

Conventional wisdom on roosting behaviour of Australian flying foxes - a critical review, and evaluation using new data

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April 12, 2021

Abstract

1. Fruit bats (Family: Pteropodidae) are animals of great ecological and economic importance, yet their populations are threatened by ongoing habitat loss and human persecution. A lack of ecological knowledge for the vast majority of Pteropodid bat species presents additional challenges for their conservation and management. 2. In Australia, populations of flying-fox species (Genus: Pteropus) are declining and management approaches are highly contentious. Australian flying-fox roosts are exposed to management regimes involving habitat modification, either through human-wildlife conflict management policies, or vegetation restoration programs. Details on the fine-scale roosting ecology of flying-foxes are not sufficiently known to provide evidence-based guidance for these regimes and the impact on flying-foxes of these habitat modifications is poorly understood. 3. We seek to identify and test commonly held understandings about the roosting ecology of Australian flying-foxes to inform practical recommendations and guide and refine management practices at flying-fox roosts. 4. We identify 31 statements relevant to understanding of flying-fox roosting structure, and synthesise these in the context of existing literature. We then contribute contemporary data on the fine-scale roosting structure of flying-fox species in south-eastern Queensland and north-eastern New South Wales, presenting a 13-month dataset from 2,522 spatially referenced roost trees across eight sites. 5. We show evidence of sympatry and indirect competition between species, including spatial segregation of black and grey-headed flying-foxes within roosts and seasonal displacement of both species by little red flying-foxes. We demonstrate roost-specific annual trends in occupancy and abundance and provide updated demographic information including the spatial and temporal distributions of males and females within roosts. 6. Insights from our systematic and quantitative study will be important to guide evidence-based recommendations on restoration and management and will be crucial for the implementation of priority recovery actions for the preservation of these species into the future.

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5. We show evidence of sympatry and indirect competition between species, including spatial segregation of black and grey-headed flying-foxes within roosts and seasonal displacement of both species by little red flying-foxes. We demonstrate roost-specific annual trends in occupancy and abundance and provide updated demographic information including the spatial and temporal distributions of males and females within roosts.
6. Insights from our systematic and quantitative study will be important to guide evidence-based recommendations on restoration and management and will be crucial for the implementation of priority recovery actions for the preservation of these species into the future.

Keywords : Pteropodidae; fruit bat; camp; habitat; management; conservation

Introduction

Fruit bats (Family: Pteropodidae) are animals of extraordinary ecological and economic importance (Fujita & Tuttle 1991). As long distance seed dispersers and pollinators, fruit bats play a crucial role in the maintenance and regeneration of forest ecosystems (Shilton *et al.* 1999; Hodgkison *et al.* 2003; Oleksy, Racey & Jones 2015). Moreover, fruit bats are responsible for the propagation of at least 289 plant species, 186 of which have economic value, making fruit bats important contributors to the sustainability of human livelihoods (Fujita & Tuttle 1991). Despite their importance, many fruit bat species are in severe decline. Half are listed as near threatened to extinct according to the IUCN (88 of the 177 species with sufficient data) (IUCN 2020), with human persecution and habitat loss identified as two of the largest threats imposed on these species (Jenkins *et al.* 2007; Acharya, Bumrungsri & Racey 2011; Andrianaivoarivelo *et al.* 2011; IUCN 2020). While measures have been taken in some countries to reverse this trend – including increased legislative protection (Eby & Lunney 2002b; Thiriet 2010; Aziz *et al.* 2016) and community awareness campaigns (Carroll & Feistner 1996; Trewhella *et al.* 2005; Anthony, Tatayah & De Chazal 2018) – conservation and management efforts for the majority of these species remain hindered by an enduring absence of ecological knowledge

(Fujita & Tuttle 1991; Mickleburgh, Hutson & Racey 2002) and ongoing conflict with humans (Aziz *et al.* 2016; Currey *et al.* 2018).

These same conservation challenges persist for Australian flying-foxes (Genus: *Pteropus*) despite improved levels of protection. Indiscriminate and widespread persecution and killing of flying-foxes were persistent until the ~1990's (Ratcliffe 1931; Fujita & Tuttle 1991; Hall 2002). Species listed as threatened are now afforded national protection under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) (Department of Agriculture Water and the Environment 1999) and other species are protected from harm under state-level native species legislations (Department of Environment and Primary Industries State Government of Victoria 1988; Queensland Government 1992; New South Wales Government 2016). However, loss and degradation of roosting habitat continues to pose a substantial threat, and management of these species must additionally balance conservation outcomes with negative public perception and human-wildlife conflict (e.g. BBC News Australia 2017; Kohut 2017; Welle 2021).

A major challenge for these species is that policies for conservation and conflict management are often in direct contrast. The identification, management and protection of roosting habitat are listed as priority recovery actions for the Vulnerable grey-headed flying-fox (*Pteropus poliocephalus*) and Endangered spectacled flying-fox (*P. conspicillatus*) (Commonwealth of Australia 2017a). Yet in direct contrast, roost management policies and guidelines that aim to reduce human-wildlife conflict often promote removal of roost trees to create perimeter buffers between the roost and private properties, which can exceed 50 meters in some cases (State of NSW and Office of Environment and Heritage 2018). In more extreme cases, flying-fox roost management permits can be granted to disturb, drive away or destroy flying-fox roosts entirely (Mo *et al.* 2020a; Mo *et al.* 2020b).

Management challenges in Australia are being further compounded by an emerging and accelerating trend of urbanisation of flying-fox roost sites, and fragmentation of roost populations (Williams *et al.* 2006; Tait *et al.* 2014). Roost structures are transitioning from large roosts that are seasonally occupied by nomadic individuals into smaller, continuously occupied roosts in urban areas (Van der Ree *et al.* 2006; Eby *et al.* in review). This fragmentation, or fissioning, of roost populations has been attributed to environmental change, both land clearing of winter flowering native species in south-eastern Australia (Eby *et al.* 1999) and the concurrent increase in availability of exotic winter food resources in urban areas (Parry-Jones & Augee 2001; Williams *et al.* 2006). As a consequence, increasing numbers of roosts have formed near residential housing, particularly in metropolitan areas like Sydney, the Gold Coast and Brisbane, despite overall population declines (Tait *et al.* 2014). These urban roosts often develop into sites of ongoing conflict with neighbours (Commonwealth of Australia 2017b) and there has been growing demand to reduce the impact of roosts on local communities through active management of flying-fox camps (Currey *et al.* 2018). Similar changes with fragmentation and urbanisation have been observed elsewhere (Hahn *et al.* 2014a; Hahn *et al.* 2014b; Peel *et al.* 2017) suggesting that this occurrence is likely representative of other systems across the range of Pteropodids.

A second major challenge for management of these species is that systematically informed, baseline ecological knowledge is limited, so the impact and effectiveness of efforts to contribute to either conservation (roost restoration) or conflict (roost modification) goals are unknown. Roosting requirements of these species are not well understood (Commonwealth of Australia 2017a) beyond broad scale trends in roosting patterns (e.g. Tidemann *et al.* 1999; Vardon & Tidemann 1999), migration (Eby 1991; Eby *et al.* 1999) and studies on sociality and behaviour (Nelson 1965b; Welbergen 2005; Klose *et al.* 2009). Detailed (fine-scale) spatio-temporal patterns in animal density and tree-use remain unquantified (Commonwealth of Australia 2017a), and knowledge on historical usage patterns (e.g. Ratcliffe 1931; Nelson 1965b; Tidemann *et al.* 1999; Vardon & Tidemann 1999) may be inconsistent with current usage patterns. This lack of detailed information is of particular concern, as current conservation strategies that aim to identify, protect and restore important roosting habitat, and practices for managing conflict, are necessarily founded on observations that may not fully reflect the habitat requirements of the animals. In this context, the number of flying-fox roosts exposed to programs of vegetation modification is increasing rapidly in Australia, yet the potential impact

of modifications to roosting habitat on flying-foxes is largely unknown. More information is needed to provide baseline ecological data in this time of rapid ecological change, and to guide and support vegetation management practices and decision-making criteria to provide a realistic representation of the roosting habitat needs and preferences of flying-foxes. Systematic and comprehensive examination of multiple species in Australia may also help identify whether generalities exist among Pteropodids, and guide understanding in systems where more limited data and resources are available.

In this paper, we seek to identify and evaluate commonly held understandings about the roosting ecology of Australian flying-foxes, focusing on species on the Australian mainland. We first review ‘grey literature’ (management, recovery and restoration plans or reports published by state government and local groups) to identify commonly held understandings concerning flying-fox roosting structure. We then review the existing empirical literature, to critically evaluate the extent of empirical support for these statements and highlight gaps in empirical evidence. Lastly, we utilise high resolution spatial mapping techniques and monthly field observations to systematically and quantitatively document spatial and intra-annual temporal patterns in flying-fox roost and tree use in south-east Queensland and north-east New South Wales. This approach allows us to highlight where quantitative information on flying-fox roosting has been missing, and where updated information may be required. Our new dataset is the first to capture fine-scale spatial and temporal dynamics of flying-fox roost use in a structured, repeatable design, and provides baseline information in a time of rapid ecological change. Such systematic and quantitative study will be important for informing evidence-based recommendations to guide vegetation modification practices and improve roost management strategies for flying-fox conservation. This will be crucial for implementation of effective habitat restoration projects, to successfully balance the management of these threatened, contentious and urbanising wildlife, and to guide comparable approaches in other Pteropodid species across their range.

Methods

Review of grey literature

Flying-fox management is generally undertaken in line with site-specific roost management plans (e.g. Ecological 2014; Scenic Rim Regional Council 2015; Council of Ipswich 2016), which are adopted by local government councils based on their state’s flying-fox camp management policy (e.g. Queensland: SEQ Catchments (2012), State of Queensland Department of Environment and Science (2020); and New South Wales: State of NSW and Office of Environment and Heritage (2018)). We focused on statements made in state-level documents, as these are the primary resource for individual roost plans. We identified common statements/understandings across these documents, with particular emphasis on those that pertain to 1) routine vegetation management activities (weed removal and trimming under-storey vegetation); 2) creation of buffers (either by clearing/trimming canopy trees, or disturbing animals at the roost boundary); and 3) restoration interventions.

Review of existing empirical support

We conducted a systematic literature search of peer-reviewed published literature using ISI’s Web of Knowledge (July 27th2020). Keywords were chosen to target studies evaluating the within- and between-roost structure of Australian flying-foxes (Table S1). This included any studies relevant to 1) the physical structure of roosts (e.g. area, tree structure, tree/roost selection), 2) the social structure of roosts (e.g. demographic and species structuring), 3) roosting behaviour (e.g. territoriality and fidelity of individuals), 4) movement and migration relating to occupancy and abundance of roosts, and 5) roost microclimate. In addition to the literature search, reference lists and relevant studies already known to the authors were also screened to identify potentially relevant studies not captured by our initial search. We also included empirical support from key unpublished sources (e.g. theses).

Empirical data collection

We collected data on roosting structure at eight sites in south-east Queensland and north-east New South Wales (Figure 1). These sites were chosen to represent a gradient of habitats utilised by flying-foxes, ranging from metropolitan areas of Brisbane and the Gold Coast, to roosts in peri-urban and rural areas (Figure 1, Table 1). All sites were previously documented as having a continuous population of grey-headed or black flying-foxes. Little red flying-foxes visited some roost sites intermittently, however no roost sites occurred within the distribution of spectacled flying-foxes (National Flying-Fox Monitoring Program 2017).

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) per roost site. Trees were mapped and tagged using tree survey methods described in the “Ausplots Forest Monitoring Network, Large Tree Survey Protocol” (Wood *et al.* 2015). To evaluate spatio-temporal patterns in roosting, we revisited all tagged trees and scored the extent of species occupancy using the following tree abundance index: 0= zero bats; 1= 1-5 bats; 2=6-10 bats; 3=11-20 bats; 4=21-50 bats; 5=51-100 bats, 6=101-200 bats, 7= >200 bats. For a subset of trees (N=60 per site, consistent through time) absolute counts and minimum/maximum roosting heights of each species were taken. Overall roost perimeter (perimeter of area occupied) was mapped with GPS (accurate to 10 meters) immediately after the tree survey to estimate perimeter length and roost area. Total abundance at each roost was also 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 emerged in the evening from their roosts (“fly-out”), as per recommendations in 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 1965b). Because roost estimates become more unreliable with increasing abundance we also converted the total estimated abundance into an index estimate for use in analyses, as per values used by the National Flying-Fox Monitoring Program (2017). Census 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. Roosting surveys were repeated once a month for 13 months (August 2018 - August 2019). More detailed methods of empirical data collection can be found in Appendix S1 in the Supporting Information.

Statistical analyses

The main statistical comparisons tested with our empirical data were: 1) whether frequency of occupation is greater for subplots in ‘core’ areas of the roost compared with subplots in irregularly occupied ‘peripheral’ areas (defined by occupation greater than or less than 80% of surveys respectively (Appendix S1); 2) whether bat occupation decreases with distance from the roost centre (per species); 3) whether bat species segregate in vertical space; and 4) whether dominant individuals occupy the centre of roosts, and subdominant individuals the outer area (per species). We also provide qualitative comparisons of 5) seasonal patterns of abundance and occupancy per species; and 6) whether bat species segregate in horizontal space.

We utilised generalized additive models for all statistical comparisons to allow for nonlinearity, with random effects modelled with smooth functions. Roost site and subplot were modelled using a standard random effects smoothing function. Session was modelled using a cyclic cubic regression spline in cases where seasonality in the time series was evident (all comparisons except those involving the proportion of male black, male grey-headed and combined male bats per tree), otherwise session was modelled with a standard random effects smoothing function. We accounted for non-independence (nesting) of random effects by including an autoregressive model for errors in the model (Yang *et al.* 2012; Laurinec 2017). For the comparisons involving evaluation of species, models were run separately for each species owing to differences in seasonality of occupation (and so, differences in the fit of cyclic cubic regression splines). Error distribution for comparisons were specified according to data type and extent of zero-inflation (as per Crawley 2013). We fit the models and performed checks of standardised residuals in R (Version 4.0.2), using the ‘mgcv’ package (functions ‘gamm’ and ‘gam.check’) (as per Wood 2017). See Appendix S1 in the Supporting Information for more detailed information on modelling decisions and a summary table of comparisons. Summarised data and annotated R code are available on GitHub at: < <https://github.com/TamikaLunn/FF-roost-ecology> >.

Results

From our review of management, recovery and restoration documents published by state government, we highlighted 31 commonly held understandings relevant to flying-fox roosting structure (Table 2). From our systematic search for empirical literature we generated a total of 79 search results. Of these, 52 were removed through screening (10 being outside the Australian mainland, 4 on non-Pteropus species, and 38 focused on topics other than roost structure). An additional 18 published studies and 4 honours/PhD theses were included from citations and the author’s reference collections, giving 49 included studies in total (Appendix S1). Lastly, we generated an empirical dataset consisting of 13 monthly repeat measures from 2,522 trees across eight roost sites. Roost sites contained 118-474 measured and tagged trees each, with an average of 2 (sparsely structured) to 75 (densely structured) trees per 20x20 meter subplot. Tree roosting height and count was recorded for 9,056 trees out of 32,206 repeat measures. (Note that our total repeat measures were less than 32,786 owing to cases of tree removal through the duration of the survey.) We report model outputs of main interest in the main text, but see Appendix S2 in the Supporting Information for full model output.

Below, and in Table 2, we synthesise how commonly held understandings compare with existing literature and new data from our study.

Use of area

“Some areas of permanent camps are more consistently occupied (‘core areas’) than others”

This understanding was generally reported by previous studies, with none contradicting it (Table 2). Consistent with these other studies (e.g. Nelson 1965b; Welbergen 2005) we observed some areas of roosts to be more consistently occupied than others (Figure 2). Occupancy of subplots ranged between 100% (30 subplots) to under 10% (15 subplots) across surveys when bats were present in roosts.

“‘Core areas’ are more densely occupied than ‘peripheral areas’”

Existing empirical data broadly supported this statement (Table 2). In our study, peripheral areas (those occupied less than 80% of the time) generally were less densely occupied than core areas, though density varied substantially across roost site, subplot and session (all contributed substantially as random effects). Here, lower density refers to both a lower number of bats per subplot in peripheral subplots (-0.581 ± 0.177 , $p = 0.001$, Figure 3), and a lower proportion of occupied trees (-0.222 ± 0.078 , $p = 0.005$,

Appendix S2). Within subplots, we also note that some trees were more consistently used than others, including trees that were occupied in 100% of surveys where bats were present at the roost (Appendix S1). The number of bats per tree in irregularly occupied trees (occupied less than 80% of the time) were typically lower than for regularly occupied trees (-0.606 ± 0.034 , $p < 0.001$).

We observed negative relationships between bat occupation metrics and distance from the roost centre, including in the number of bats per occupied subplot (-1.639 ± 0.016 , $p < 0.001$, Figure 4) and proportion of occupied trees per subplot (-0.315 ± 0.034 , $p < 0.001$, Appendix S2). This decline with distance from the centre of subplot was largely driven by little red flying-foxes (Figure 4). Roost site, subplot and session also all contributed substantially as random effects (Appendix S2).

“Roost area fluctuates with total abundance”

Studies have previously reported changes to total roosting area, but none to date have formally quantified the relationship between area and abundance (Table 2). From our data, we observed substantial fluctuations in total roost area within some roost sites across monthly surveys, and overall, a positive relationship with total roost abundance. The extent of variation was variable across roosts, however (Figure 5). We note that relationships between total abundance and area were likely masked in many roosts by the large span of population values in some index categories (e.g. index 6 spans 16,000 - 49,999 bats). It is probable that data

of finer resolution may have detected this relationship more strongly for roosts in this size range, but are not available in this dataset.

Spatial segregation of species

Results from our new dataset included systematic recording of the three species that occur in south-east Queensland – *P. alecto*, *P. poliocephalus* and *P. scapulatus*. The majority of observations were made of *P. alecto*, and *P. poliocephalus*, which occupy this region continuously through the year. *P. scapulatus* was found irregularly at some roosts, which is consistent with the seasonal migration patterns of this species (Nelson 1965a). Fine-scale spatial overlap between species was evaluated during surveys when multiple species were present (N=73, 70.2% of surveys). Black and grey-headed flying-foxes co-occurred in 65 surveys (62.5%), black and little red flying-foxes co-occurred in 17 surveys (16.3%), and grey-headed and little red flying-foxes co-occurred in 9 surveys (8.7%). We observed roost-dependent support for spatial segregation of species.

“Species share roosts sites, but segregate spatially within”

Observations from previous studies commonly report co-occupation of roosts by multiple species, with anecdotal observations of inconsistent overlap or separation within and between trees (Table 2). We observed some horizontal spatial segregation of species, with species showing preference for discrete areas in roosts. In the ‘Lismore’ roost, for example, black flying-foxes were commonly distributed toward the eastern part of the roost and grey-headed flying-foxes in the western part of the roost (Appendix S3). Likewise, in the ‘Clunes’ roost, black flying-foxes were commonly observed toward the north-eastern part of the roost and grey-headed flying-foxes in the south-western part of the roost (Appendix S3). Of 659 occupied subplots across the survey period, only 34.1% (225, binomial confidence interval: 0.31-0.38) showed co-occupation by two different species (Figure 6A). Co-occupation of individual trees by two different species was also relatively low – across surveys where two species were present, 4.6%-7.9% of occupied trees were co-occupied by two species, versus 92.1-95.4% that were occupied by only one species (Figure 6B). Only six trees were ever observed to occupy all three species at once.

“Large influxes of species into roosts (especially little red flying-foxes) can displace other species”

Only one previous study had reported displacement by species, reporting an anecdotal observation of black and grey-headed flying-foxes being displaced by little red flying-foxes (Table 2). Our quantitative data document changing distribution of regular species occupants in response to (‘invading’) irregular species occupants, supporting this prior observation. Little red flying-foxes, in particular, were observed to displace black and grey-headed flying-foxes from their usual roosting locations (most notably at the ‘Redcliffe’ roost: Appendix S3). Black and grey-headed flying-foxes tended to co-occur in roosts without too much impact on each other (Appendix S3).

“Species roost at different heights”

Previously only one study had formally documented differences in roosting height between species (Table 2). This included record of black flying-foxes and grey-headed flying-foxes only, and did not provide measures of absolute height (rather, roosting in different quadrants of trees) (Welbergen 2005). From our new dataset, we observed segregation of species by roosting height, with black flying-foxes typically showing the highest roosting heights (average maximum height with interquartile range: 18.0, 14.6-21.0; average minimum height with interquartile range: 14.3, 11.3-17.2), followed by grey-headed (maximum: 15.1, 11.2-18.9; minimum: 12.6, 8.8-16.2), then little red flying-foxes (when present) (maximum: 11.4, 9.2-13.6; minimum: 8.8, 7.1-10.4) (Figure 7). Note, however, that topographical variation within roosts was not taken into consideration in measures of height. Differences in heights presented here reflect a relative difference in roosting heights from the ground within trees, but may not reflect true, realised height relative of the canopy.

Demographic/social structure

“The majority of roost trees are occupied by mixed groups of adults, with territories comprised of a single

male and one or more females and their dependent young”

We commonly observed roost trees to be occupied by mixed groups of sexes, with a single tree occupied by one or more males, and one or more females and their dependent young. This is inconsistent with general knowledge based on historical studies like Nelson (1965a) and Nelson (1965b), but consistent with more contemporary observations (Table 2). We also observed cases where trees were occupied by entirely male individuals (consistent with reports of ‘bachelor male’ trees in Markus (2002)). We would note here that a single tree may contain multiple male territories (Markus 2002; Connell 2003) and the survey methods did not allow inference on the composition of individual territories, only individual trees. The proportion of males per tree appeared to follow seasonal patterns that was mostly consistent between black and grey-headed flying-foxes within roosts (Appendix S2). Some roosts (‘Toowoomba’, ‘Avondale’, ‘Lismore’) showed an increase in the proportion of males per tree after parturition in September/October, while other roosts (‘Sunnybank’, ‘Canungra’) decreased immediately after this time. We also did not observe complete segregation of sexes at any time of the year, in contrast to Nelson (1965b) who noted complete segregation between September until early December, and March to April.

“Dominant individuals (defined as reproducing males and females) occupy the centre of roosts and subdominant individuals (defined as non-reproducing males and females) the outer area”

Prior studies reported inconsistent spatial patterns in flying-fox occupation (Table 2). From our new dataset, we observed that the proportion of males per tree increased with distance from the roost centre (0.15 ± 0.039 , $p < 0.001$), though this effect was relatively small and variable across roosts and species (Figure 8). If we assume that only dominant males share their territory with females and their young (Markus 2002; Welbergen 2005), a lower proportion of males in trees closer to the centre of roosts may indicate that dominant individuals occupy the centre of some roosts and subdominant individuals the outer area. The small effect sizes observed would suggest that there is no clear spatial structure to reproductive groupings or dominance groupings. This can be seen also in maps showing male composition by tree relative to the roost perimeter, given in Appendix S4 in the Supporting Information.

Roost abundance/occupancy

“Individual roosts have distinguishable seasonal patterns of abundance and occupation.” & “Intra- and inter-annual variations in abundance can be extreme” & “Roost abundance peaks in March”

Prior studies reported inconsistent patterns in occupancy and abundance (Table 2). In our dataset, seasonal patterns in abundance and density were roost specific (Figure 9). Some roosts showed patterns consistent with the general notion that total roost abundance peaks towards March (Nelson 1965b; State of NSW and Office of Environment and Heritage 2018) (e.g. ‘Redcliffe’, ‘Canungra’ and ‘Clunes’). Others showed no considerable fluctuation in abundance (‘Burleigh’) or peaks at other times (‘Toowoomba’, ‘Sunnybank’, ‘Avondale’, ‘Lismore’) (Figure 9). The latter cases potentially highlight that population dynamics are more strongly driven by local dynamics in these roosts (e.g. food availability) (Parry-Jones & Augee 1992; Eby *et al.* 1999; Parry-Jones & Augee 2001; Giles *et al.* 2016), than reproductive cycles as described in Nelson (1965b). Little red flying-foxes showed seasonal trends in occupancy and density, peaking in February-March (Appendix S2). Seasonal trends in grey-headed and black flying-fox numbers were less consistent between roost sites (Appendix S2).

Discussion

The success of efforts to conserve Pteropodid bats across their distribution relies on effective population and habitat management. Pivotal to this is a baseline understanding of species ecology and behaviour, which is currently lacking for the majority of these species (Fujita & Tuttle 1991; Mickleburgh, Hutson & Racey 2002). Here we provide a synthesis on all existing literature, as well as an unprecedented empirical dataset, to meet that need for Australian species of *Pteropus*. We highlight that many existing beliefs on

which conservation and management decisions are based, are unsupported or outdated, and suggest that management plans should be updated to incorporate improved knowledge. Most importantly, we highlight that a one-size-fits-all approach to roost management will be inappropriate, given the extent of variation between sites even within a regional area. Roost management guidelines need to be changed to promote a more tailored approach that requires preliminary data acquisition before management plans are formulated and approved.

Existing understanding not supported

“Individual roosts have distinguishable seasonal patterns of abundance and occupation”

All roost sites in our empirical dataset were occupied continuously throughout the year by adults and juveniles/sub-adults of both sexes. This type of roost occupation has been noted from 1981 onwards (Puddicombe 1981; Parry-Jones 1985) and has become common in recent decades (e.g. Aston 1987; Eby 1991; Larsen *et al.* 2002; Van der Ree *et al.* 2006). This pattern of occupation contrasts to the ‘summer’ and ‘winter’ pattern described historically by Nelson (1965a) and Nelson (1965b) and cited in the *Flying-fox Roost Management Guideline* for Queensland, where ‘summer roosts’ of reproducing individuals would form between ~September/October and April/May, and ‘winter roosts’ of dispersed animals would form between April/May and September (Ratcliffe 1931; Nelson 1965a; Nelson 1965b; Parry-Jones & Augee 1991; Parry-Jones & Augee 1992). For these roost types, overwintering animals at summer roosts were rare, and when present, were documented as being predominantly juveniles or lone adult males (Nelson 1965b).

While seasonally occupied colonies are still observed (e.g. Klose *et al.* 2009), an increasing number of roosts are now consistently occupied year around, particularly in urban areas (Parry-Jones & Augee 2001; Tait *et al.* 2014). The cyclic patterns of summer aggregation and winter dispersal were originally thought to reflect social drivers and availability of resources (Parry-Jones & Augee 1992). Specifically, territory formation (from January) and conception (from ~March) (*P. poliocephalus* and *P. alecto*) (Welbergen 2005) coupled with abundant flowering of native flora in these months (Nelson 1965a), were understood to drive and support aggregative living in summer/autumn, while decreased food availability and the cessation of mating from ~May triggered the animals to disperse and adopt a less-gregarious living style in winter (Parry-Jones & Augee 1992). This ecology has changed in more recent decades, where continuous availability of exotic foods in urban areas has reduced the need for migratory behaviours and allows aggregate groups to remain year round (Parry-Jones & Augee 2001; Williams *et al.* 2006).

Policy documents containing only historical information on flying-fox occupation patterns (including the most recent *Flying-fox Roost Management Guideline* for Queensland: State of Queensland Department of Environment and Science (2020)) are of concern, as recommendations based on historical usage patterns may be inconsistent with current usage patterns, particularly in urban areas where occupation patterns have changed the most (Larsen *et al.* 2002; Tait *et al.* 2014), and where human-bat conflict is often the highest (Kung *et al.* 2015). Roost monitoring prior to management actions should encompass every season, and not assume that bats will disperse in winter. Similarly, contemporary overwintering roosts commonly contain individuals from all age and sex groups and may be consistently utilised through time (Larsen *et al.* 2002; Tait *et al.* 2014).

“The majority of roost trees are occupied by mixed groups of adults, with territories comprised of a single male and one or more females and their dependent young” & “Dominant individuals (defined as reproducing males and females) occupy the centre of roosts and subdominant individuals (defined as non-reproducing males and females) the outer area”

These historic perspectives also describe complete separation of males and females between September until early December (the period immediately before parturition, during lactation, and before conception) and again post March (after conception) (Nelson 1965a; Nelson 1965b). During these times, animals were historically noted to segregate by tree or height, such that all social contacts were between individuals of the same sex. However, these observations contrast with more recent observations of flying-fox social groupings (Puddicombe 1981; McWilliam 1984; Eby *et al.* 1999; Welbergen 2005), and observations from this study. In

contemporary roosts, mixed-sex groups are commonly present all year around, such that males and females co-occur in the roost and within trees year around.

Historically, during the times that males and females co-occurred within roosts, four types of social groupings were noted: 1) guard groups on the outsides of roosts, 2) family groups of one male, one female and one young, 3) other adult groups including polygamous males, 4) groups of juveniles. More recent observations, and results from this study suggest, however, that there is no clear spatial structure in the distribution of the sexes within the roost. Puddicombe (1981) notes that reproductive groups (mixed groups of males, females and their young) were uniformly distributed through the camp and present in peripheral areas (McWilliam 1984). Additionally, in this study we observed randomly distributed groups of mixed males and females, and groups of males. This potentially reflects the change in occupancy patterns in flying-fox roosts, where aggregative living was historically believed to be driven by strong social drivers (i.e. mating), whereas aggregative living in contemporary roosts is thought to be driven by continuous resource availability in the urban environment (Parry-Jones & Augee 2001; Williams *et al.* 2006). The observations will have implications for current management plans. Specifically, in support of current guidelines, managers should avoid management actions during times of the year when females are in late stages of gestation and have dependant young that cannot fly on their own (as per Commonwealth of Australia 2015; Department of Environment and Science 2020a). Importantly (and in contrast to current guidelines), actions scheduled within this time should note that restricting work to edges of roosts will likely not circumvent disturbances to gestating females and dependant young

Existing understanding supported, but conditional on roost site and local conditions

“Roost abundance peaks in March” & “Intra- and inter-annual variations in abundance can be extreme”

March was identified in some management documents as being the time for peak abundance in flying-fox roosts (e.g. State of Queensland Department of Environment and Science 2020). However, studies on *P. poliocephalus* and *P. alecto* identify a typical pattern of increasing abundance from September-October (when females give birth) until a peak in January-February (when the season’s young are able to fly independently) (Nelson 1965b; Eby 1991; Eby & Palmer 1991; Parry-Jones & Augee 2001). Roost sizes then decrease during March-April (the period of mating) to low winter counts in continuously occupied/overwintering roosts, or zero winter counts in seasonally occupied summer roosts (Nelson 1965b; Eby 1991; Eby & Palmer 1991). These studies note that cyclical patterns of occupation are driven by reproductive factors (i.e. timing of birth and independent flight), but highlight that irregular, local dynamics of food availability can superimpose variability into these patterns of abundance (Parry-Jones & Augee 1992). Indeed, many studies note high intra- and inter-annual variability in abundance. Parry-Jones and Augee (2001), for example, note that animals from their study roost appeared to migrate away and decrease in abundance in response to a blossoming event, presumably to move to a roost in closer proximity to the blossoming.

In our study, some roosts showed patterns consistent with a total roost abundance peak towards March (e.g. ‘Redcliffe’, ‘Canungra’ and ‘Clunes’). Others showed either no considerable fluctuation in abundance (‘Burleigh’) or peaks at other times (‘Toowoomba’, ‘Sunnybank’, ‘Avondale’, ‘Lismore’). Drivers of peaks were variable between roosts. For the ‘Redcliffe’ roost, seasonal migration of little red flying-foxes from ~January 2019 contributed to a peak in abundance around March (see species abundance plots in

Appendix S2). For the ‘Lismore’ roost, a blossoming event in winter 2018 triggered an influx of nomadic bats into the population, driving the peak observed in August 2018. Dynamics observed in other roosts were likely the result of local dynamics of food availability.

We note also that estimates of abundance from our study were much smaller than those of historical estimates. Ratcliffe (1931) describes ‘small’ roosts as ~5,000-10,000 animals, ‘medium’ as 10,000-50,000, and ‘large’ as anything over this size. Ratcliffe (1931) also report roosts in northern Queensland with bats ‘into the millions’ (Red River) and ‘exceeded a quarter of a million, possibly considerably’ (Burnett River). Likewise, Lunney and Moon (1997) report historical observations of flying-foxes in the Richmond Valley (1870’s) as into the millions. The maximum roost site observed in this current study was ~ 95,000, recorded at the Lismore roost

in August 2018 in response to a local eucalyptus flowering event. Roost sizes of <5,000 were more common for the roost sites surveyed and, extending from the sizes in Ratcliffe (1931), may constitute a new category of ‘very small’. Local management areas should expect that local conditions can change substantially and rapidly for flying-fox populations, resulting in population changes outside of times predicted by demographic driven dynamics alone. An understanding of the timing and productivity of flower resources within the feeding range of roosts is likely to be of greater importance to forecasting and interpreting large population fluctuations than are reproductive considerations.

Existing understanding supported

“Some areas of permanent camps are more consistently occupied (‘core areas’) than others” & “‘Core areas’ are more densely occupied than ‘peripheral areas’” & “Roost area fluctuates with total abundance”

Variability in the usage and occupation of areas within roosts have been highlighted in management documents (e.g. SEQ Catchments 2012). This includes more persistent usage of ‘core’ areas, higher occupation of ‘core’ areas, and variability in the roost perimeter (reflecting expansion and contraction from the core area). All existing literature (to our knowledge) and the new data from our study support these understandings. We would note however, the distinction between a ‘core/peripheral’ roost area and a ‘central/edge’ roost area. We defined the core area based on consistency of occupation, not spatial location. Areas identified to be ‘core’ were not necessarily in the centre of the roost (see location of roost centroid relative to the roost perimeter and surveyed subplots, in Appendix S3). This distinction has not necessarily been made in literature and management plans to date but has important implications for the interpretation of ‘core’ roosting areas, and management recommendations specific for ‘core/central’ or ‘peripheral/edge’ areas. For example, it cannot be assumed that buffer creation via vegetation removal from the roost edge will not affect a ‘core’ area of bat roosting, and so will not have a substantial impact of flying-foxes. Management activities should be prescribed for specific zones in roosts, based on prior monitoring of the roost, and recognising the ecological importance of different areas (Pallin 2000; Ku-ring-gai Council 2018). In addition, prior monitoring of core/peripheral roosting areas will be important to inform the location and potential effectiveness of buffer creation. Given the potential for roost area to fluctuate with abundance, creation of buffers via vegetation removal may reduce the area of normal roost habitat available, and result in an expansion into new areas when flying-fox numbers increase (as noted in Currey *et al.* 2018). The prescription of buffers should be planned with care to avoid unintended outcomes during periods of high population abundance.

“Species share roosts sites, but segregate spatially within” & “Large influxes of species into roosts (especially little red flying-foxes) can displace other species” & “Species roost at different heights”

The range of black flying-foxes underwent a phase of rapid southern expansion in the late 1990s and early 2000s, increasing the area of overlap with grey-headed flying-foxes (Roberts *et al.* 2012a). As the two species co-occupy roosts where their distributions overlap, this process has substantially increased the number of roosts occupied by both species, and thereby increased the pertinence of understanding the structure of mixed species roosts. There has been relatively little formal documentation of species overlap and segregation within roosts. Ratcliffe (1932) noted that sections of roosts were occupied by different species - specifically, that little red flying-foxes and black flying-foxes occupied different areas. Some horizontal separation has also been noted by Nelson (1965b) and Klose *et al.* (2009), and notes of displacement by little red flying-fox have been described in Birt and Markus (1999). We contribute quantitative, spatial information on the extent and overlap little red flying-fox, black flying-fox and grey-headed flying-fox, extending on the predominantly anecdotal observations underlying management documents to date. Findings from our data support common understandings of flying-fox roost structure: species commonly showed preferences for discrete areas of roosts, and even more commonly, preference for occupation of separate trees. We also observed segregation of species by roosting height, with black flying-foxes showing the highest roosting, followed by grey-headed flying-foxes and little red flying-foxes. These findings flag the importance of species monitoring of roost sites prior to management interventions. It cannot be assumed, for example, that species occupy areas of the roost uniformly, and management actions need to consider areas that may be more or less important to vulnerable species, like the grey-headed flying-fox. These results also give interesting insights into understanding disease

transmission dynamics within roosts, relating to the extent of mixing of primary host species (e.g. black flying-foxes for Hendra virus) and other species presumed to be incidental hosts (e.g. grey-headed and little red flying-foxes).

Final comments and implications for roost management

State-level management guidelines, including the *Flying-fox Camp Management Policy* (State of NSW and Office of Environment and Heritage 2018) and the *Flying-fox Roost Management Guideline* (State of Queensland Department of Environment and Science 2020) outline several camp-based management approaches that involve the modification or removal of vegetation within roost sites. ‘Routine camp management actions’ include the removal of tree branches or whole trees, weed removal, trimming of understorey vegetation, and minor habitat augmentation. The aim of such actions are often to encourage roosting in alternative areas of the roost (e.g. Geolink 2010; EcoLogical 2014), or to increase the sustainability of existing roosting habitat for flying-foxes (e.g. Ku-ring-gai Council 2018). These actions are considered to be low impact activities (Department of Environment and Science 2020b) and do not require referral under the EPCB act (Commonwealth of Australia 2015), however these actions may considerably alter the structure of roost vegetation and decrease the suitability of a roost as habitat (Ku-ring-gai Council 2018). For example, the removal of mature weed vines in the canopy and midstory, as well as the clearing of understory, can reduce the structural complexity of roost vegetation. This may have immediate and direct effects on roosting flying-foxes, and may accidentally cause bats to disperse or adjust use of roost trees in ways contradictory to conflict management. This may also have long-term, indirect implications for the ability of flying-foxes to survive extreme weather events, by altering roost macroclimate and removing physical refuge needed at times of extreme heat (Welbergen *et al.* 2008).

Individual and council-level roost management plans developed by local governments under the guidance of these policies, commonly utilise these vegetation management measures (e.g. EcoLogical 2014; Logan City Council 2015; Sunshine Coast Regional Council 2016; Ku-ring-gai Council 2018), though the long-term implications for flying-foxes of vegetation works are rarely noted (with the exception of Ku-ring-gai Council 2018). We recommend that vegetation removal should not be considered low impact by default. Routine management actions should follow a mosaic pattern (State of NSW and Department of Planning Industry and Environment 2019), or target weeding on a weed-by-weed case basis (Ku-ring-gai Council 2018), and seek to maintain refuges in the mid- and lower storeys at all times. Special care not to disturb bats should be taken in identified core areas of the roost.

Conclusion

This study takes a thorough, multifaceted approach to better understand the ecology of flying-fox roost use and structure in Australia. We build upon broad-scale knowledge of historic roosting occupancy and abundance patterns, and provide updated baseline information on roosting structure in urban and peri-urban roosts by providing fine-scale spatial, and temporal data on roost and tree use. Specifically, we demonstrate high variation in patterns of occupancy and abundance between roosts sites, and provide updated demographic information including the spatial and temporal distributions of males and females within roosts. We also show evidence of sympatry and indirect competition between species, including spatial segregation of black and grey-headed flying-foxes within roosts, and seasonal displacement of both species by little red flying-foxes. The outcomes of this research will be of immediate, practical benefit to management and conservation of flying-fox roosts in Australia, and meets research needs specifically identified in the draft Recovery Plan for the Vulnerable grey-headed flying-fox. The level of spatial and temporal detail provided in our empirical study will be important in designing management plans that are sensitive to flying-fox habitat needs, and in identifying and protecting important habitat areas within roosts that are reflective of current movements and preferences. Most importantly, we highlight that a one-size-fits-all approach to roost management will be inappropriate, given the extent of variation between sites even within a regional area. Fine-scale information on roost tree preferences will also improve understanding of the potential impacts

of existing conflict management strategies involving vegetation removal, including buffer creation, and can guide vegetation removal efforts to heed these habitat requirements. This information is timely, and much needed in advance of the recently announced Environmental Trust grants program for flying-fox habitat restoration, and in the face of continued and increasing urbanisation of flying-foxes in Australia.

Acknowledgements

We would like to thank Beccy Abbot, Kirk Silas, Devin Jones, Liam Chirio, Rachel Smethurst and Cara Parsons for their assistance in the field. Fieldwork for this work was supported by a Paddy Pallin Research Grant and a ‘Grants in Need’ science grant awarded to TJL, sponsored by the Paddy Pallin Foundation, The Royal Zoological Society of NSW and The Foundation for National Parks and Wildlife, and the National Science Foundation (a Coupled Dynamics of Natural and Human Systems grant DEB1716698 and a DARPA PREEMPT program Cooperative Agreement #D18AC00031). TJL was supported by an Endeavour Postgraduate Leadership Award and a Research Training Program scholarship sponsored by the Australian Government, AJP was supported by an ARC DECRA fellowship (DE190100710) and a Queensland Government Accelerate Postdoctoral Research Fellowship, RB was supported by a Griffith University Honours Allowance and an EFRI Honours Thesis Write-Up Scholarship, and RKP was supported by USDA National Institute of Food and Agriculture (Hatch project 1015891). This research was conducted under a Griffith University Animal Research Authority permit (DEB-1716698), a Scientific Purposes Permit from the Queensland Department of Environment and Heritage Protection (WISP17455716), a permit to Take, Use, Keep or Interfere with Cultural or Natural Resources (Scientific Purpose) from the Department of National Parks, Sport and Racing (WITK18590417), a Scientific Licence from the New South Wales Parks and Wildlife Service (SL101800) and general and products liability protection permit (GRI 18 GPL), and with permission to undertake research on council and private land. The content of the information does not necessarily reflect the position or the policy of the U.S. government, and no official endorsement should be inferred. We acknowledge the Danggan Balun, Kabi Kabi, Turrbal, Widjabul Wia-bal, Yugambeh and Yuggera Ugarapul people, who are the Traditional Custodians of the land upon which this work was conducted.

Data Accessibility Statement

Summarised data and annotated R code will be made available on GitHub at: <https://github.com/TamikaLunn/FF-roost-ecology>. Summarised data will also be made available on Dryad after publication.

Competing Interests Statement

The authors have no competing interests to declare.

Author Contributions

TJL and PE conceived and designed the research; TJL acquired funding for the research 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.

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Tables

Table 1: Information on roost sites included in the study. Contemporary roost types (features greyed) are characterised by: being a new overwintering site (defined as having either formed since 2007 or changed to an overwintering site since 2007), having a high number of neighbouring roosts within 45 km, having a high proportion of surrounding urban land-cover, and by being in close proximity to urban land-cover. Foraging radii enclose 45 km from roost study sites (as per Giles *et al.* 2018).

Roost site	Type	Year of formation/new overwintering	Number of neighbouring roosts within
	<i>Within 45 km foraging radius</i>	<i>Within 45 km foraging radius</i>	<i>Within 45 km foraging radius</i>
Toowoomba		2009	9
Redcliffe		2003	41
Sunnybank	Contemporary	2009	67
Avondale	Contemporary	2008	68
Burleigh	Contemporary	2013	50
Canungra		1996	59

Roost site	Type	Year of formation/new overwintering	Number of neighbouring roosts within
Clunes		2014	40
Lismore		2007	37

Table 2: Common understandings in state-level management documents. Note that additional evidence from our 13-month empirical study only addresses questions that require less than one year of data (i.e. intra-annual patterns in roost structure). Statements not addressed with our empirical data are coloured grey. An extended version of this table with details on study results is provided in

Appendix S2 in the Supporting Information.

Understandings	Referenced by	Empirical evidence	Empirical evidence	Additional evidence (this study)	Additional evidence (this study)
		Support	Contradict	Support	Contradict
Use of area:					
Some areas of permanent camps are more consistently occupied ('core areas') than others	SEQ Catchments (2012); EcoLogical (2014)	Welbergen (2005); Richards (2002); Nelson (1965b)		Figure 2	
'Core areas' are more densely occupied than 'peripheral areas'	SEQ Catchments (2012)	Nelson (1965b); Welbergen (2005)		Figure 3; Figure 4; Appendix S2	
Roost area fluctuates with total abundance	SEQ Catchments (2012); EcoLogical (2014)	Welbergen (2005); Pallin (2000); Larsen <i>et al.</i> (2002)		Figure 5	
Flying-foxes adjust the location of 'core areas' through time	SEQ Catchments (2012)	Hall (2002) & Pallin (2000)	Welbergen (2005)		
Areas outside of the 'core area' are used by more transient animals	SEQ Catchments (2012)	Welbergen (2005)			
Spatial segregation of species:					

Understandings	Referenced by	Empirical evidence	Empirical evidence	Additional evidence (this study)	Additional evidence (this study)
Species share roosts sites, but segregate spatially within	Commonwealth of Australia (2017a)	Welbergen (2005); Ratcliffe (1932); Parsons <i>et al.</i> (2010); Nelson (1965b); Klose <i>et al.</i> (2009)	Parsons <i>et al.</i> (2010); Markus (2002)	Figure 6; Appendix S3	
Large influxes of species into roosts (especially little red flying-foxes) can displace other species		Birt and Markus (1999)		Appendix S3	
Species roost at different heights	Geolink (2010)	Welbergen (2005); Roberts (2005)		Figure 7	
Indirect competition favours black flying-foxes over grey-headed flying-foxes	Commonwealth of Australia (2017a); EcoLogical (2014)	Ratcliffe (1931)	Markus (2002); Roberts (2005)		
Demographic/social structure:					
The majority of roost trees are occupied by mixed groups of adults, with territories comprised of a single male and one or more females and their dependent young	SEQ Catchments (2012); State of Queensland Department of Environment and Science (2020)	Welbergen (2005); Puddicombe (1981); Nelson (1965b); Nelson (1965a); Markus and Blackshaw (2002); Markus (2002); Eby <i>et al.</i> (1999); McWilliam (1984); Connell (2003)	Welbergen (2005); Nelson (1965b); Nelson (1965a)	Figure 8	

Understandings	Referenced by	Empirical evidence	Empirical evidence	Additional evidence (this study)	Additional evidence (this study)
Dominant individuals (defined as reproducing males and females) occupy the centre of roosts and subdominant individuals (defined as non-reproducing males and females) the outer area	State of Queensland Department of Environment and Science (2020)	Nelson (1965b); Welbergen (2005)	Puddicombe (1981); Markus and Blackshaw (2002)		Figure 8; Appendix S4
Individuals at the periphery of groups act as ‘guards’	State of Queensland Department of Environment and Science (2020)	Nelson (1965b); Klose <i>et al.</i> (2009)			
Juveniles wean and leave their mothers from January and form groups on the edge of their existing roost or at another site	State of Queensland Department of Environment and Science (2020)		Welbergen (2005); Nelson (1965b); Nelson (1965a); Markus and Blackshaw (2002); Eby <i>et al.</i> (1999); Connell (2003)		
The roosting positions of individual males are highly consistent and animals return to the same branch of a tree over many weeks or months	SEQ Catchments (2012)	Welbergen (2005); Markus and Blackshaw (2002); Markus (2002)	Tidemann and Nelson (2004); Roberts <i>et al.</i> (2012b); Parsons, Robson and Shilton (2011)		
Roost abundance/occupancy:					

Understandings	Referenced by	Empirical evidence	Empirical evidence	Additional evidence (this study)	Additional evidence (this study)
Individual roosts have distinguishable seasonal patterns of abundance and occupation.	<i>Abundance:</i> Commonwealth of Australia (2017a); <i>Occupation:</i> State of Queensland Department of Environment and Science (2020)	<i>Abundance</i> Westcott <i>et al.</i> (2018); Welbergen (2005); Tait <i>et al.</i> (2014); Parry-Jones and Augee (2001); Parry-Jones and Augee (1992); Nelson (1965b); Nelson (1965a); Meade <i>et al.</i> (2019) <i>Occupation</i> Welbergen (2005); Vardon and Tidemann (1999); Parry-Jones and Augee (1992); Parry-Jones (1985); Nelson (1965b) & Nelson (1965a); Nelson (1965b) & Nelson (1965a); Klose <i>et al.</i> (2009); Puddicombe (1981); Roberts (2005)	<i>Abundance</i> Shilton <i>et al.</i> (2008); Richards (2002); Roberts (2005) <i>Occupation</i> Van der Ree <i>et al.</i> (2006); Richards (2002); Puddicombe (1981); Shilton <i>et al.</i> (2008)	Figure 9	

Understandings	Referenced by	Empirical evidence	Empirical evidence	Additional evidence (this study)	Additional evidence (this study)
Intra- and inter-annual variations in abundance can be extreme	Commonwealth of Australia (2017a)	Westcott and McKeown (2004); Tait <i>et al.</i> (2014); Welbergen (2008); Welbergen (2005); Vardon and Tidemann (1999); Ratcliffe (1931); Ratcliffe (1932); Eby (1991); Eby and Palmer (1991); Van der Ree <i>et al.</i> (2006); Eby and Lunney (2002a); Roberts <i>et al.</i> (2012a); Richards (2002); Parry-Jones and Augee (2001); Parry-Jones and Augee (1992); Pallin (2000); Meade <i>et al.</i> (2019); Loughland (1998); Giles <i>et al.</i> (2016); Forsyth, Scroggie and McDonald-Madden (2006); Eby <i>et al.</i> (1999); Lunney and Moon (1997)	Roberts (2005)	Figure 9	

Understandings	Referenced by	Empirical evidence	Empirical evidence	Additional evidence (this study)	Additional evidence (this study)
Roost abundance peaks in March	State of Queensland Department of Environment and Science (2020)	Van der Ree <i>et al.</i> (2006); Tait <i>et al.</i> (2014); Meade <i>et al.</i> (2019); Eby (1991); Eby and Palmer (1991); Nelson (1965a)	Westcott <i>et al.</i> (2018); Welbergen (2005); Vardon and Tidemann (1999); Vardon <i>et al.</i> (2001); Roberts <i>et al.</i> (2012a); Richards (2002); Parry-Jones and Augee (2001); Parry-Jones and Augee (1992); Pallin (2000) (citing personal communication with M. Beck); Nelson (1965b); Nelson (1965a)		Figure 9; Appendix S2
Consistent (inter-annual) patterns in abundance and use are more commonly observed in roosts located in 1) extensive areas of rainforest, and 2) urban areas	SEQ Catchments (2012); Commonwealth of Australia (2017a)	<i>Extensive rainforest</i> Parry-Jones (1985) <i>Urban areas</i> Tait <i>et al.</i> (2014); Welbergen (2005); Van der Ree <i>et al.</i> (2006); Richards (2002); Williams <i>et al.</i> (2006); Parry-Jones and Augee (2001); Parry-Jones and Augee (1992)			
Habitat preferences:			Stager and Hall (1983)		

Understandings	Referenced by	Empirical evidence	Empirical evidence	Additional evidence (this study)	Additional evidence (this study)
The habitat patch must be at least 1ha in size but be large enough to accommodate and sustain large numbers of flying-foxes. For a small roost (10,000 bats) the area needed is approximately 3ha and for a large roost (50,000) the area needed is 10ha	SEQ Catchments (2012); State of NSW and Department of Planning Industry and Environment (2019) as per State of NSW and Office of Environment and Heritage (2018); EcoLogical (2014)	Pallin (2000); Roberts (2005)			
Flying-foxes prefer complex vegetation structure (upper, mid- and understorey layers)	SEQ Catchments (2012); State of NSW and Department of Planning Industry and Environment (2019) as per State of NSW and Office of Environment and Heritage (2018)	Pallin (2000) (citing report by Buchanan)			
Flying-foxes prefer dense vegetation	SEQ Catchments (2012)	Roberts (2005)			
Flying-foxes prefer a dense understory	SEQ Catchments (2012)	Roberts (2005)			

Understandings	Referenced by	Empirical evidence	Empirical evidence	Additional evidence (this study)	Additional evidence (this study)
Flying-foxes prefer a closed canopy at least 3-5m high	SEQ Catchments (2012); State of NSW and Department of Planning Industry and Environment (2019) as per State of NSW and Office of Environment and Heritage (2018); EcoLogical (2014)	Tidemann <i>et al.</i> (1999); Tidemann (1999); Roberts (2005)	Welbergen (2005)		
The structure of roost-wide vegetation is more important than the characteristics of individual roost trees (e.g. species, canopy cover)	SEQ Catchments (2012)	Palmer and Woinarski (1999); Pallin (2000); Vardon <i>et al.</i> (2001); Tidemann <i>et al.</i> (1999); Vardon and Tidemann (1999); Hall and Richards (2000); Roberts (2005)			
Flying-foxes prefer level topography (<5° incline)	SEQ Catchments (2012); State of NSW and Department of Planning Industry and Environment (2019) as per State of NSW and Office of Environment and Heritage (2018)	Roberts (2005)			

Understandings	Referenced by	Empirical evidence	Empirical evidence	Additional evidence (this study)	Additional evidence (this study)
Flying-foxes prefer to roost within 50 km of the coastline or at an elevation <65 m above sea level	SEQ Catchments (2012); State of NSW and Department of Planning Industry and Environment (2019) as per State of NSW and Office of Environment and Heritage (2018)	Hall and Richards (2000); Roberts (2005)	Ratcliffe (1931); Ratcliffe (1932)		
Roost macroclimate:					
The mid-storey vegetation within roosts is critical for maintaining a cool, humid and sheltered environment that is stable against the outside environment	SEQ Catchments (2012); State of NSW and Department of Planning Industry and Environment (2019) as per State of NSW and Office of Environment and Heritage (2018)	Loughland (1998)	Snoyman and Brown (2010)		
Negative impacts from flying-foxes:					
Impacts sustained over several years of flying-fox occupancy can lead to damage and/or death of individual roost trees	SEQ Catchments (2012); State of Queensland Department of Environment and Science (2020)	Welbergen (2005); Richards (2002); Pallin (2000); McWilliam (1984); Hall (2002)			

Understandings	Referenced by	Empirical evidence	Empirical evidence	Additional evidence (this study)	Additional evidence (this study)
Some tree species are more resilient to damage by flying-fox roosting than others	SEQ Catchments (2012)				
In small remnant patches, the process of opening the canopy (from tree damage by roosting) will increase the impact of invasive weeds	SEQ Catchments (2012); State of Queensland Department of Environment and Science (2020)	Pallin (2000); McWilliam (1984); Hall (2002)			
Where sufficient roosting space is available, flying-foxes shift their roosting areas, which lessens their damage to vegetation over time	SEQ Catchments (2012); EcoLogical (2014)	Pallin (2000); Hall (2002)			

Figure Legends

Figure 1: Map of roost sites included in the study. Grey shading indicates urban land cover of dense human habitation (as per Schneider, Friedl & Potere 2009) and grey circles are locations of flying-fox roosts. Circles show 45km foraging radii from roost study sites (as per Giles *et al.* 2018). GIS land-cover data was downloaded from Natural Earth (2020) and flying-fox roost locations obtained from the National Flying-Fox Monitoring Program (2017).

Figure 2: Occupancy of subplots across survey period, for surveys when at least one bat was present. A) shows the total number of bats per subplot, and B) shows the proportion of surveys the subplot was occupied. Facets/colour indicates separate roost sites. “C” indicates roosts that have features of contemporary roost types (see Table 1). Note that construction works at the ‘Avondale’ roost during the survey caused the bats to shift their roosting location, such that only one subplot was utilised thereafter.

Figure 3: Occupancy of subplots in ‘core’ and ‘peripheral’ areas, shown by average total number of bats per occupied subplot across the survey period. Data is filtered to show numbers of bats when subplots were occupied (i.e. unoccupied subplots are removed). ‘Core’ subplots were identified as those occupied in at least 80% of surveys (when bats present at the roost), and ‘peripheral’ subplots as those occupied less than 80%

of the time. A) Shows areas split by roost site (facet and colour), and B) shows all roosts combined. Area displayed in subplot has been cropped to remove extreme outliers. “C” indicates roosts that have features of contemporary roost types (see Table 1).

Figure 4: Distance from roost centre and occupancy of bats, shown by the average total number of bats per occupied subplot during the survey period. Data is filtered to show numbers of bats when trees are occupied (i.e. unoccupied subplots are removed). Roost centre is calculated for each survey as the centroid of the roost area at the time of the survey. Distance from the centre is calculated as the mean distance of trees in each subplot from this centroid, scaled by the maximum observed distance value per session. A) shows values per species (line type) split by roost (facets); and B) shows species and roost combined. Trend line is by loess fit (local polynomial regression fit) with standard error bands (grey shading). “C” indicates roosts that have features of contemporary roost types (see Table 1).

Figure 5: Relationship between total roost abundance (x axis) and total roost area (y axis) for each roost site. A) shows relationship split by roost (facets) and B) shows relationship with roosts combined. Trend line is by loess fit (local polynomial regression fit) with standard error bands (grey shading). Note that trend lines could not be fitted for all sites and are omitted. “C” indicates roosts that have features of contemporary roost types (see Table 1).

Figure 6: Co-occupation of subplots (A) and individual trees (B) by species. Total subplots/total trees observed are shown in text labels and include subplots/trees across sessions where every bat species in the species comparison were present. (e.g. for the black and grey-headed flying-fox comparison, only sessions where both black and grey-headed flying-fox were present were included in the subplot/tree tally). ‘BFF’ refers to black-flying-fox, ‘GHFF’ grey-headed flying-fox and ‘LRFF’ little red flying-fox. Confidence intervals are binomial, calculated with a Wilson test.

Figure 7: Difference in roosting height per species, over time. Fill shows average roosting height range per species (minimum height to maximum height). Fill boundaries (minimum and maximum curves) are by loess fit (local polynomial regression fit). A) shows relationship split by roost (facets) and B) shows relationship with roosts combined. In A), dashed line represents the average canopy height per site; for roost sites where species occupy distinctly different areas (‘Clunes’ and ‘Lismore’), canopy height is split by areas the species predominantly occupy. “C” indicates roosts that have features of contemporary roost types (see Table 1). Note that height data are taken from the tree subset only (up to N=60 per roost site), and that trend lines could not be fitted for all site by species combinations and are omitted.

Figure 8: Proportion of male bats per occupied tree versus distance of tree from the roost centre, scaled by the maximum distance value observed per session. A) shows values per species (row facet) split by roost (column facet); B) shows combined species value pooled by roost. Trend line is by loess fit (local polynomial regression fit) with standard error bands (grey shading). ‘BFF’ refers to black-flying-fox, ‘GHFF’ grey-headed flying-fox and ‘LRFF’ little red flying-fox. “C” indicates roosts that have features of contemporary roost types (see Table 1).

Figure 9: Different scales of bat abundance measures through time. A) shows total roost abundance; B) shows total roost area; C) shows the proportion of occupied trees per subplot; D) shows the total abundance of occupied subplots. Total roost abundance is measured by an index score of abundance: 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.

Figures











