A metapopulation model of Little Red Flying Fox population dynamics across Queensland

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Abstract: The Little Red Flying Fox (*Pteropus scapulatus*) is native to large coastal areas of northern and eastern Australia. A primary food source for this species is the nectar from *Eucalyptus* and *Corymbia* blossoms. There is only partial understanding of their roosting locations (known as "camps") and movement, being semi-nomadic in nature to move between flowering events and camps. This creates a complexity in modelling the Little Red Flying Fox population. However, through stacked data including monthly spatial estimates of nectar availability, we can begin to understand how the bats move with these events.

To investigate the population dynamics, we use a metapopulation model, coupling the spatial data of average monthly nectar availability through a radiation model for movement between camps. We couple the approximately 1 × 1km spatial nectar data using Voronoi diagrams based on known camp locations. The radiation model then considers a combination of camp distance and nectar availability to determine which patch leaving bats move to. We use a combination of density and caloric needs approach to limit the population in a patch.

We compare our modelled population with historic camp survey data of population estimates. We show this relatively simple metapopulation model results in emergent behaviour aligned with the observation of ecologists, particularly to do with movement and patch numbers around pupping season. We showcase two areas of interest, regions across Cape Yorke and around Brisbane, where seasonal trends are expected to be substantially different.

This metapopulation model based on nectar availability will form the basis of further work exploring infectious diseases risks, such as Hendra or Leptospirosis. Our model can be extended to consider the spatio-temporal availability of other resources, such as fresh water, vegetation coverage, and other environmental factors (temperature, humidity, aridity, etc.).

Keywords: *Little Red Flying Fox, metapopulation model, radiation model, Queensland*

1 INTRODUCTION

The Little Red Flying Fox (LRFF) (*Pteropus scapulatus*) have multiple behaviours that make them a species of interest when considering potential (re)emerging infectious diseases such as Hendra, namely they are known to be highly mobile (Welbergen et al. 2020), are more likely to co-locate resulting in the displacement of other species (Lunn et al. 2021). Furthermore, the way they cluster is unique in that they cluster close together in large camps, sometimes even breaking the tree limbs they are clinging to. Their most prominent food source is nectar from *Myrtacaea* Trees, such as Eucalyptus.

There have been instances from the surveying done by the National Flying Fox Monitoring Program (NFFMP) of camps hosting an estimated 3 million individuals (Australian Government 2021). The estimated extent of the LRFF is across the Northern coastline and down the east coast as far as Victoria, though they have also been observed in Adelaide, South Australia, and North of Perth, WA (Macdonald et al. 2021). They are nomadic and frequently 'decamp' – that is leave their current camp for a new one – some even suggesting that they follow annual flowering patterns of feed trees. An estimated foraging distance is roughly 40km per night (80km return) (Macdonald et al. 2021), while bats have been known to travel over 400km to decamp to a new location (Welbergen et al. 2020). The biggest decamping event is thought to occur during pupping season (May – June), when large counts have been observed (Australian Government 2021).

We explore how the historic spatiotemporal fluxes of nectar availability affect the pattern of the flying fox populations across Queensland, including exploring the camps observed to be unusually populous during pupping season.

2 METHODS

2.1 Data on Little Red Flying Foxes and nectar availability

Observations of the camp locations (latitude and longitude) and estimated population numbers of the bats come from the NFFMP (Australian Government 2021). The NFFMP has been active since November 2012, and was launched as a collaborative project between Australian, NSW, Queensland, Victorian, South Australian and ACT Governments and CSIRO Land and Water (Australian Government 2021).

Additionally, we use raster estimates of the historical availability of nectar per month on approximately a 1×1km grid across Queensland. This estimate is based on the presence of the trees LRFFs prefer to feed on, the flowering patterns of various *Myrtacaea* species, amongst other factors. For further information on how nectar availability is estimated, see (Westcott et al. 2020).

Figure 1. Voronoi regions of known LRFF camps (circles) in Queensland, Australia for the raw data (left) and when explicitly taking into account the estimated 40km foraging distance (right). Note the colours are only to aid visual clarity of the polygon borders.

2.2 Determining the spatial patches

As the historic nectar availability data is for Queensland, our study area is Queensland. We further mask the geographic region of Queensland by the estimated spatial extent of LRFFs, as shown in Figure 1 of Macdonald et al. (2021).

Using the point estimates of the camp locations (167 total camps), we developed Voronoi diagrams to give a representation of the local areas where bats are likely to forage within a night without moving camps. The camp location data was cleaned to find the midpoint that were within 40km of each other, based on the typical foraging distance of LRFFs (see, for example, Welbergen et al. (2020)). The Voronoi regions were subsequently generated using `geovoronoi` Konrad (2022), Python 3.9, and other dependent packages. The difference between the observed camp locations and this merged approach is depicted in Figure 1. This merging results in 72 patches. Where camps were merged, survey estimates for the LRFF population were summed.

The merging depicted in Figure 1 reduced the number of patches from 167 to 72, reducing computational requirements. The merging of the camps is non-unique but systematic and reproducible. The choice of merging distance is to reflect the observed typical foraging behaviour, otherwise estimates of population dynamics based on historic nectar availability would likely be greatly underestimated in areas with many camps within small areas, such as the inset region.

2.3 Relating historic nectar availability estimates to the LRFF population

Given the camp locations are point data and the nectar estimates are rasters, we first summed the estimated available nectar in a month using the voronoi polygons. As the Voronoi polygons in Figure 1 represent the spatial regions LRFFs are expected to forage in a night, we summed the nectar availability for a total estimate each month using a combination of `geopandas`, `shapely.geometry`, Python 3.9, and other package dependencies. The larger patches towards central Queensland (away from the coastline) implicitly allow for foraging further than 40kms, which is a limitation of this approach.

To relate the nectar to a carrying capacity $K_i(t)$ in patch i at time t, we approximated a maximum enclosing envelope using a piecewise linear function of the relationship between the population number and estimated total nectar in a patch each month,

$$K_i(N(t)) = \begin{cases} \frac{1500000}{62176} N_i(t), & 0 \le N_i(t) < 62176 \\ 3000000, & N_i(t) \ge 62176 \end{cases}. \tag{1}$$

The specific numbers, such as 62176, arise from the empirical approximation. This does not take into account noise in the count estimates of the population size, instead assuming no patch population is above three million.

2.4 The LRFF metapopulation model

Let the population dynamics for the LRFF population in patch i at time t are governed by a metapopulation model with crowding-based deaths ($\mu P_i/K_i(t)$, with $K_i(t)$ the carrying capacity based on nectar availability) and seasonal births ($b(t)$), with a radiation model of migration for dispersion both in and out of patches (see, for example, Alis et al. (2021), Simini et al. (2012)), resulting in the following system of ordinary differential equations (ODEs),

$$\frac{dP_i}{dt} = P_i(t)\left(b(t) - \mu \frac{P_i(t)}{K_i(t)}\right) - \sum_{j, i \ne j} \langle T_{i \to j} \rangle(t) + \sum_{j, i \ne j} \langle T_{j \to i} \rangle(t), \tag{2}$$

where $\langle T_{i \to j} \rangle$ is the flux between patches at each time step t,

$$\langle T_{i \to j} \rangle(t) = \ell_i(t)P_i(t) \frac{N_i(t)N_j(t)}{(N_i(t) + s_{i \to j}(t))(N_i(t) + N_j(t) + s_{i \to j}(t))}, \tag{3}$$

$N_i(t)$ is the total nectar available in patch i at time t, $\ell_i(t)P_i(t)$ is the number of individuals leaving site i, and $s_{i \to j}$ represents the sum of the nectar available that month in all other patches within radius r_{ij} centred at patch i (given by the distance between patch i and j). To capture the birthing period being between the two months of May and June, we set $b(t) = b_c$ during those months, and zero otherwise.

Initial conditions for the model were based on the earliest available survey estimate for a given camp (or camps where merged). The model was implemented in Python 3.9, with the system of ODEs solved using `scipy.integrate.solve_ivp`.

Table 1. Detail about the model parameters for System (2). Note all rates are in units of per day.

Symbol	Description	Baseline (explored)	Source
b_c	birth rate during non-zero months	$\frac{1-\delta}{61 \times 15}$ (0.5/61)	Estimated
δ	equaliser for births over 61 days to equal deaths over year	9.42/10	Calculated
μ	1/average lifespan	1/10950	Macdonald et al. (2021)
$K_i(t)$	carrying capacity of patch i at time t	Equation (1)	Estimated
$\ell_i(t)$	leaving rate from patch i at time t	0.41 (0.1)	Macdonald et al. (2021)
$r_{\max}$	maximum movement distance for radiation	450km	Welbergen et al. (2020)

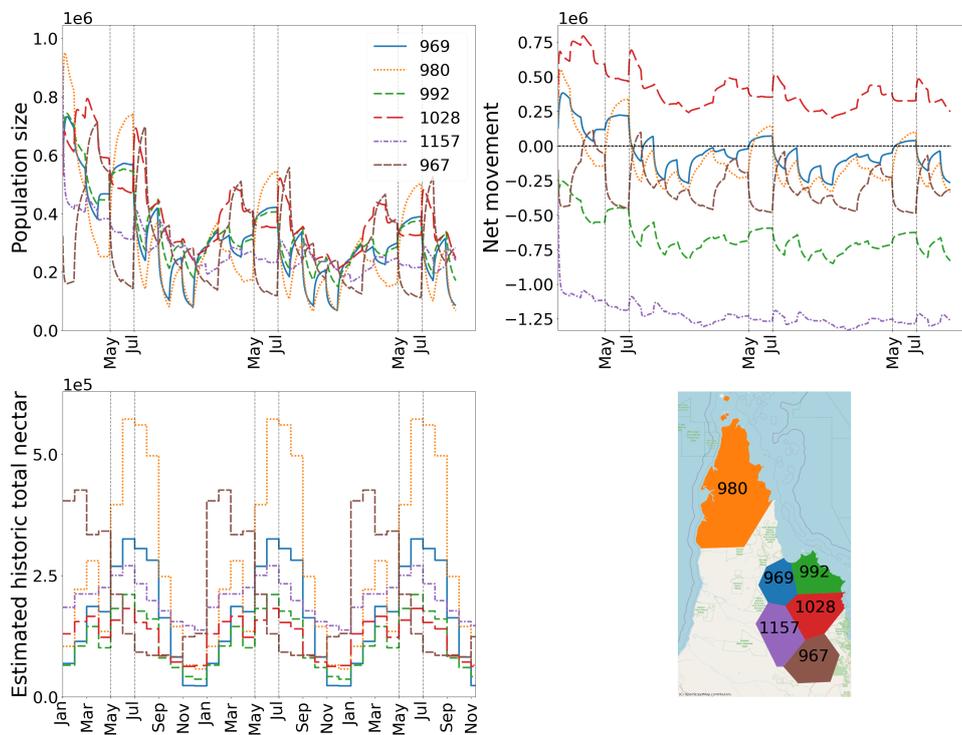## 3   SPATIOTEMPORAL DYNAMICS OF THE MODEL

Figure 2.   Model dynamics for selected patches in Cape Yorke, with colours corresponding to the patches displayed in the map (bottom right) and the legend in the top left figure relates the line types to those patch numbers. The top left shows the modelled LRFF population size versus time (days). The bottom left shows the estimated historic nectar available each month in the respective patch. The top right shows the net movement into a patch through time (positive values result in an increasing population, and conversely negative a reducing population). Note the y-axis scale is scaled by $1e6$ for the top figures, and $1e5$ for the bottom left.

We first explore the spatiotemporal dynamics of the LRFF population, net movement, and nectar availability, for select patches across Queensland with baseline parameter values. The patches selected represent areas known to either be favoured for breeding (Cape Yorke, Figure 2) or not (just north of Brisbane, Figure 3). The baseline parameter values are reported in Table 1.

The breakdown of the dynamics in Figures 2 and 3 show the radiation term for movement is dominating, with several patches showing a strong decline in population size even when there are large amounts of nectar available. This dominance of movement over nectar availability was surprising since, per Equation (3), movement is determined by a combination of distance and nectar availability, with distance represented through the $s_{i \to j}$ terms. For example, patch 161 (Figure 3) has a the largest population during periods when the nectar availability is low, such as May–July. Patch 980 in Figure 2 has almost as much nectar available in July as June, yet there is a steep decrease in population size. This particular patch is a known pupping site, and shows strong growth during the May–July period. One aspect of the dynamics across Cape Yorke of interest is the nectar availability in the patches near 980 are also reasonably high in the months the pups would first be expected to forage for themselves.
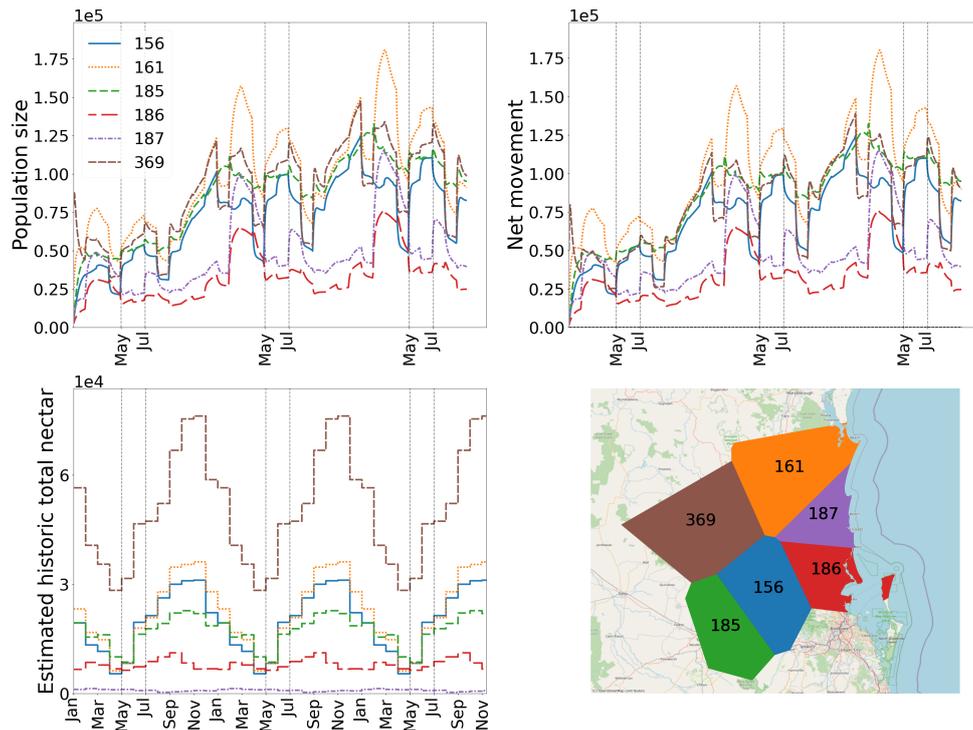

Figure 3.   Model dynamics for selected patches just north of Brisbane, with colours corresponding to the patches displayed in the map (bottom right) and the legend in the top left figure relates the line types to those patch numbers. The top left is the LRFF population size versus time (days). The bottom left is the estimated historic nectar available each month in the respective patch. The top right shows the net movement into a patch through time (positive values result in an increasing population, and conversely negative a reducing population). Note the y-axis scale is scaled by $1e5$ for the top figures, and by $1e4$ for the bottom left.

4   EXPLORATION OF THE EFFECT OF KEY PARAMETERS ON THE DYNAMICS

There were discrepancies in the literature about how often LRFFs move camps, with Macdonald et al. (2021) suggesting 41% ($\pm$21%) move each day, and Welbergen et al. (2020) estimating they move every 10–14 days. As such, we use the 0.41 estimate as the baseline, but explore the effect of the substantially lower leaving rate of 0.1, with this difference shown in the top row of Figure 4 (baseline model values minus decreased leaving rate model values). The longer term differences as a result of the reduced leaving rate are small, with the effect earlier on likely due to a mismatch in initial conditions as a result of not having survey estimates for all patches in the same years. In particular, the difference in patch 980 (orange) is small during the pupping season.
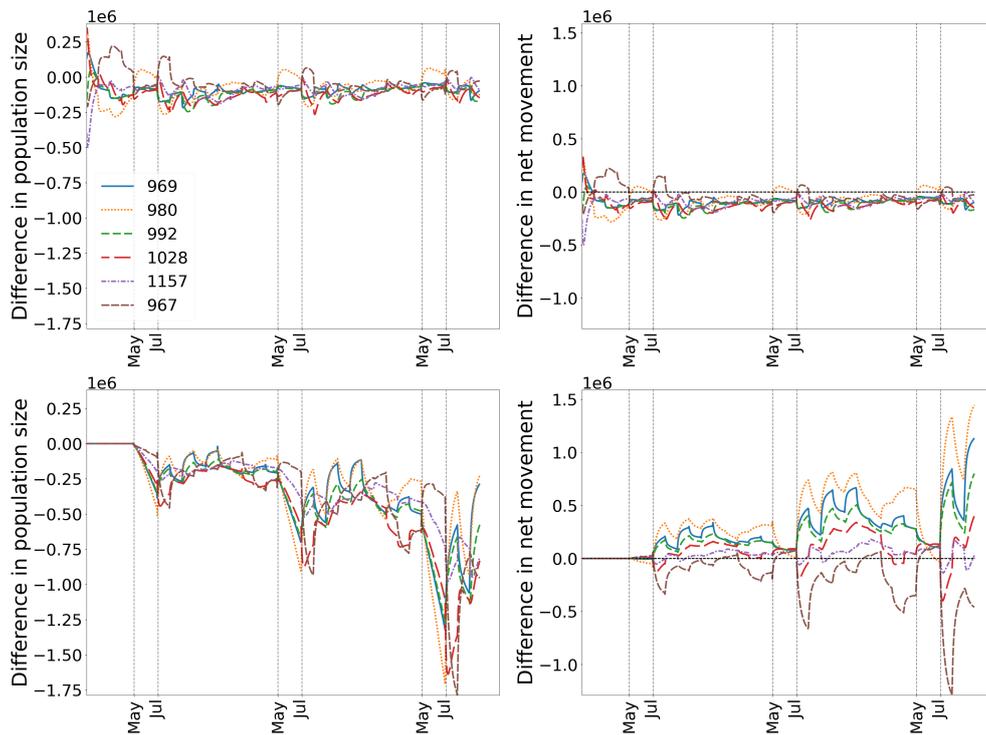
Figure 4. Differences in the model dynamics for selected patches across Cape York, with colours corresponding to the patches displayed in the bottom right map of Figure 2 and the legend in the top left figure relates the line types to those patch numbers. The top row depicts the difference between the baseline leaving rate ($\ell = 0.41$) and a lower leaving rate ($\ell = 0.1$). The bottom row is the difference between the constant population size assumption and a growing population, with left the baseline LRFF population size minus growing population, and the right the difference in net movement. Note the y-axis multiplier of $1e6$.

One knowledge gap of the LRFF population in Queensland is how the total population varies through time. As such, we explore an approximately stable population (across the course of a year) as the baseline, and how the spatiotemporal dynamics are affected when we instead assume an optimistic birth rate (all females breed each year and constitute half the population), resulting in a growing population. The difference between the baseline constant population and a growing population are shown in the bottom row of Figure 4 (baseline model values minus growth model values). The differences are increasing through time, as to be expected with the growth model. However, even though the trend is larger, the patterns relative to the patches remain consistent. For example, the strongest growth period for patch 980 (orange) is still during the pupping season, though the growth is more strongly driven by births and less by movement.

5 DISCUSSION

We found that a relatively simple metapopulation model describing population dynamics and movement based on historic nectar availability results in emergent properties aligned with observations. In particular, it is interesting that the known preferred breeding site (patch 980) shows such strong growth during the pupping season, despite the choices in birth or leaving rates.

The key strength of our approach is its relative simplicity, and ability to recreate the observed strong trend of LRFFs moving towards Cape Yorke with no explicit forcing term. Prior models have used an explicit forcing function. This is a simple population and movement model based on estimates of historic nectar availability

per month. That nectar availability is likely to fluctuate year to year, based on climatic factors such as rainfall. This limited our ability to do any model fitting. We have subsequently explored the effect of varying some of the key model parameters on the population size and movement, namely the birth rate and leaving rate. Although we did not perform model fitting, our approach is still data and biologically-based, with interesting outcomes warranting further investigation.

6 CONCLUSIONS

LRFFs are an important species in Australia for a variety of reasons, especially their role in pollination, but some of their behaviours mean they may be particularly vulnerable to the introduction of, or helping spread an introduction of, key pathogens. This is a straightforward modelling approach used to explore population dynamics across a region of interest based on known camp locations, loosely on population estimates from surveys, and on estimates of historic nectar availability. This approach resulted in large population centres and movements of the bats aligning with observations more closely than expected.

We think this approach could be used as a foundation to help infer missing camp locations. There are many opportunities to expand on this approach, such as the effect of the foraging distance, and different camp aggregation algorithms.

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