellation approach allowed us to estimate crown area for a large number of trees which would not have been feasible with field methods. While this approach could be influenced by the choice of maximum crown area set for edge trees and trees in open areas, we show that neither estimated tree-level 3-D density, nor model outputs, varied substantially under different values realistic for eucalyptus species (Verma *et al.* 2014) (Appendix S5).

Framework for heterogenous contact structures in bat-pathogen interactions

Taken together, the information in this study emphasises that models of bat disease dynamics that assume contact rate is density-dependent, but assume transmission scales with total roost abundance, may not represent actual contact structures. Such inadequate specification of transmission may produce substantially biased estimates of the basic reproductive number (R_0) and propagate error to model predictions like the probability of pathogen invasion and persistence, predicted peak and timing of epidemics, and estimates of the force of infection (Borremans *et al.* 2017; Hopkins *et al.* 2020).

Intermediate, non-linear or hybrid transmission functions are a possible alternative to standard density-dependence (e.g. Antonovics, Iwasa & Hassell 1995; Ryder *et al.* 2007; Cross *et al.* 2013; Orlofske *et al.* 2017), but these may not reveal underlying mechanisms for the relationship, and as a result, may be hard to select*a priori* based on ecological information, and may not be generalisable or predictive between bat roosts of the same species (Smith *et al.* 2009; Ferrari *et al.* 2011). Instead of modifying the transmission function, it may be better to investigate alternative approaches to integrating contact structure within host-pathogen models at ecologically relevant scales (De Jong 2002). We therefore propose a framework (Fig. 3) to help guide the incorporation of heterogenous contact structures into infectious disease models of bats in ecologically relevant ways – for example by structuring groups within roosts as metapopulations, with separate ecological processes defining contacts within and between groups. Our framework prompts ecological questions that may be relevant for specifying transmission within wildlife disease models. They include whether hosts mix homogenously throughout the roost or mix within smaller subgroups; how population or group contacts are expected to change with increasing abundance; and whether roost or group area fluctuates with abundance.

Given a roost has fluctuating abundance or density, the first step in the framework is to consider the nature of mixing in bat roosts. That is, whether bats mix evenly/randomly throughout the roost, mix within smaller subgroups, or have other structured contact networks. This will determine what scale is ecologically relevant for transmission, and so, what scale(s) the model should consider. If bats mix throughout the roost (i.e. all individuals have equal likelihood of coming into contact) the mechanisms driving contact rate will fall more simply to a choice between density-dependent and frequency-dependent expected dynamics. If occupied area changes with abundance, models will be best parameterised by density at this roost scale, otherwise, by either abundance or density.

In cases where individuals interact within aggregate groups that include only a proportion of the population, transmission mechanisms may need to be more nuanced to include special structuring within the roost. This is because the structure of the host population (and the strength of coupling between local groups) may drive transmission between groups, and be different to (and/or independent of) the nature of within-group contacts (Jong, Diekmann & Heesterbeek 1995; Ferrari *et al.*2011). In other mammal systems, this paradox has led to cases where dynamics appear to be density-dependent at the within-group scale, but frequency dependent at the between-group scale (Ferrari *et al.*2011; Cross, Caillaud & Heisey 2013). In these cases, models that can distinguish within- and between-group transmission pathways may be useful (e.g. metapopulation models). If mixing is non-random and based on individual contact networks, individual based models may provide a good framework. Of course, the complexity of adopted models should be driven by the objective of the investigation, and reflect a parsimonious attempt to reproduce transmission patterns relevant to the system and question. This need not necessarily capture every single mechanism in the real system.

Consideration of these questions will provide a more ecologically informed, mechanistic basis for specifying transmission, but will require more data and more computational power. This may or may not be achievable for many host species, for which basic ecological information is lacking. Even if ecologically informed specification of transmission is not possible, consideration of our framework will help to highlight cases where traditional density-dependent transmission may fail to reproduce data, and why. If integrated into research programmes, this could create the opportunity for a model guided fieldwork approach (Restif *et al.* 2012) and represent bat-disease systems in a more holistic approach. This framework also assumes transmission between bats is direct and occurs predominantly within the roost. This is consistent with our knowledge of bat-virus systems of zoonotic importance (Plowright *et al.* 2015). Nevertheless, understanding the nature of density at transmission-relevant scales, and building this into transmission dynamics, will be important to gain more realistic predictions of pathogen invasion and persistence in bat populations. This will be crucial for accurately forecasting disease risk from these animals.

Conclusion

Transmission is the focal process in host-pathogen interactions. The nature of infectious contacts, and how transmission scales with animal density, is complex for host species whose population structures are heterogenous and underpinned by ecological processes across different scales. Using a high-profile bat-virus system, we show that basic bat population measures from larger scales were not strongly predictive of local scale measures where viral transmission occurs. We also suggest that the highly aggregative spatial structuring of bats is likely to add substantial heterogeneity to the contact structure of roosting populations, further complicating models of pathogen transmission. We urge researchers to carefully consider which scale and modelling method is most relevant for transmission in bat-virus models. More broadly, we propose a framework to guide the structuring of transmission in more ecologically relevant contexts. This approach can apply to many species that occupy communal breeding or resting sites, and has an advantage over other statistically based approaches by allowing selection of scale and transmission structure *a priori* based on ecological information. Outputs using this ecologically informed approach will be more generalisable and predictive of infection patterns, and can be used to gain mechanistic insight into the drivers of transmission, local epidemics and pathogen spillover risk.

Authors contributions

TJL conceived and designed the research, acquired funding and led project administration; TJL and RB collected and curated the data; TJL, AJP and HM analysed and visualised the data; AJP, HM, RKP and PE provided supervision; TJL drafted the manuscript, and all authors participated in review and editing of drafts.

Data Availability Statement

Summarised data will be made available on GitHub at: < https://github.com/TamikaLunn/FF-roost-structure >. Data will also be made available from the Dryad Digital Repository upon publication.

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Tables and Figures

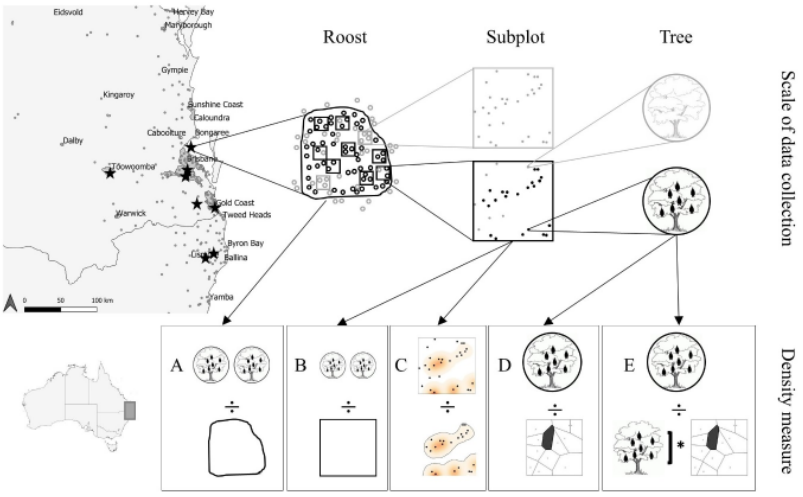
Table 1: Model comparison of candidate model set. Best candidate models, as given by Akaike information criterion (AIC), are bolded (ΔAIC<2).

	Response variable	**Response variable**
	Tree-level 3-D density	**Tree-level 3-D dens**
Model structure	**R^2**	**AIC**
Roost level		
Roost Index Abundance * Roost Area	**0.064**	**8552.2**
Roost Index Abundance * Roost Area + Mean density of trees in roost	0.064	8560.6
Null model	0.061	8727.2

	Response variable	**Response variable**
Mean density of trees in roost	0.06	8740.7
Sublot level		
Sublot Abundance * %Trees Occupied + Tree Density	**0.116**	**7986.9**
Sublot Abundance * %Trees Occupied	0.113	8011.4
Null model	0.078	8464
Tree Density	0.077	8470.2
Tree level		
Null model	**0.078**	**8464**
Tree preference	0.124	8493.5

Table 2: Parameter estimates for best model at each level.

	Tree-level 3-D density	**Tree-level 3-D density**	**Tree-level 3-D**
Variable	**Coef (± se)**	**T value**	**F value**
Roost level			
Intercept	-0.345 (0.32)	-1.079	
Roost Index Abundance	-0.084 (0.059)	-1.409	
Roost Area	0 (0)	-2.469	
Roost Index Abundance * Roost Area	0 (0)	2.3039	
Session			<0.001
Site			25.046
Subplot level			
Intercept	-2.481 (0.261)	-9.497	
Subplot Abundance	-0.001 (0.001)	-1.31	
Proportion trees occupied	1.067 (0.301)	3.5442	
Subplot Tree Density	9.665 (1.492)	6.4772	
Subplot Abundance * Proportion trees occupied	0.001 (0.001)	1.9682	
Session			0.2584
Site			13.395
Subplot			10.433
Tree level			
Intercept	-1.052 (0.218)	-4.8226	
Tree preference (irregularly occupied)			
Session			0
Site			43.109
Subplot			15.814



		Spatial replicates		Temporal replicates
Density measure	**Overall**	**Per roost**	**Per subplot**	
A) Roost-level density (/m²)	8	1	NA	13
B) Subplot-level density (/m²)	80	10	1	13
C) Subplot-level kernel density (/m²)	80	10	1	13
D) Tree-level 3-D density (/m²)	2,522*	118-474	2-75	13
E) Tree-level 3-D density (/m³)	480*	60*	6*	13
Abundance measure				
Tree-level abundance	2,522*	118-474	2-75	13

*Up to this number of replicates. Some measures could not be calculated where there were either no bats or a single bat in the tree (e.g. height range). Some trees were also removed or fell during the survey period (N=52).

Figure 1: Schematic summarising the scales of data collection (roost, subplot and tree) and density measures (A-E) with table highlighting spatial and temporal replicates of density measures within the data. Roost-level density (A) was calculated by dividing the total roost abundance by roost area. Subplot-level density was calculated either from total subplot count and subplot area (B), or from fixed-bandwidth kernel estimates (C), calculated from tree locations weighted by abundance (index values). For (C) shading showing the kernel density estimates (light shading = lower density, dark shading = higher density). Average kernel density per subplot was calculated from occupied pixels only. Tree-level 2-D density (D) was estimated from within tree abundance and canopy area (estimated by Dirichlet-Voronoi tessellations), while tree-level 3-D density (E) was calculated as the absolute count of bats in a single tree divided by the approximate volume of tree occupied (height range occupied multiplied by crown area). Tree-level 3-D density was calculated for the randomly selected subset of trees in the full dataset for which absolute count and height measures were available. The total number of datapoints for each measure can be calculated by the number of spatial replicates per roost multiplied by the number of temporal replicates. Grey colouring in measure visuals indicates where bats were absent and not included in mean calculations. Grey colouring on the map shows urban areas.

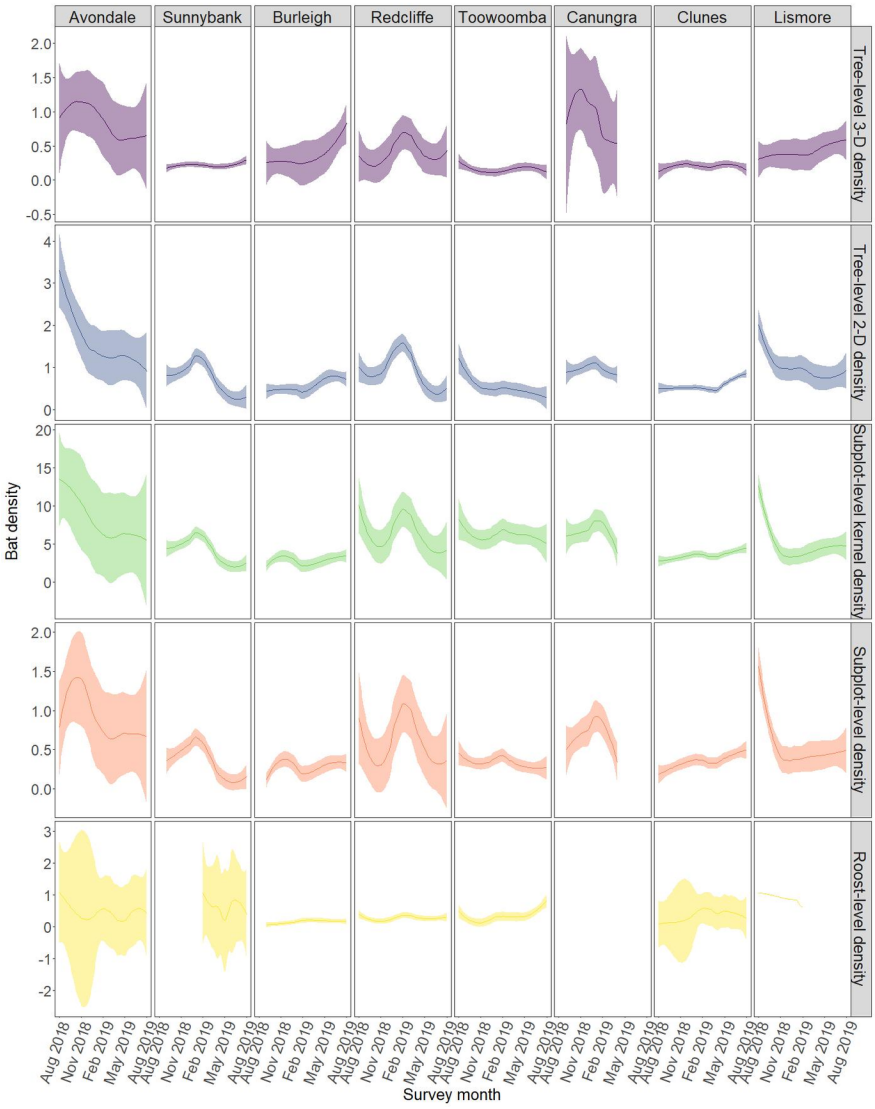


Figure 2: Comparison of density estimates across scales. Note that tree-level 2-D density, roost- and subplot-level density measures do not consider the vertical distribution of bats (bats /m^2) where tree-level 3-D density does (bats /m^3).

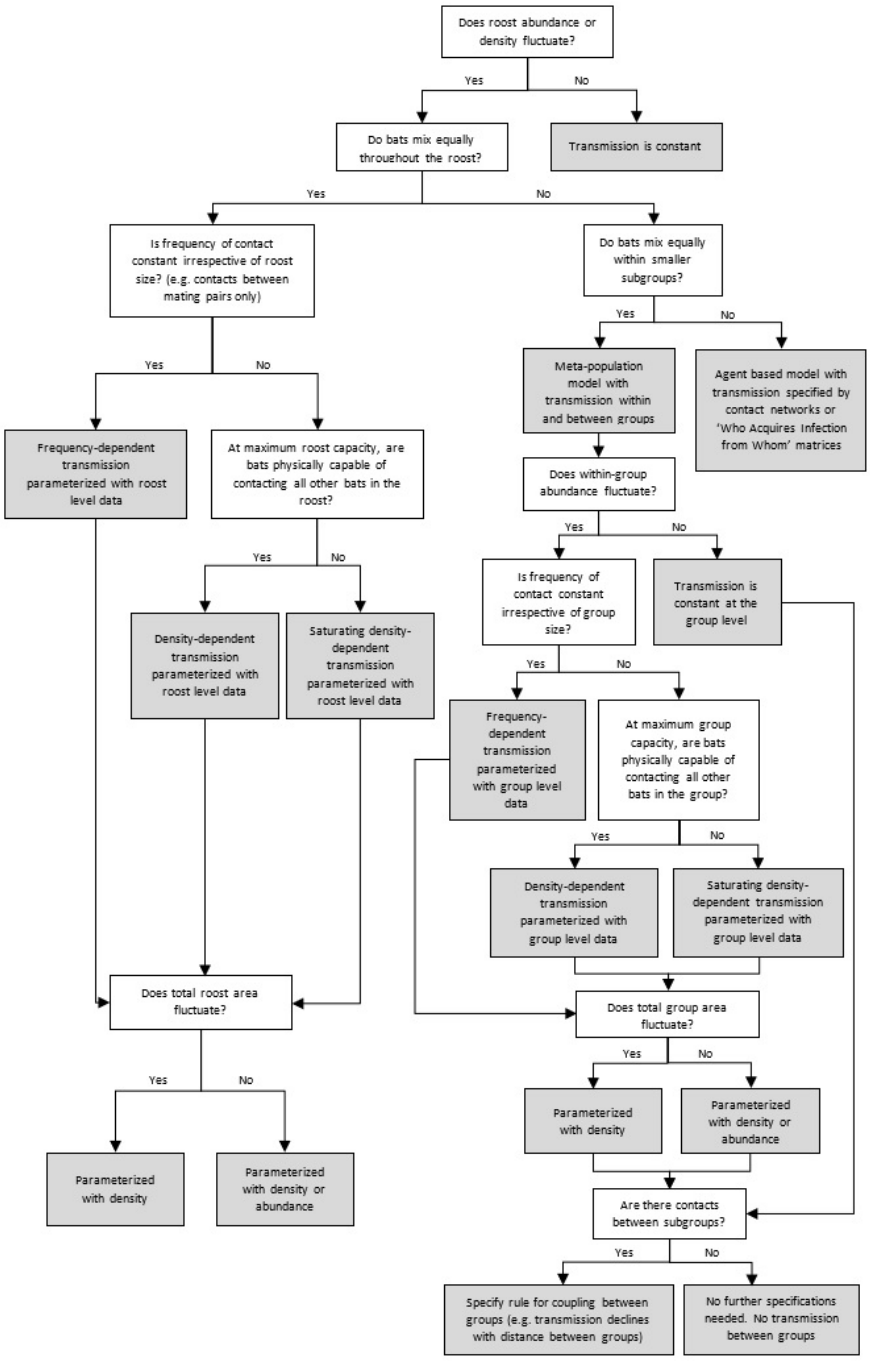


Figure 3: Suggested framework for incorporating contact structure (abundance and density data) into infectious disease models in ecologically informed ways. Whilst the framework is based on our particular bat–virus system, it should be broadly applicable, with minor modifications, to other systems. Suggestions for transmission structure are in grey. Continue the length of the decision tree for the full suggestion on transmission specification (i.e. to get combined scale and parameter choice). This framework is not exhaustive but instead aims to highlight the types of ecological questions that may be relevant for specifying contact structure within models. This framework assumes transmission is through direct contact. Note that

this framework focusses on contact structure only as a driver of transmission, but other heterogeneities in the transmission process could exist (e.g. viral load and the probability of an individual becoming infected given an infective dose, see Lunn*et al.* (2019) and McCallum *et al.* (2017)).

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