

Foraging resource use by grey-headed flying-foxes in urban and non-urban Australia

Submitted by

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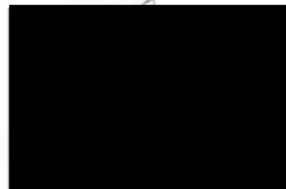
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Statement of authentication

The work presented in this thesis is, to the best of my knowledge and belief, original except as acknowledged in the text. I hereby declare that I have not submitted this material, either in full or in part, for a degree at this or any other institution.



.....
(Samantha Yabsley)

Table of contents

Acknowledgments.....	ii
Statement of authentication	iv
Table of contents.....	v
List of tables	vii
List of figures.....	viii
List of appendices	xi
List of abbreviations.....	xiii
COVID-19 Impact Statement	xiv
Summary.....	xv
Chapter 1: Wildlife urbanisation: threats, opportunities and implications for management.....	1
1.1 Wildlife urbanisation	1
1.2 How is wildlife urbanisation managed globally?	7
1.2.1 Ex situ management strategies.....	8
1.2.2 In situ management strategies.....	10
Chapter 2: Flying-foxes and urbanisation	20
2.1 Introduction to flying-foxes	20
2.2 Threats to flying-foxes.....	23
2.3 Flying-fox urbanisation.....	24
2.4 Urban human versus flying-fox conflicts.....	27
2.5 Current management of human versus flying-fox conflict.....	29
2.5.1 Lethal management	29
2.5.2 Forced eviction.....	32
2.5.3 In-situ management.....	34
2.6 Study aims	37
2.7 Thesis structure.....	38
Chapter 3: Human-modified landscapes provide key foraging areas for a threatened flying mammal: the grey-headed flying-fox.....	40
3.1 Abstract	40
3.2 Introduction	41
3.3 Methods.....	44

3.3.1 Capture and deployment of transmitters.....	44
3.3.2 Data handling and analysis	45
3.4 Results.....	49
3.4.1 Vegetation type preferences.....	51
3.4.2 Habitat quality rank preferences	55
3.4.3 Food plant species	57
3.5 Discussion	60
Chapter 4: Grey-headed flying-foxes (<i>Pteropus poliocephalus</i>) exhibit greater dietary breadth when feeding within versus outside of urban environments	66
4.1 Abstract.....	66
4.2 Introduction	67
4.3 Methods.....	72
4.3.1 Study area	72
4.3.2 Capture and deployment of transmitters.....	74
4.3.3 Data collection	75
4.3.4 Data sub-setting.....	78
4.3.5 Identifying feeding fixes.....	78
4.3.6 Identifying food plant species	79
4.3.7 Data analysis	82
4.4 Results.....	85
4.4.1 Land-use preferences.....	85
4.4.2 Food plant species	88
4.4.3 Phenology of food plant species	90
4.5 Discussion	94
Chapter 5: Conclusion.....	100
5.1 Main Findings.....	100
5.2 Drivers of flying-fox urbanisation, and implications for flying-fox management and conservation	101
5.2.1 Urban areas as ‘ecological traps’	103
5.2.2 Increased human-wildlife conflict.....	103
5.2.3 Ecosystem services provided by flying-foxes.....	104
5.3 Potential application of results and future research directions.....	105
Appendices	108
References	117

List of tables

Table 4.1 The number of <i>P. poliocephalus</i> feeding fixes, and the duration each transmitter recorded GPS and accelerometer data for each individual (n = 9). Individual FFOX05 left the study area (within a 75 km radius from the center of the Adelaide Botanic Park roost; - 34.916, 138.607) before the transmitter began collecting data and hence this individual produced no usable data.	77
Table 4.2 The flowering and fruiting phenology of the food plant species visited by <i>P. poliocephalus</i> in residential areas, and linear landscape features including road-side trees. Boxes are coloured to indicate months in which plant species have ever been recorded to flower/fruit. Dark shading represents periods of likely peak flowering or occurrence of ripe fruit, and moderate shading represents moderate flowering/fruiting. Blank spaces represent months in which food plant species have not been recorded to flower/fruit and hence are unlikely to contribute to the <i>P. poliocephalus</i> diet during these times. Asterisks represent species that are not known food plant species to <i>P. poliocephalus</i> . Colours indicate geographic origin; green indicates locally indigenous species, blue indicates non-indigenous Australian native species, and red represents non-Australian species. Where data were available, the flowering/fruiting duration is shown in months and annual reliability of flowering/fruiting is shown as a proportion of years when flowering occurs.	92

List of figures

Figure 2.1 Grey-headed flying-fox (<i>P. poliocephalus</i>) feeding on blossom. Pollen covers the face while foraging and is deposited on the stamens of the next foraging tree as they feed on the flowers. Image credit Mandy Griffith.	22
Figure 2.1 Flying-foxes (<i>P. poliocephalus</i>) roosting near a human settlement in Boonah, Queensland. Image credit Justin Welbergen.	25
Figure 2.1 Grey headed flying-foxes (<i>P. poliocephalus</i>), roosting at Sydney Botanic Gardens. Image credit Justin Welbergen.....	26
Figure 2.2 Dispersal actions conducted near Charters Towers, Queensland, in an attempt to evict flying-foxes from a local roost. Image credit Australasian Bat Society.....	34
Figure 3.1 Map of <i>P. poliocephalus</i> roost sites. Red points indicate the location of roosts in major-urban areas, yellow dots indicate roosts in minor-urban areas, and white dots indicate roosts in non-urban areas. Major-urban areas are indicated by dark blue shading, minor-urban areas are indicated by mid-blue shading. Lines indicate State boundaries. Shaded grey area shows <i>P. poliocephalus</i> ' range in Australia. Inset, map of Australia with box indicating area used in this study.....	50
Figure 3.2 Vegetation class preferences. The proportion of (A) each vegetation class in the study area, and (B) of positional fixes (n = 1,236) recorded from <i>P. poliocephalus</i> roosting in non-urban colonies in each vegetation class, (C) of positional fixes (n = 974) recorded from <i>P. poliocephalus</i> roosting in minor-urban colonies in each vegetation class, (D) of positional fixes (n = 1,988) recorded from <i>P. poliocephalus</i> roosting in major-urban colonies in each vegetation class.	52
Figure 3.3 Predicted changes in vegetation class preferences with distance from urban areas. The predicted change in proportion of vegetation types visited by foraging <i>P. poliocephalus</i> roosting at non-urban colonies as the distance from the roost site to the nearest urban polygon increases. Predictions are taken from a multinomial logistic regression model. Grey polygons indicate 95% confidence intervals. Vegetation types that made up <1% of foraging fixes were excluded from the graph.....	54
Figure 3.4 Habitat quality preferences. The proportion of (A) each habitat quality rank in the sampled area, (B) of positional fixes (n = 1031) recorded from <i>P. poliocephalus</i> roosting in non-urban colonies in each habitat quality rank, (C) of positional fixes (n = 770) recorded from <i>P. poliocephalus</i> roosting in minor-urban colonies in each habitat quality rank, and (D) of positional fixes (n = 1956) recorded from <i>P. poliocephalus</i> roosting in major-urban	

colonies in each habitat quality rank. Habitat quality was ranked from 1-4: where rank 1 is good quality foraging habitat, rank 4 is poor quality foraging habitat, and rank 0 is habitat where the recorded dominant and subdominant plant species are not known to be part of the *P. poliocephalus* diet. 56

Figure 3.5 Likely food plant species. The identified likely food plant species overall when *P. poliocephalus* roosted in non-urban, minor-urban and major-urban areas. A maximum of 18 different food plant species were included in each graph. n = the number of foraging fixes used to calculate proportions. ‘No species’ indicate additional fixes for the particular bi-month that fell in the sampled area, but for which the recorded dominant and subdominant plant species were not known to be part of the *P. poliocephalus* diet. 58

Figure 4.1 The distribution of grey-headed flying-fox (*P. poliocephalus*) roosts in Australia. Image extracted from the National flying-fox monitoring viewer; Australian Government: Department of Agriculture, Water and the Environment. The size of the markers represents an estimate of colony size in terms of the number of individuals recorded there. 74

Figure 4.2 Example photographs taken of locally indigenous, non-indigenous Australian native (non-endemic to South Australia but endemic to Australia), and non-Australian food plant species visited by n = 9 GPS tracked *P. poliocephalus* roosting in Adelaide, South Australia. A) *Eucalyptus leucoxylon*, B) *E. camaldulensis*, C) *Lophostemon confertus*, D) *Corymbia citriodora*, E) *Phoenix canariensis*, and F) *Ficus carica*. 81

Figure 4.3 Study area; the Adelaide region. Feeding fixes are represented by yellow markers. All feeding fixes are 500m - 75km from the center of the roost; -34.916, 138.607, depicted by the red circle. Image created in ArcGIS. 83

Figure 4.4 A) the expected proportion of *P. poliocephalus* feeding fixes in each land-use category based on areal availability (grey bars), and the observed proportion of feeding fixes in each land-use category overall (white bars), and B) the observed proportion of feeding fixes in each land-use category shown for each of the 9 individuals. Data (n = 489) were obtained from GPS tracked *P. poliocephalus* collected between December 2019 and May 2020. 87

Figure 4.5 The number of plant species visitations (n = 265) by *Pteropus poliocephalus*. The top panel (A) shows the total number of plant species visitation across all land-use categories. The following panels show the number of visits in each land-use category separately: (B) residential (n = 90), (C) road/river (n = 46), (D) reserve (n = 38), (E) primary production (n = 34), (F) utilities (n = 23), (G) vacant (n = 14), (H) recreation (n = 11), (I) institution (n = 8), (J) mining (n = 1). Plant species are listed in order of most feeding visitations overall. Locally

indigenous plant species are shown in green, non-indigenous Australian native species are shown in blue, non-Australian species are shown in pink, and those with unknown geographic origin are shown in yellow. Data were obtained from 9 GPS tracked *P. poliocephalus* roosting in the Adelaide region (-34.916, 138.607) from December 2019 – May 2020..... 90

List of appendices

Appendix 1. Distribution of non-urban roosts in relation to the distance to the nearest urban polygon.....	108
Appendix 2. The numbers of visiting individuals for all combinations of roost types ($N_{\text{total}} = 98$ individuals, satellite tracked over up to 5 years between 2012-2017).	109
Appendix 3. The proportion of (A) each vegetation class in the study area, and (B) of <i>P. poliocephalus</i> foraging positional fixes ($n = 4,233$) recorded in each vegetation class. Satellite tracking data were collected between 2012-2017 and is representative of 98 individuals. ..	110
Appendix 4. Estimated regression parameters, standard errors, z values, and p-values for the best fitting multinomial logistic regression. Cleared land is the reference category.	111
Appendix 5. The proportion of (A) each habitat quality rank in the area sampled, and (B) of foraging positional fixes ($n = 3,773$) recorded in each habitat quality rank. Habitat quality was ranked from 1-4: where 1 is good quality foraging habitat, rank 4 is poor quality foraging habitat, and ‘No species’ is habitat where the recorded dominant and subdominant plant species were not known to be part of the <i>P. poliocephalus</i> diet.....	112
Appendix 6. Likely <i>P. poliocephalus</i> food plant species in each bi-month where individuals roosted in non-urban areas. A maximum of 10 different food plant species were included in each graph. n = the number of foraging fixes used to calculate proportions. ‘No species’ indicate additional fixes for the particular bi-month that fell in the sampled area, but for which the recorded dominant and subdominant plant species were not known to be part of the <i>P. poliocephalus</i> diet.....	113
Appendix 7. Likely <i>P. poliocephalus</i> food plant species in each bi-month where individuals roosted in minor-urban areas. A maximum of 10 different food plant species were included in each graph. n = the number of foraging fixes used to calculate proportions. ‘No species’ indicate additional fixes for the particular bi-month that fell in the sampled area, but for which the recorded dominant and subdominant plant species were not known to be part of the <i>P. poliocephalus</i> diet.....	114
Appendix 8. Likely <i>P. poliocephalus</i> food plant species in each bi-month where individuals roosted in major-urban areas. A maximum of 10 different food plant species were included in each graph. n = the number of foraging fixes used to calculate proportions. ‘No species’ indicate additional fixes for the particular bi-month that fell in the sampled area, but for which the recorded dominant and subdominant plant species were not known to be part of the <i>P. poliocephalus</i> diet.....	115

Appendix 9. Inaccessible GPS feeding fixes (n = 35), the land-use categories they pertain to and the reason for inaccessibility.	116
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List of abbreviations

GPS	Global positioning system
GPRS	General Packet Radio Service
UHF	Ultra-high frequency
FTP	File transfer protocol
GSM	Global system for mobile
PCA	Principal component analysis
IPFM	Interpeak frequency minimum
CBD	Central business district

COVID-19 Impact Statement

The original intention for Chapter 4 was to conduct extensive fieldwork along the East coast of Australia and collect scat samples from 5 urban and 5 non-urban colonies of roosting grey-headed flying-foxes (*Pteropus poliocephalus*). My original aim was to investigate the diet of *P. poliocephalus* in urban and non-urban areas using laboratory-based pollen and seed analysis. Unfortunately, due to COVID-19 restrictions, I was not able to travel to these locations to perform such fieldwork, and this was further complicated by university laboratory closures. This resulted in substantial changes of originally planned approaches and associated methodologies, and required incorporation of alternative data sources. The latter included the use of GPS and accelerometry data collected as part of the ARC Discovery Project (DP170104272) awarded to my supervisory panel. These data were used to identify food plant species that were visited by *P. poliocephalus* in Chapter 4; however, it still required in-person visitations to identify the tree species each feeding fix pertained to. Unfortunately, due to the interstate travel restrictions and border closures, I was unable to travel to Adelaide between March 2020 – February 2021, and thus collaborated with personnel at Adelaide University whom were able to collect a subset of my tree species data. I was fortunate enough to be able to visit Adelaide for a short time when restrictions eased, collecting an additional subsample of data. However, as a result of the COVID-19 restrictions, tree species data collection in Chapter 4 was a collaborative effort with Tom Hibburt, Dr Wayne Boardman, and myself.

Summary

Urbanisation is a major threat to ecosystems globally, resulting in habitat loss and habitat fragmentation, reduced biodiversity, and/or species extinction. However, urban habitats also create opportunities for exploitation by adaptable species, and this often leads to unbalanced management actions that have little regard for species conservation. Better understanding of the underlying drivers of wildlife species urbanisation will assist wildlife managers in developing effective and balanced conservation-management strategies.

The grey-headed flying-fox (*Pteropus poliocephalus*), is a large, highly mobile species, that is becoming increasingly dependent on urban areas. Flying-fox urbanisation has been hypothesised to be a result of loss of natural foraging habitat, an attraction to increased spatiotemporal stability of food resources in urban areas, and/or both. Yet, little is known about how *P. poliocephalus* utilise urban areas for foraging.

This study aims to investigate foraging resource availability as a driver of the documented *P. poliocephalus* urbanisation. Foraging habitat use was assessed using a large satellite tracking dataset from 98 individuals between 2012-2017. These data were combined with vegetation type data, and published indices of *P. poliocephalus* habitat quality to assess foraging habitat preferences. Tracked individuals were overwhelmingly dependent on human-modified landscapes for foraging, particularly where they roosted in major-urban areas. To identify the specific food plant species that support *P. poliocephalus* in urban areas, paired GPS and accelerometer data were used to identify trees visited by foraging individuals roosting in Adelaide. Tracked individuals preferentially visited residential areas and road-side habitats. Individuals visited a relatively high diversity of food plant species in these habitats, and flowering/fruiting phenology records indicated collective year-round availability of food resources for *P. poliocephalus*. This study suggests that *P. poliocephalus* urbanisation is, at least in part, driven by spatiotemporal availability and stability of food resources.

Chapter 1: Wildlife urbanisation: threats, opportunities and implications for management

1.1 Wildlife urbanisation

The human population is increasing at an alarming rate and there is a trend towards more people living in urban areas than ever before (Hooke et al., 2012; Magle et al., 2012).

Urbanisation and the rapid rate at which urban areas are expanding are major threats to wildlife populations due to processes including habitat loss and habitat fragmentation (Marzluff and Ewing, 2001; McKinney, 2002). Urbanisation can also promote changes in local abiotic and biotic conditions (Bar-Massada et al., 2014). Firstly, urban areas are characterised by increased local temperatures via the urban heat island effect (Magee et al., 1999); changes in soil nutrient content caused by disturbances from clearing, pollutants, and the use of fertilisers; and soil moisture via artificial watering and runoff (Sukopp, 2004; Neil and Wu, 2006). Increased temperature, soil nutrients and soil moisture have been hypothesised to have a positive effect on the growth and flowering phenology of urban plants, in some cases leading to enhanced growth (Zhao et al., 2016), and more regular, intense flowering (Handreck, 1997; Williams et al., 2003; Neil and Wu, 2006; Neil et al., 2014; Davis et al., 2016). Soil disturbance from processes such as land clearing, can promote an increase in ‘weedy’ disturbance-tolerant plant species and a decrease in re-establishment of native species through competitive exclusion (Deák et al., 2016). Additionally, urban pollutants can alter the acidity of soils, making it difficult for particular plant species that are sensitive to changes in soil composition to grow in such urban environments (Sukopp, 2004). Urban environments are also characterised by decreased vegetation cover, structure and complexity as a result of physical landscape changes such as extensive areas of impervious surfaces (Le Roux et al., 2014). Furthermore, anthropogenic plantings of regionally non-

endemic and exotic plant species alter the vegetation composition of urban habitats. As such, urban habitats often exhibit increased abundance of non-native plant species and a decrease in native plant species (McKinney, 2008). Research suggests that ‘moderately disturbed’ areas including suburbia, exhibit higher plant species diversity than surrounding rural, ‘less-disturbed’ areas (McKinney, 2008). This is because suburban areas are highly diverse in terms of land-use (McKinney, 2008). Streets, parks, public and private gardens, for example, comprise a range of locally indigenous, non-indigenous, and exotic species; and greenspaces can retain remnant natural vegetation, resulting in a potential increase in plant species diversity (McKinney, 2008). In addition, urban habitats also provide non-seasonal water sources such as recreational lakes, that are available throughout the year (Šálek et al., 2015). Therefore, in general urban expansion results in the decline of natural habitats and the introduction of ‘new’ habitats (McKinney, 2002) that exhibit unique abiotic and biotic conditions (Bar-Massada et al., 2014).

Urbanisation, and the associated decline of native habitats and establishment of ‘new’ habitats can result in changes to the composition of urban wildlife species assemblages in many taxa including birds, mammals, and insects (McKinney, 2006). Firstly, wildlife species vary in their ability to adapt to urban habitats (McKinney, 2002); urbanisation tends to provide a selective advantage for diet and habitat generalist species (often referred to as ‘urban adapters’ or ‘urban exploiters’) as these species are better able to adapt to the unique conditions of the urban habitat (Öckinger et al., 2010; Lizée et al., 2011; Callaghan et al., 2019b). Urban-dwelling orb-weaving spiders (*Nephila plumipes*) for example, are larger and exhibit higher fecundity than non-urban individuals; theorised to be a result of increased growth under warmer temperatures associated with the urban heat island effect (Lowe et al., 2014). However, for habitat and diet specialist species, poorly mobile species, and/or species that rely on dense vegetation, the expanding urban landscape is often largely unsuitable (see

Concepción et al., 2015). Thus, species with narrow niche breadths are less likely to occur in urban environments (Kellner et al., 2019); and these species are often referred to as ‘urban avoiders’ (McKinney, 2002). In addition, the abundance of native species tends to decline along rural-urban gradients (McKinney, 2006). This is thought to be a result of increased intentional and unintentional importation of non-native plant and animal species, drastic changes in vegetation structure and/or abiotic conditions in urban environments that can provide exotic species with a competitive advantage (McKinney, 2006). However, native endangered species sometimes occur in urban habitats (Ives et al., 2016), and this can have important implications for conservation management. Thus, urbanisation can result in changes to the composition of urban wildlife species assemblages.

The composition of urban wildlife species assemblages can also be altered by changed predator-prey relationships (Fischer et al., 2012; Eötvös et al., 2018). Predator-prey dynamics naturally fluctuate in a cyclic manner whereby predator and prey species’ densities are closely linked; populations dip and recover through time in response to one another (e.g. Bode and Possingham, 2007). In unmodified environments, predator-prey dynamics are relatively stable as species can move between populations and thus spatial factors weaken the effect of population peaks and troughs (Bode and Possingham, 2007). However, in smaller habitat patches, including habitat fragments (and thus likely also in urban habitats), predator-prey dynamics have a greater impact on species density (Bode and Possingham, 2007). Therefore, the composition of urban species assemblages and predator-prey population densities, can be vastly different from natural counterparts.

There are two broad mechanisms that are thought to influence wildlife species colonisation of urban areas: ‘push’ and ‘pull’ factors (Hassan et al., 2017). ‘Push’ factors are those relating to loss and modification of natural habitat; the ability of the natural habitat to support the current population of a species decreases with habitat loss, resulting in animals

finding refuge in urban habitats (Hassan et al., 2017). For example, studies have hypothesised that the urbanisation of Pteropodid bats is, at least in part, driven by habitat loss as a push factor (Páez et al., 2018). Push factors may have particular implications for territorial species as habitat loss can alter territorial defense behaviours, potentially heightening conflict between neighbouring individuals (e.g. Hardman and Dalesman, 2018), increasing the number of ‘intruders’ due to reductions in the space available to establish new territories, or altering territory size (Christensen and Radford, 2018). Therefore, due to a lack of resources including food, shelter and unoccupied space in the natural habitat resulting from habitat loss, animals may be ‘forced’ to find refuge within urban habitats.

While habitat loss can ‘push’ wildlife to become more reliant on urban areas, wildlife species may also be attracted to urban areas by ‘pull’ factors. Pull factors may include an attraction to increased availability of resources via a ‘bottom-up’ effect (increased resource abundance at lower trophic levels can have a cascading effect throughout entire food webs) (Shochat et al., 2010), the absence of resource competition (Lill, 2009), and/or a reduction in predation pressure (Fischer et al., 2012). The diversity of flora in urban and suburban ‘green spaces’ such as parks and gardens, including native, locally non-endemic, exotic, and hybridised plant species (McKinney, 2008), can provide a wider range of foraging opportunities that are more spatiotemporally stable and abundant than natural areas on average, and this can attract urban adaptable species (e.g. Williams et al., 2006; Lill, 2009). Furthermore, humans generally choose to plant species based on traits such as the aesthetic appeal of their flowers, and/or the colour of their foliage (Kendal et al., 2012), which can be particularly attractive to nectivorous animals. For instance, some highly mobile nectivorous species including birds (e.g. Evans et al., 2012) and bats (e.g. Meade et al., 2021), remain for longer in urban habitats, a likely result of increased availability and stability of urban resources. Additionally, anthropogenic resources such as rubbish, litter, and roadkill may

attract some scavenger species including black bears (*Ursus americanus*; Lewis et al., 2015), racoons (*Procyon lotor*; Bozek et al., 2007), and red foxes (*Vulpes vulpes*; Doncaster et al., 1990). Similarly, bald eagles (*Haliaeetus leucocephalus*) are known to take advantage of urban landfills; primarily as sites for rest, and juveniles appear to obtain much of their energy requirements from urban landfill (Elliott et al., 2006). In addition, intentional resource provisioning by urban human residents, such as via the use of bird feeders, can further attract wildlife (Galbraith et al., 2017). Furthermore, artificial light sources associated with developed urban areas can attract large aggregations of insects that can be appealing to some insectivorous microbat species. For example, studies have shown increased levels of Gould's wattled bat (*Chalinolobus gouldii*) and *Mormopterus* species activity in artificially lit urban areas in Australia (Scanlon and Petit, 2008). Additionally, colonies of Kuhl's pipistrelle (*Pipistrellus kuhlii*) roosting in urban areas in Italy, particularly near artificially lit areas or water sources, have shown advanced parturition time and produce greater numbers of pups, thus exhibiting higher reproductive success than their non-urban counterparts (Ancillotto et al., 2016b). Therefore, urban adaptable species can be attracted to anthropogenic food resources offered in urban areas as they either provide relief during food shortages and/or require reduced foraging effort.

Interspecific interactions can also be important factors that influence wildlife urbanisation (Shochat et al., 2010). For example, an observational study on rainbow lorikeets (*Trichoglossus haematodus*), musk lorikeets (*Glossopsitta concinna*), and red-rumped parrots (*Psephotus haematonotus*) in Melbourne, Australia, have found that these species feed predominantly on urban foraging resources that include locally non-native Eucalypts (lorikeets) and turf grasses (red-rumped parrots) planted in urban parks and gardens (Lill, 2009). They also found reduced interspecific competition for these resources in urban habitats (Lill, 2009). Therefore, it is likely that a combination of the availability of urban

resources and the absence of interspecific competition, has influenced the successful colonisation of these wildlife species in Melbourne. However, interspecific competition can also limit the success of some wildlife species in urban areas (e.g. Charter et al., 2016). For example, the breeding success of native birds such as the great tit (*Parus major*) and house sparrow (*Passer domesticus*) in Israel is negatively affected by interspecific competition for nesting cavities by introduced species (Charter et al., 2016). Similarly, invasive ring-necked parakeets (*Psittacula krameri*) have been shown to out-compete native scops owls (*Otus scops*) for nesting cavities in urban Italy (Mori et al., 2017). In these ways, interspecific competition is an important factor contributing to the dynamics of wildlife urbanisation.

Predator-prey interactions may also act as push and pull factors influencing wildlife urbanisation (Fischer et al., 2012). However, this is quite a complicated and contradictory area of research to the extent that researchers have developed the term ‘predation paradox’ (Fischer et al., 2012). Some studies report overall higher predator abundances in urban areas than natural habitats (Fischer et al., 2012), while other studies suggest a ‘predator relaxation’ in urban habitat, as prey species’ survival rates appear to increase with urbanisation (Fischer et al., 2012; Eötvös et al., 2018). There are now many theories to explain these findings. For example, research shows that some dietary-generalist carnivorous avian predators show a diet shift in urban areas, generally feeding on the most abundant prey species (Eötvös et al., 2018), which is theorised to result in a relaxation of predation pressure on other potential prey species (Eötvös et al., 2018). Other theories suggest that anthropogenic resources available in urban areas support a hyperabundance of prey species and that this weakens the top-down control of predation on the overall urban prey population (Fischer et al., 2012). In the case of the ‘predator relaxation’ hypothesis, urban areas may act as refuges from natural predators and hence facilitate the successful urbanisation of prey species. Other research suggests that despite the natural predation relaxation in urban areas, human activities can be perceived as a

‘predation risk’ and that animals may modify their behaviour to compensate for those perceived risks (e.g. house finches; Valcarcel and Fernández-Juricic, 2009). Therefore, altered predator-prey relationships may promote wildlife urbanisation by weakening top-down controls, whereas perceived predation risks including those associated with human activities can potentially impede the urban success of certain wildlife species.

As demonstrated above, the urbanisation of wildlife species can be influenced by various push and pull factors, including natural habitat loss, an attraction to increased availability and stability of urban food resources, reduction in intra- and interspecific competition for resources and/or reduced predation pressures. Understanding the underlying factors that drive wildlife urbanisation is critical in order to develop conservation-management strategies that are effective throughout time and space (Allen and Singh, 2016).

1.2 How is wildlife urbanisation managed globally?

Interactions between humans and wildlife have existed from before the beginning of civilisation (Miquelle et al., 2005; Anand and Radhakrishna, 2017). In many respects, the presence of wildlife in urban environments is perceived as beneficial for human psychology; making us feel closer to the natural world (Fuller et al., 2007; Carrus et al., 2015; Soulsbury and White, 2015). However, conflicts can arise between humans and wildlife species where there is; competition for resources including food crop or livestock depredation (Tillman et al., 2000; Michalski et al., 2006; Aziz et al., 2017a); damage to property (Delahay et al., 2009); loss of social amenity (Kung et al., 2015); perceived risk of disease transmission to livestock or humans (Plowright et al., 2011; Wood et al., 2012; Mackenstedt et al., 2015); and/or any other threat to human health and wellbeing (Soulsbury and White, 2015). The potential for human-wildlife conflict increases with wildlife urbanisation as there are greater opportunities for humans and wildlife to interact.

Previous attempts to manage the urbanisation of wildlife have often focused on ways to mitigate the impact of wildlife species on humans, rather than focusing on understanding the underlying drivers of wildlife urbanisation to develop methods aimed at reducing the ‘attractiveness’ of urban areas to the conflict species. Two broad classes of urban wildlife management are currently used; 1) ex situ management, and 2) in situ management.

1.2.1 Ex situ management strategies

Forced eviction, is a common method used to exclude wildlife species from urban sites (Stevens et al., 1998; Holevinski et al., 2007; Vantassel et al., 2013; Germano et al., 2015). In Australia, for example, a combination of smoke, light and noise is used to disperse flying-foxes roosting in conflict areas (Westcott, 2010; Roberts et al., 2011; Welbergen et al., 2020; Roberts et al., 2021), and in countries including China, aerosol irritants are used to prevent the habituation of bird species (Stevens et al., 1998). In the United States, urban coyotes (*Canis latrans*) display enhanced boldness and aggressive behaviour towards humans and pets (Breck et al., 2017). Inducing fear by aggressively approaching a coyote, throwing objects and yelling is promoted as a way of evicting such animals from urban sites (Bonnell and Breck, 2016). However, these methods often have little regard for conservation and without extensive biological understanding of each conflict animal species, current methods of forced eviction are often unsuccessful (e.g. Roberts et al., 2011; Roberts et al., 2021). For instance, wildlife species can become desensitised to aversive stimuli; learning through repeated exposure to a non-lethal sensory disturbance that there is no negative consequence (Blumstein, 2016). Furthermore, rather than resolving conflict, forced eviction may simply shift the conflict to an alternative location (e.g. Roberts et al., 2011).

Another ex-situ management technique involves the translocation of wildlife species from conflict zones to alternative habitat. Translocation as a human-wildlife conflict mitigation tool is generally regarded as the most humane option of managing ‘nuisance’

wildlife (Germano et al., 2015). However, translocations used as conflict mitigation tools are economically rather than scientifically driven and thus, they often have little regard for species conservation (Germano et al., 2015). Firstly, translocation can have detrimental effects on the survivability of translocated populations and on resident animal populations at target locations (Craven et al., 1998; Annis et al., 2007; Pinter-Wollman et al., 2009); including considerable increases in mortality rates in translocated adult and calf African elephants (*Loxodonta africana*; Pinter-Wollman et al., 2009), black bears (Annis et al., 2007), and racoons (Rosatte and MacInnes, 1989). Increased mortality rates are thought to be a result of factors including stress caused by capture, transportation and disorientation in the new habitat; increased intraspecific conflict with resident animals, particularly in territorial species (e.g. Eymann et al., 2006); challenges locating food and shelter; difficulty establishing due to unsuitable habitat; dispersal of animal populations beyond the release site; and increased disease transmission between translocated and resident animals (Massei et al., 2010). For example, nuisance racoons translocated from Florida to Virginia in the United States, resulted in an epizootic of rabies, threatening the health and wellbeing of humans and pets (Nettles et al., 1979; Craven et al., 1998). Further, translocation can also result in the continuation of the ‘nuisance’ behaviour at the translocation site and surrounding areas, thus proliferating the conflict rather than reducing it (e.g. Craven et al., 1998). For example, studies have reported that almost 50% of translocated black bears continued nuisance behaviour post-release (Annis et al., 2007), and leopard (*Panthera pardus fusca*) translocations resulted in increased frequency and severity of attacks on humans (Athreya et al., 2011). Moreover, for species that have large home ranges and/or are capable of long-distance movements, relocations may have little long-term benefit in conflict mitigation, as translocation may potentially result in the return of translocated animals to the capture site (e.g. Gila monsters (*Heloderma suspectum*), diamond-backed rattlesnakes (*Crotalus atrox*);

Sullivan et al., 2015). Therefore, successful translocation requires careful consideration of the potential impacts on the translocation and resident species (Massei et al., 2010), the biological needs and habitat suitability of each conflict species (Letty et al., 2007), as well as the consideration of species-specific movement patterns (Annis et al., 2007; Sullivan et al., 2015). Implementing support strategies such as acclimation pens and monitoring the health of translocated animals may increase survivability post translocation (Massei et al., 2010). However, it may be difficult to gain support for and implement such strategies due to the additional financial costs they incur. Furthermore, due to the risks associated with mitigation translocation, this procedure may further impact the survivability of vulnerable conflict species.

1.2.2 In situ management strategies

The management of human-wildlife conflict in general, has historically focused on lethal control of wildlife by direct culling (Treves and Naughton-Treves, 2005), or selective killing of animals that display unwanted behaviours (Breck et al., 2017). Culling is the process by which numbers of a target species are killed with the aim of reducing the overall population, assuming this will result in a corresponding reduction in conflict (Treves and Naughton-Treves, 2005). Lethal control methods include the use of baits (Morgan and Hickling, 2000), traps (Warburton and Orchard, 1996), fumigants (Hadjisterkotis, 2006; Fellowes et al., 2020), or the use of guns (Choquenot et al., 1999; Mason et al., 2002). In some historical cases, lethal management incorporated economic incentives (i.e. bounties) to increase the impact of culling efforts (e.g. rabbits (*Oryctolagus cuniculus*); Braysher et al., 1996; Tasmanian tigers (*Thylacinus cynocephalus*); Bulte et al., 2003; Danish harbour seals (*Phoca vitulina*); Olsen et al., 2018).

Lethal control as a conflict mitigation strategy is widespread and has applications in response to wildlife exploitation of anthropogenic resources from farms, homes, cars, and

stealing directly from people (e.g. chacma baboons (*Papio ursinus*); Fehlmann et al., 2017); damage to personal property (e.g. badgers (*Meles meles*); Delahay et al., 2009; African elephants; Scrizzi et al., 2018; moles (*Talpa europaea*); Fellowes et al., 2020); as a response to perceived disease risk (e.g. badgers; Carter et al., 2007; Riordan et al., 2011); and/or to reduce unwanted behaviours including aggression towards humans (e.g. coyotes; Breck et al., 2017). However, despite its extensive use, research indicates that lethal control is largely ineffective in reducing human-wildlife conflicts for several reasons. Firstly, the occurrence and severity of conflict is not always directly associated with the population density of a conflict species (Treves and Naughton-Treves, 2005), and without addressing the ‘attractant’ or cause of the unwanted behaviour, other members of the conflict species may replace those that are killed (e.g. moles; Adams and Lindsey, 2010). Thus, lethal control in conflict management may be ineffective without achieving a significant reduction in the overall population of a species, which leads to a series of animal-welfare and conservation implications (Treves and Naughton-Treves, 2005). Secondly, research has indicated that lethal control can worsen human-wildlife conflict such as causing increased aggression in animals including dingoes (O’Neill et al., 2017), and stress-mediated immunosuppression leading to increased prevalence of infectious disease transmission (Woodroffe et al., 2008; Riordan et al., 2011). Therefore, lethal control is often ineffective at reducing human-wildlife conflict, and may in fact exacerbate the conflict it aims to resolve.

The widespread use of lethal control (both historically and presently), has had drastic impacts on wildlife populations, leading to the decline and in some cases, the local, regional or even global extinction, of species around the world (Breitenmoser, 1998; Treves and Naughton-Treves, 2005). Lethal control can also result in unpredicted impacts on remaining animal populations including stress-related increases in mortality (e.g. African elephants; Slotow et al., 2008; dingoes (*Canis dingo*); O’Neill et al., 2017), social disruption (e.g.

elephants; Shannon et al., 2013; dingoes; O'Neill et al., 2017), and influence changes in animal movement patterns and home range size (e.g. badgers; Tuytens et al., 2000; Riordan et al., 2011). Thus, lethal control can lead to unpredicted impacts on animal populations that not only result in serious long-term implications for wildlife species but may also worsen human-wildlife conflicts.

Due to associated negative implications for animal welfare and species rights (Liordos et al., 2017), lethal control is now a highly contentious procedure and in many places it is now prohibited and/or used only as a precautionary measure to protect human health and wellbeing (Delahay et al., 2009). However, this has important implications, as where vulnerable species threaten human health and wellbeing, it is often human interests that take precedence over conservation (e.g. Florens and Baider, 2019). Additionally, where lethal control is prohibited, or where engaging in lethal control requires a conditional license, there is often little or no enforcement, particularly in developing countries, and this can result in illegal shooting and non-compliance of license conditions (Jenkins and Racey, 2008; Rahaingodrahety et al., 2008; Divljan et al., 2011). Therefore, there is an urgent need for the development of effective, non-lethal control strategies, as well as stricter enforcement of current regulations.

There is growing interest in the use of non-lethal alternatives to control wildlife populations at the center of human-wildlife conflict, including partial or complete fertility control and sterilisation (Fagerstone et al., 2010; Massei and Cowan, 2014; Tribe et al., 2014). As these techniques are focused on reducing birth rates rather than increasing mortality rates, this method is often perceived as more 'socially acceptable' and 'less inhumane' (Lauber et al., 2007). There are many different methods of fertility control and sterilisation that include: surgical sterilisation (e.g. overabundant koalas (*Phascolarctos cinereus*); Duka and Masters, 2005), hormonal contraceptives (e.g. pigeons (*Columbia livia*);

Massei and Cowan, 2014), immunocontraception (e.g. eastern grey kangaroos (*Macropus giganteus*); Kitchener et al., 2009; deer, bison, horses, elephants; Kirkpatrick et al., 2011), and the use of bacterial or viral pathogens that cause infertility (Cooper and Herbert, 2001; Massei and Cowan, 2014). However, fertility control measures may also have animal welfare implications, for example, surgical sterilisation and surgeries involved with the deployment of slow-release hormone implants can cause increased mortality as a result of stress induced by the capture, anesthesia and/or potential surgical complications (Spence et al., 1999); hormonal contraceptives may have pharmaceutical repercussions including behavioural changes, and potential impacts on already pregnant females (Kirkpatrick et al., 2011); immunocontraceptives and may interfere with disease resistance in targeted animal populations (Cooper and Herbert, 2001); and the use of ‘bacterial ghosts’(virus-like particles and genetically modified organisms to induce infertility) have potential risks including causing infertility in non-target species, and thus has not proceeded to field testing (Tyndale-Biscoe, 1991; Massei and Cowan, 2014). Additionally, sterilisation and fertility control methods can have other undesired impacts of wildlife populations including behavioural changes related to a reduction in sexual activity that alter group cohesion and/or the social hierarchy of the species (Cooper and Herbert, 2001), potentially leading to increased vulnerability. Furthermore, sterilisation and fertility control are not viable options for species already in decline as it would be further detrimental to the overall survival of the species. Therefore, these methods vary in their effectiveness, duration of effect, and potential risk for the target species, and thus require extensive species-specific consideration. Moreover, these methods of population control will not immediately reduce human-wildlife conflicts as they work to reduce population growth and therefore the population will only decrease at the rate of natural mortality.

Preventative measures are also implemented in an attempt to mitigate human-animal conflicts. Where wildlife species are attracted to anthropogenic resources such as rubbish and fruit trees in urban settings, preventative measures have been employed, including the removal of fruit crops from high risk areas and the introduction of scavenger proof bins (Lewis et al., 2015), and signage to deter supplementary feeding of wildlife species (Marschall et al., 2017). In the United States for example, the removal of fruit trees in urban areas, particularly those close to riparian habitat, has been suggested as a mitigation tool to minimise the appeal of urban foraging to black bears (Lewis et al., 2015). Additionally, bear resistant bins are employed to reduce anthropogenic scavenging on rubbish (Lewis et al., 2015). However, the effectiveness of bear-resistant rubbish bins relies on training and enforcement to ensure adequate securing of the bins is achieved (Lewis et al., 2015). A combination of these techniques may reduce urban foraging; however, urbanisation is predicted to increase and along with predicted worsening of future food shortages driven by climate change, and hence the prevalence of species such as black bears in human-dominated environments is likely to increase accordingly (Baruch-Mordo et al., 2014). Therefore, it is important to develop methods that simultaneously limit urban food resources and improve natural food resources, and thus, address the underlying cause of wildlife urbanisation.

Other species-specific measures have been suggested to mitigate human-wildlife conflict in urban areas. For example, the use of bone-oil as a repellent to deter European moles, may be a suitable small-scale alternative to lethal control in this species (Atkinson and MacDonald, 1994). Additional mole deterrent strategies include the use of aluminium sheeting to prevent tunneling through garden beds, and/or compacting the soil using rollers and by reducing irrigation to discourage tunneling (Davis and Mengak, 2007). However, these practices vary in their effectiveness, initial economic cost and labour involved (Davis and Mengak, 2007). In Australia, brushtail possums (*Trichosurus vulpecula*) nesting in roof

cavities and the associated noise and smell of faeces is a common cause of human-wildlife conflict (Eymann et al., 2006). Residents who report conflict with possums are given advice on how to use preventative measures to mitigate conflict. Strategies include sealing roof cavities, removal of branches overhanging rooves, use of tree guards, and the removal of garden plants that are known to attract possums (Eymann et al., 2006). The installation of possum boxes is also recommended, to provide alternative nesting habitat; however, they are often unsuccessful if sealing of roofs is not undertaken simultaneously (Eymann et al., 2006). Unfortunately, possum deterrent strategies are rarely adopted by the public, likely due to a lack of education (Hill et al., 2007), and often result in illegal translocations which can cause increased mortality and territory-driven possum-possum conflict (Eymann et al., 2006). This highlights the importance of education-based programs, to teach residents how to effectively use preventative strategies to reduce conflict, and inform them about why alternate strategies are ineffective and/or inhumane (Eymann et al., 2006). In addition, there is growing interest in incorporating human social science in human-animal conflict mitigation in order to maximise the effectiveness of non-lethal preventative practices. Social scientists that are trained in human conflict resolution, persuasion theory, and human behavioural conditioning, could help wildlife conservationists improve management strategies by conducting human-based research aimed at changing human behaviour (Baruch-Mordo et al., 2009). Therefore, species-specific conflict preventative strategies could be a successful non-lethal strategy to mitigate human-wildlife conflicts in urban areas, particularly if used alongside extensive community education and human behavioural approaches.

Wildlife management agencies have the difficult task of trying to balance the perspectives of numerous stakeholders including local residents, wildlife species and conservationists (Madden, 2004). Where the perspectives of each stakeholder are not considered carefully, human-wildlife conflict can intensify, and/or can result in conflict

between humans about wildlife, particularly if people believe animal conservation takes priority over their own needs (Madden, 2004). Where there is overwhelming support for a particular action (e.g. lethal control) due to negative public perception of a species or where the perceived severity of the conflict is high, these opinions can influence the type of control method employed to mitigate the conflict (e.g. Florens and Baider, 2019). In some cases, human perspectives can overshadow the ecological importance and conservation status of the conflict species resulting in ‘blind’ employment of lethal management (e.g. Florens and Baider, 2019).

Education is a powerful tool that can be used to improve public perceptions of a species (Hoffmaster et al., 2016; Cailly Arnulphi et al., 2017; Marley et al., 2017). For example, education can be used to improve public perception of a wildlife species; research has shown that people who are more knowledgeable about bat biology are less likely to fear them (Prokop et al., 2009), and thus, more likely to support their conservation. Education programs also have the potential to spread information to local communities in the centre of human-wildlife conflict about the importance of species conservation, provide information regarding why current control methods are largely unsuccessful in conflict mitigation and the power of alternative non-lethal options. For example, model-based research has suggested that using an education program focused on effective bear deterrent methods and proper waste management can reduce the probability of human versus black bear conflicts in America (Marley et al., 2017). However, where such methods are employed, there is limited empirical evidence to support the effectiveness of education programs (Baruch-Mordo et al., 2011). Nonetheless, where a species is central to human-wildlife conflict, educational programs could be more effective where they acknowledge the economic revenue potential of the species including wildlife tourism (Vannelli et al., 2019), ecological benefits such as assistance in improved crop yields via pollination and seed dispersal (Tuttle, 2013; Aziz et

al., 2017b), or the value of natural insect control (Castilla et al., 2020). Education programs, may further improve attitudes for conflict species, reduce conflict with humans, and/or increase support for conservation by local communities.

Recent research has suggested that the unique nature of urban habitats (either supporting or excluding wildlife species), human-wildlife conflicts and the way in which conflict species are managed, may drive evolutionary change in urbanised species (Schell et al., 2020). Urban habitats generally provide a selective advantage for generalist species, for example, and management procedures such as culling and translocation, remove individuals with particular undesirable traits (Schell et al., 2020). Furthermore, wildlife populations may adapt to management actions potentially negating long-term goals and the efficacy of such management strategies; influencing a ‘co-evolution’ between human management and wildlife conflict in urban areas (Schell et al., 2020). It is therefore imperative to understand the long-term evolutionary effects of current lethal and non-lethal management strategies.

The limitations of the current conflict management techniques explained throughout this section, highlight the need to better understand the drivers of wildlife movements and urbanisation. Once we gain an understanding of the ‘push’ and ‘pull’ factors that drive species movements into urban areas, management strategies that focus on landscape management rather than species management can be implemented. Such strategies consider the ecological and biological needs of each species and therefore may provide more effective, long-term solutions to human-wildlife conflict mitigation and species conservation.

Landscape modification is already being implemented in several countries in an attempt to improve urban biodiversity. In the United Kingdom, for example, research into how urban biodiversity can be improved in existing green spaces such as ‘road verges’ or ‘nature strips’ has been conducted (O'Sullivan et al., 2017). Planting more trees and shrubbery as opposed to grasses that require much maintenance, could have multiple ecological and environmental

benefits (O'Sullivan et al., 2017). Enhancing the biodiversity of road verges will improve foraging resource availability for species in urban areas, better connect fragmented landscapes, enhance local air quality, stabilise air temperature, increase carbon sequestration, reduce flood risk, reduce noise pollution and potentially reduce time and financial cost associated with maintenance of existing lawns (O'Sullivan et al., 2017). In other countries, innovative approaches to increase the amount of green space are being implemented. In Switzerland for example, the urban foraging landscape is being improved by implementing green roofs as mandatory for new buildings with flat roofs (Brenneisen, 2006). The purpose of green roofs in this context is to increase biodiversity in urban areas as well as attempt to support threatened species (Brenneisen, 2006). In China, urban growth and the need for the development of new infrastructure, including roads and railway lines, is carefully planned to minimise the impact such development will have on biodiversity (Xu et al., 2011). In particular, the construction of new roads is carefully planned to avoid certain habitat, including natural waterways, and cleared trees are saved and replanted adjacent to new roads in order to minimise the environmental impact of expanding infrastructure; these are known as 'greenways' (Xu et al., 2011). These strategies could potentially be used in urban conflict mitigation. The use of greenways where there is need to expand or create new infrastructure could be implemented to reduce further impact of urbanisation on the natural environment. This could reduce the rate of habitat loss, potentially reducing the effect of habitat loss as a 'push' factor of wildlife urbanisation. The vegetation that is incorporated into green spaces and green roofs could consider the species-specific foraging resource use of conflict animals, for example, 'attractive' plant species could be limited near conflict zones and actively planted in alternative areas, essentially aiming to redirect foraging of problem species. A limitation of the use of green roofs and green spaces in this way is that they may only be accessible to volant species including birds and bats (Brenneisen, 2006). Tree planting

schemes, as have already been suggested as a conflict mitigation strategy to reduce Australian flying-fox dependence on orchards during food shortages (Law et al., 2002; Eby, 2016), could be employed in a similar way. Therefore, the existing foraging habitat could be modified in ways that both improve foraging habitat in natural areas and reduce foraging habitat in problem areas to simultaneously support animals in their natural habitat and encourage foraging away from conflict zones.

The current chapter highlights that wildlife urbanisation is an important and growing issue for conservation management and human-wildlife conflict mitigation. Current management actions are often ineffective and detrimental to the survival of wildlife populations, and thus, effective, balanced conservation management approaches rely on better understanding of the underlying factors that drive wildlife urbanisation. In the next chapter, I will review wildlife urbanisation, and its implications for conflict mitigation and species conservation with a specific focus on flying-foxes (*Pteropus* spp.).

Chapter 2: Flying-foxes and urbanisation

Flying-fox (*Pteropus* spp.) urbanisation involves many of the issues highlighted in Chapter 1, and as such provides a good model for investigating the factors supporting the increasing persistence of wildlife in cities and towns. Flying-fox urbanisation is particularly well-documented in Australia (Williams et al., 2006; Tait et al., 2014), and although there is limited research showing increasing prevalence of flying-foxes in urban areas in other countries, there is a large body of literature documenting human versus flying-fox conflicts globally, suggesting that management of flying-fox populations is a worldwide conservation management issue (Harrison et al., 2011; Rego et al., 2015; Islam et al., 2016; Aziz et al., 2017a; Florens and Baider, 2019). Here, in this chapter, I will focus on flying-fox urbanisation. I will begin by introducing flying-foxes, their ecological roles and importance, and current threats. Next, I will discuss urban human versus flying-fox conflict, the current management strategies that aim to address this along with their limitations, and illustrate the importance of understanding the driving factors of flying-fox urbanisation for the development of balanced conservation management of flying-fox populations.

2.1 Introduction to flying-foxes

Flying-foxes are large, highly mobile species of bat belonging to the Pteropodidae family (order: Chiroptera), consisting of 186 species (Simmons, 2005; Almeida et al., 2011). Flying-foxes are geographically dispersed, existing throughout the Mediterranean, Africa, Asia, Australia, and the Indian and western Pacific Ocean islands (Mickleburgh et al., 1992; Hall and Richards, 2000). They are highly social animals that forage during the night and aggregate in arboreal colonies known as roosts (or ‘camps’) during the day (Hall and Richards, 2000). Flying-foxes are considered nomadic, well known for their ability to travel long distances (Welbergen et al., 2020) in response to fluctuations in floral resources (Eby, 1991). For example, nightly foraging return visits of up to 80 km have been recorded in

Pteropus poliocephalus (Eby, 1991; Field et al., 2016). The flying-fox diet consists of the nectar, pollen, fruits and occasional supplementation of bark and leaves of several native and non-native plants, albeit the relative contributions of these various food sources vary from species to species (Parry-Jones and Augee, 1991a; Hall and Richards, 2000; Markus and Hall, 2004). They are generally regarded as dietary generalist or ‘sequential specialist’ species, feeding on their diet plants seasonally and opportunistically, in a hierarchical manner (Marshall, 1983; Parry-Jones and Augee, 1991b).

Flying-foxes deliver critical long-distance pollination and seed dispersal services as a result of their natural foraging behaviour and extreme mobility (Fujita and Tuttle, 1991; Aziz et al., 2021). During foraging, either by direct consumption of pollen or indirectly while feeding on nectar or fruits, pollen can adhere to the fur of flying-fox individuals (Figure 2.1; Marshall, 1983). Flying-foxes can then deposit pollen on the stamens of the next food plant they visit as they feed on other flowers (Fujita and Tuttle, 1991). When foraging for fruit, flying-foxes often carry the fruit in their mouths away from the foraging tree (Marshall, 1983; Richards, 1990). Additionally, they often do not consume the entire fruit, rather crushing it in their mouths to extract the juice before dropping the remaining ‘ejecta’ that contains larger seeds and pulp (Marshall, 1983). Small seeds can be ingested throughout this process (Marshall, 1983), and studies have shown gut retention times of *Ficus* spp. seeds in some *Pteropus* species of up to 12 hours (Shilton et al., 1999). Thus, via their droppings (including both scat and ejecta), flying-foxes have a natural ability to engage in seed dispersal (Fujita and Tuttle, 1991; Shilton et al., 1999). The extreme mobility exhibited by *Pteropus* species enhances their important role in long-distance pollination and seed dispersal (Fujita and Tuttle 1991).



Figure 2.1 Grey-headed flying-fox (*P. poliocephalus*) feeding on blossom. Pollen covers the face while foraging and is deposited on the stamens of the next foraging tree as they feed on the flowers. Image credit Mandy Griffith.

The ecosystem services provided by flying-foxes are critical to the maintenance of genetic diversity of native ecosystems, the genetic connectivity of forest fragments, and to forest regeneration (Fujita and Tuttle, 1991; Trakhtenbrot et al., 2005; Aziz et al., 2021). These ecological services are of particular importance for island ecosystems as they are geographically and reproductively isolated, and often exhibit high rates of endemism and naturally low genetic diversity (Braeutigam and Elmqvist, 1990; Cox et al., 1992). Additionally, island ecosystems generally have low diversity of animal pollinators, particularly nocturnal pollinators, and therefore many island plants are totally dependent on flying-fox pollination (Braeutigam and Elmqvist, 1990). Thus, flying-fox ecosystem services are critical to the maintenance of genetic diversity of flora and the extinction of these species

would have catastrophic flow-on impacts, particularly for the island flora and fauna that exclusively rely on their services (Braeutigam and Elmqvist, 1990; Cox et al., 1992).

Flying-foxes also pollinate numerous economically important crops including bananas, mangoes, guava, cashews, dates, figs (Pennisi et al., 2004), and durian (Aziz et al., 2017b). Other products derived from flying-fox-visited plants include hardwood timbers used in construction and medicinal products (Pennisi et al., 2004). These services are invaluable and can impact local and global markets (Wiles and Fujita, 1992). The extent of the benefits provided by flying-fox pollination and seed dispersal services has been largely overlooked and the loss of such species is likely to have drastic ecological and economic impacts.

2.2 Threats to flying-foxes

Of the 65 known *Pteropus* species 36 are currently listed as threatened, 5 as Data Deficient, and 6 as Extinct (IUCN, 2021). Contributing factors include loss of natural foraging and roosting habitat (Mohd-Azlan et al., 2001; Jenkins et al., 2007), bushfires (Baranowski et al., 2021), climate change related extreme heat events (Welbergen et al., 2008), other climatic events including cyclones (Banack and Grant, 2002), culling in response to fruit crop depredation (Florens and Baider, 2019), hunting for sport, bushmeat and/or medicines (Brooke and Tschapka, 2002; Jenkins et al., 2007), and other anthropogenic impacts including barbed wire or fruit netting entanglement and electrocution by power lines (Tidemann and Nelson, 2011; Scheelings and Frith, 2015; Mo et al., 2020b; Tella et al., 2020). Extreme heat events alone, can have enormous impacts on overall flying-fox populations, with records indicating mass mortality of up to tens of thousands caused by a single extreme heat event (Welbergen et al., 2008). Recent research has reported minimum mortality rates of more than 72, 000 Australian flying-fox individuals during the 2019-2020 summer alone (Mo et al., 2021). Lactating females and juveniles are more susceptible to the effects of extreme heat events due to a predicted lower ability to thermoregulate during these

life stages (Welbergen et al., 2008). This is likely to have disproportionate effects on the breeding population and thus, reduce the population's ability to recover after such disturbances (Welbergen et al., 2008). Furthermore, under current climate change models, extreme heat events are expected to increase in frequency and intensity in the future (IPCC, 2021), posing a serious risk to the survival of flying-fox populations. Moreover, flying-foxes generally have a low reproductive ability to recover from population declines as they generally exhibit slow sexual maturity, long gestation, and low reproductive output with mature females usually only producing one pup per mating season (McIlwee and Martin, 2002; Welbergen, 2005). Thus, flying-fox species are faced with several threatening factors, and due to their slow life histories, are considerably vulnerable to threats including extreme heat events as they have a limited ability to recover from population declines.

2.3 Flying-fox urbanisation

Flying-foxes are becoming increasingly urbanised and this is particularly well-documented in Australia (Figure 2.2, 2.3; Williams et al., 2006; Plowright et al., 2011; Tait et al., 2014; Páez et al., 2018; Meade et al., 2021). Models indicate that flying-foxes roost closer to human-dominated areas than would be expected by chance (Tait et al., 2014), and many urban roosts are now occupied year-round (Plowright et al., 2011). While there is limited research elucidating the urbanisation of flying-foxes further afield, studies researching human-flying-fox conflicts are extensive, indicating that the human versus flying-fox interface is a global conservation management issue (Harrison et al., 2011; Rego et al., 2015; Islam et al., 2016; Aziz et al., 2017a; Florens and Baider, 2019).

In order to effectively conserve and manage flying-fox populations, it is essential to first investigate the underlying drivers of their movement patterns and urbanisation. Flying-fox urbanisation has been hypothesised to be a result of loss of native foraging habitat (Markus and Hall, 2004; Páez et al., 2018), a behavioural response to increased availability

and spatiotemporal availability of urban foraging resources (Williams et al., 2006; Tait et al., 2014; Boardman et al., 2021; Meade et al., 2021), or a combination of both. Recent research has indicated that grey-headed flying-foxes (*P. poliocephalus*) preferentially roost in urban habitats (Meade et al., 2021), and that a large proportion of flying-foxes roosting in Adelaide during spring forage in residential areas where they feed on a range of species including non-natives (Boardman et al., 2021). Together, these findings suggest that availability and temporal stability of urban foraging resources is attracting flying-foxes to cities and towns. However, further research is needed to investigate how urban plantings have changed throughout time, and to understand how flying-foxes utilise the urban landscape for foraging.



Figure 2.1 Flying-foxes (*P. poliocephalus*) roosting near a human settlement in Boonah, Queensland.

Image credit Justin Welbergen.



Figure 2.1 Grey headed flying-foxes (*P. poliocephalus*), roosting at Sydney Botanic Gardens. Image credit Justin Welbergen.

The increasing prevalence of flying-foxes in urban areas may have important implications for conservation resulting from increased exposure to urban-related threats including electrocution on powerlines and entanglement in backyard fruit tree netting (Tidemann and Nelson, 2011; Scheelings and Frith, 2015; Mo et al., 2020b; Tella et al., 2020). Furthermore, urban flying-fox colonies may be more exposed to the effects of extreme heat events (Welbergen et al., 2008) due to the already warmer urban climate resulting from the urban heat island effect (Khan et al., 2020). Thus, flying-fox urbanisation could further impact their conservation. Recent research has indicated that urban roosting flying-foxes exhibit shorter foraging distances than non-urban roosting individuals (Meade et al., 2021), thereby reducing the long distance pollination and seed dispersal services they provide to natural ecosystems. Therefore, flying-fox urbanisation may have important implications for

the management of urban-related threats to these species, for the natural ecosystems they service, and for the species that rely on such ecosystems.

2.4 Urban human versus flying-fox conflicts

Personal values, negative attitudes towards bats and a longing to conform to social norms, strongly influence our behaviour as humans in response to human-bat conflict (Kingston, 2016). Bats in general, have bad reputations and are largely misunderstood; they have long been negatively represented by the media and associated with horror films and vampirism (Prokop et al., 2009; Kingston, 2016). Humans are more likely to generate animosity for animals that are most unlike us in terms of physical features and biology (Prokop et al., 2009). Bats are unique in morphology and natural history; being nocturnal animals, that hang upside-down, have backward feet and hooked thumbs, traits that are dissimilar and hence unfamiliar to humans (Prokop et al., 2009). As a result of these factors, fear and disgust for bats in general, is widespread (Kingston, 2016). Indeed, studies have revealed that humans rank bats in the ‘disgust’ category amongst cockroaches, leeches and maggots (Davey et al., 1998). Thus, in general, there is an underlying dislike of bats, and this may exacerbate negative perceptions of bats in human-bat conflict situations.

Flying-foxes have had a long negative connotation as ‘pests’ with orchardists due to their natural attraction to cultivated fruits (Ratcliffe, 1932). Fruit crop raiding is a major source of human versus flying-fox conflict, and remains a prominent management issue to this day (Aziz et al., 2016). The general dislike and fear of flying-foxes is further intensified by reports that they are natural reservoirs for a number of potentially fatal zoonotic pathogens (Mackenzie et al., 2001; Smith and Wang, 2013), albeit flying-foxes themselves rarely display any indication of diseases from these pathogens (Baker et al., 2013; Brook and Dobson, 2015). Zoonotic diseases that are potentially transmissible by flying-foxes include SARS-coronavirus, Nipah virus, Hendra Virus (Smith and Wang, 2013), Ebola virus (Leroy

et al., 2009), Menangle virus (Philbey et al., 2008) and Australian Bat Lyssavirus ABLV (Hooper et al., 1997). Furthermore, fear of bats in general has further intensified by more recent concerns related to the origins of the current COVID-19 pandemic (Rocha et al., 2020). This has resulted in deliberate attacks on some bat species in India, Australia, Peru and Indonesia (Rocha et al., 2020). Modes of disease transmission include; direct contact via bites or scratches (e.g. ABLV; Hanna et al., 2000; Francis et al., 2014), via an intermediate host (e.g. Hendra virus; Plowright et al., 2011), or by consumption of the meat of an infected animal (e.g. Ebola virus; Leroy et al., 2009). Thus, flying-foxes are central to human-wildlife conflicts largely concerning their attraction to fruit crops, and their natural ability to transmit zoonotic diseases; however, underlying fear of bats in general has likely exacerbated the way in which these conflicts are perceived.

In some cultures, such as those of Madagascar and South-East Asia, hunting flying-foxes for sport and/or the consumption of their meat is common (Jenkins and Racey, 2008; Aziz et al., 2017a). Hunting flying-foxes presents many issues for both conservation as well as human health and wellbeing. Firstly, flying-fox diurnal roosting behaviour makes them particularly conspicuous and thus vulnerable to human hunting as well as to other predators, with some studies suggesting that hunting at roost sites could deplete an entire colony of some species in a single season (Sheherazade and Tsang, 2018). Additionally, due to their slow life histories (Welbergen, 2005; Welbergen, 2010; Welbergen, 2011; Todd et al., 2018), flying-foxes are further vulnerable to overhunting (and other threats) as they are unable to recover quickly from population declines (McIlwee and Martin, 2002). In some island communities, the hunting of flying-foxes is prohibited or limited seasonally (Rahaingodrahety et al., 2008). However, there is often little or no enforcement and therefore it is largely ineffective at preventing overhunting (Rahaingodrahety et al., 2008).

Furthermore, direct contact with live or deceased animals, or the consumption of their meat is

likely to increase the incidence of zoonotic disease transmission (Smith and Wang, 2013).

Thus, hunting flying-foxes presents issues for conservation as well as human-health and wellbeing.

Flying-foxes defoliate the trees in which they roost in as a result of their natural movements within roosting trees. In some areas such as the Sydney Royal Botanic Gardens, Melbourne Botanic Gardens, and Mataranka Springs in the Northern Territory, flying-fox defoliation has had a detrimental effect on the aesthetic appeal of roost trees, some of which have cultural and historical significance, and thus flying-foxes residing in these areas have had a considerable impact on the tourism industry (Vardon et al., 1997; Perry, 2012; Glynn, 2019). Additional urban human-flying-fox conflicts relate to objectionable noise, smell of faeces and impact on social amenity (Kung et al., 2015), and consumption of backyard fruit crops (Aziz et al., 2016; Tollington et al., 2019). The increasing prevalence of flying-foxes in cities and towns is exacerbating urban human versus flying-fox conflicts, and thus, increasing the pressure on wildlife managers to mitigate such conflicts.

In response to human versus flying-fox conflicts, various, often controversial methods are used in an attempt to evict flying-foxes from urban sites (Roberts et al., 2011; Currey et al., 2018; Roberts et al., 2021). The general perception of flying-foxes as ‘nuisance’ species and/or vectors of disease make it difficult to gain support for their conservation (Rego et al., 2015; Crockford et al., 2018) and without enforcement, regulation, and education, people are more likely to support and/or engage in lethal and/or illegal means of control.

2.5 Current management of human versus flying-fox conflict

2.5.1 Lethal management

As humans, our primary response to manage a ‘pest’ species is to employ lethal control such as active culling (Hadjisterkotis, 2006; Vincenot et al., 2017). In Australia, fruit farmers have

previously attempted to control flying-fox fruit crop depredation by poisoning some of the fruits (Ratcliffe, 1932). In other countries such as Cyprus, another member of the Pteropodidae family, the threatened Egyptian fruit bat (*Rousettus aegyptiacus*) was previously classified as a ‘pest’ species, which led to the use of drastic lethal management including government incentivised fumigation poisoning and shooting (Hadjisterkotis, 2006). However, poisoning fruit and fumigation of cave roosts can have unwarranted impacts on non-target species and, in some cases, can lead to the collapse of entire ecosystems (e.g. Hadjisterkotis, 2006). For example, fumigation of *R. aegyptiacus* cave roosts, has caused unforeseen reductions of protected insectivorous microbat species which influenced population booms of their prey species, noctuid moths (Hadjisterkotis, 2006). Noctuid moths cause extensive crop damage and population booms led to the use of secondary chemical insect control, which caused heavy environmental pollution (Hadjisterkotis, 2006). Thus, lethal control including the use of chemical fumigants can have unprecedented impacts on non-target species, may cause cascading effects throughout entire food webs, and/or lead to secondary conflicts with humans.

Culling by direct shooting is another strategy used to in an attempt to mitigate human versus flying-fox conflicts in many countries (Epstein et al., 2009; Olival, 2016; Vincenot et al., 2017). In some island communities, residents engage in lethal control in an attempt to protect their fruit crop profits from flying-fox and fruit bat depredation (e.g. Florens and Baider, 2019). However, research suggests that culling flying-foxes does not increase fruit growers’ profits; rather, it is likely a result of government overestimates of losses caused by flying-fox depredation, with studies indicating considerably higher losses resulting from over-ripening and/or alien bird species (Florens and Baider, 2019). Studies have shown that flying-fox foraging on economically important crops such as durian, can actually enhance fruit growers' profits through their pollination services (Aziz et al., 2017b). Additionally,

flying-foxes tend to avoid unripe crops and fruit growers generally harvest their products before they become fully ripe. Thus, flying-foxes are more likely to consume fruits that are not usable to fruit growers, and by consuming overly ripe fruits, they could help prevent insect and fungal pests (Tuttle, 2013).

Attempts to manage zoonotic disease risk by culling bat species has been unsuccessful in several countries (e.g. rabies; Streicker et al., 2012). Culling is in fact, more likely to increase zoonotic disease transmission (Olival, 2016). Firstly, the act of culling increases direct contact with wildlife, thus increasing the risk of disease exposure in individuals engaging in such control methods (Olival, 2016). In addition, culling may alter complex disease dynamics, potentially increasing transmission risk (Olival, 2016). Furthermore, culling can influence greater inter-roost movement and/or the establishment of new roosts, potentially increasing the spread of the disease in wild populations (Olival, 2016). Moreover, the high mobility of flying-foxes and their dynamic movement patterns, using roosts as ‘staging posts’ (Welbergen et al., 2020) means that they are likely to recolonise previously culled roosts sites, whereby they may exhibit higher infection rates as a result of modified age structure in the recolonised population (Olival, 2016). Stress can also potentially increase the probability of viral shedding and/or the incidence of vectors (Olival, 2016). Therefore, instead of mitigating conflict, culling flying-fox populations may modify disease dynamics and potentially increase the risk of zoonotic disease transmission.

While culling has implications for increased disease transmission, it can also have detrimental impacts on the longevity of flying-fox populations, particularly in species that are already threatened by extinction. For example, reports have suggested that mass-culls resulted in population declines of up to 50% in an already threatened island species, the Mauritian flying-fox (*P. niger*; Vincenot et al., 2017). Such significant population declines resulting from mass culling events are cause for concern for the longevity of flying-fox and

fruit bat species. Additionally, flying-foxes provide essential ecosystem services through long-distance pollination and seed dispersal, maintaining the genetic diversity of forest ecosystems (Nyhagen et al., 2005; Chen et al., 2017; Florens et al., 2017). Therefore, population declines are also likely to have an impact on the functioning and viability of native forest ecosystems they service, with a particular concern for oceanic island ecosystems that may not have other species that engage in long-distance pollination (Florens et al., 2017).

In Australia, culling by direct shooting is now largely considered unethical and inhumane (Divljan et al., 2011), and in many states it is now illegal to kill flying-foxes, or permits given to fruit growers to protect their fruit crop from flying-fox depredation are being phased out (Waples, 2002; Australian Government, 2021); with the exception of QLD where permits are still issued (Department of Environment and Science, 2020). Female flying-foxes carry their dependent young while foraging, or at other times of the breeding cycle, will leave their young in creches while they forage (Rose, 2010). Females are often killed carrying their dependent young, or where they are left in creches and mothers are killed during foraging, their abandoned dependent young will eventually dehydrate and starve to death (Divljan et al., 2011). Thus, not only is lethal management by direct shooting arguably an inhumane and an unethical procedure that contravenes conservation law (Divljan et al., 2011), it is also an ineffective means of mitigating conflict with fruit farmers and the spread of disease (Olival, 2016).

2.5.2 Forced eviction

Another common flying-fox management strategy is the forced eviction of flying-foxes from urban sites via roost dispersal (Roberts et al., 2011; Roberts et al., 2021) and roost destruction (Edson et al., 2015). In Australia, dispersal continues to be a central course of action in the management of flying-fox populations in cities and towns (Roberts et al., 2011; Currey et al., 2018; Mo et al., 2020c). These methods involve the use of a combination of noise, smoke and

light to deter flying-foxes from settling in their original roost as they return from foraging (Figure 2.4; Currey et al., 2018; Mo et al., 2020c). However, there is growing evidence to suggest that such practices are largely unsuccessful (Roberts et al., 2011; Welbergen and Eby, 2016; Lentini and Welbergen, 2019; Roberts et al., 2021). Being a nomadic species, capable of long-distance flight, flying-foxes readily commute between roosts throughout eastern Australia, with a high turnover rate (Welbergen et al., 2020). This means that any one dispersal attempt will only successfully evict individuals residing at the conflict roost during that time, and these individuals will quickly be replaced by others. Therefore, for dispersal-based eviction of flying-foxes, the procedure must be carried out consistently, over a long period of time and this entails a significant physical and economic cost (Mo et al., 2020c). Additionally, flying-foxes generally return to the roost from foraging at dawn and are seemingly reluctant to fly long distances during daylight, possibly a result of predator avoidance and/or thermophysiological constraints (Welbergen et al., 2020). As a result, individuals often settle in trees nearby the original roost site (Roberts et al., 2011; Welbergen and Eby, 2016). This often leads to a larger number of community complaints and conflict, post roost dispersal (Roberts et al., 2011; Welbergen and Eby, 2016; Lentini and Welbergen, 2019; Roberts et al., 2021). Another issue associated with flying-fox dispersal is the concern for a potential increase in stress-mediated viral excretion, infection and transmission of zoonotic pathogens such as Hendra Virus (Plowright et al., 2011; Edson et al., 2015). However, this is difficult to quantify and is not yet well understood. Thus, methods of forced eviction are largely unsuccessful and may in fact exacerbate human-wildlife conflicts.



Figure 2.2 Dispersal actions conducted near Charters Towers, Queensland, in an attempt to evict flying-foxes from a local roost. Image credit Australasian Bat Society.

2.5.3 In-situ management

In-situ management of flying-fox conflict involves the use of buffers via removing vegetation between roosts and areas of human habitation, and the destruction of roosting trees (Currey et al., 2018; Mo et al., 2020c). Buffers have been described as successful at reducing the impact of noise and smell of faeces on social amenity; however, there are concerns about the effectiveness of this method as flying-fox numbers fluctuate throughout the year, and during peak times, flying-foxes could potentially roost in areas closer to human settlement than before due to limited space as a result of vegetation removal for the buffer (Currey et al., 2018). The use of olfactory deterrents involving python excrement, and taste aversion using fermented prawn paste have been trialed for their effect in the creation of buffers in Sydney's

CBD (Richards, 2002). These methods have shown promise; however, once the smell subsides, flying-foxes were shown to recolonise the buffer area (Richards, 2002).

Government subsidies for equipment and services are available for residents that live in close proximity to some flying-fox roosts in Australia, these include; high-pressure water cleaners, vehicle or clothesline covers, installation of air-conditioners and double-glazed windows to reduce noise, and the removal of exotic trees (Mo et al., 2020a). Recent research has analysed the effectiveness of these programs and in most cases they were effective at mitigating conflict with flying-foxes; however, they also created secondary issues associated with cost of running air-conditioners, the ongoing labour involved with continuous use of high-pressure water cleaners and issues associated with having to keep windows closed (Mo et al., 2020a). Nevertheless, government subsidised exotic forage tree removal did seem to be an effective mitigation strategy by alleviating noise and soiling impacts associated with foraging flying-foxes, and did not result in the need for continual mitigation (Mo et al., 2020a). Thus, although there is potential to use exotic tree removal as an urban conflict mitigation strategy where tree species that attract flying-foxes to high conflict areas are known, many other government subsidised mitigation strategies can lead to secondary issues and thus, do not completely resolve the underlying conflict.

Current management practices can have serious implications for flying-fox conservation. Culling by direct shooting may lead to imbalances in population age and sex ratios due to suggested disproportionate impacts on females and the impacts on dependent young (Divljan et al., 2011). As a result, lethal control can have an impact on population growth and recruitment. In addition, stress caused by roost dispersal and/or destruction is thought to increase the prevalence of zoonotic diseases and increase the risk of spillover events (Edson et al., 2015), and this is likely to exacerbate human-health and wellbeing concerns and increased public demands for culling and dispersal. Therefore, current

management techniques are largely unsuccessful (Hadjisterkotis, 2006; Roberts et al., 2011; Streicker et al., 2012; Olival, 2016; Florens and Baider, 2019), are detrimental to species conservation (Florens et al., 2017), and often proliferate conflicts rather than mitigate them (Roberts et al., 2011; Roberts et al., 2021). This highlights the urgent need to develop non-lethal, balanced conservation-management strategies.

Some recent research has already focused on understanding how to reduce the attractiveness of cultivated fruits to flying-foxes by improving the availability of native foraging resources. For example, it is thought that the presence of invasive plant species negatively impact the availability of native foraging resources including fruits, via competitive exclusion (Krivek et al., 2020). Recent research has found that weeding invasive plant species in native habitats can improve the native foraging habitat quality for Mauritian flying-foxes, thereby increasing native fruit production and foraging in natural habitats (Krivek et al., 2020). This suggests that invasive plant control could reduce the dependence of Mauritian flying-foxes on commercial fruit crops and consequently reduce associated conflict with humans (Krivek et al., 2020). Tree planting schemes have also been suggested to mitigate conflict with Australian flying-foxes and orchardists (Law et al., 2002; Eby, 2016). In some regions, spring-flowering floral resources for flying-foxes have been cleared and it is thought that replanting such species could reduce flying-fox reliance on fruit crops and thereby reduce conflicts with fruit growers (Law et al., 2002). Thus, landscape-based management approaches are a promising method to reduce conflict with fruit growers while supporting the conservation of flying-fox species.

Landscape-based management approaches could potentially be used in urban conflict mitigation, by manipulating the availability of resources throughout the urban landscape; excluding food resources in order to discourage foraging in conflict zones, and increasing food availability in native habitats to encourage foraging away from cities and towns. It has

been theorised that flying-foxes persist in urban areas as a result of increased spatiotemporal stability and availability of foraging resources (Boardman et al., 2021; Meade et al., 2021), mediated by increased dietary variety from anthropogenic urban plantings (Tait et al., 2005) and enhanced flowering due to the urban heat island effect and other urban abiotic factors (Davis et al., 2016), respectively. However, little is known about how flying-foxes use urban landscapes for foraging, in terms of foraging habitat utilisation across time and space, and the composition of their diet in urban areas. As such, we do not know what supports flying-fox urbanisation, which poses serious impediments for the management and conservation of this threatened species, as discussed throughout this chapter. Gaining a better understanding of flying-fox foraging resource use in urban landscapes and how this differs in non-urban landscapes could help us identify what attracts flying-foxes to cities and towns, and thus, provide wildlife managers with conservation ‘handles’ to effectively manage urban human versus flying-fox conflicts while supporting the conservation of these ecologically important species. This involves first, investigating whether individuals use urban and non-urban landscapes for foraging differently, and second, identifying the food resources that support flying-foxes in cities and towns.

2.6 Study aims

The overarching aim of this thesis is to better understand foraging resource availability and temporal stability as a driver of flying-fox urbanisation, and to inform effective, balanced, conservation-management strategies for urban flying-fox populations. The specific aims of this thesis are to:

1. Determine the foraging habitat use of the grey-headed flying-fox in urban versus non-urban Australia.

2. Investigate the food plant resources (and temporal stability of food resources) that sustain grey-headed flying-foxes in urban areas.

2.7 Thesis structure

This MRes thesis consists of five main bodies of work, comprising two review chapters (Chapters 1 & 2), two data chapters (Chapter 3 & 4), and one concluding chapter (Chapter 5).

In the first two chapters I review the issue of wildlife urbanisation, along with the threats and opportunities it poses for wildlife, and its implications for wildlife management (Chapter 1), and how this issue affects the management and conservation of flying-foxes (Chapter 2).

In Chapter 3, I present results on the foraging habitat preferences of 98 *P. poliocephalus* satellite tracked across the East coast of New South Wales over up to five years and compare the results where individuals roosted in major-, minor- and non-urban areas. The findings indicated clear differences in major-urban and non-urban foraging landscape utilisation and highlighted the overwhelming importance of human-modified landscapes for *P. poliocephalus* foraging, particularly when individuals roosted in major-urban areas. The findings also suggest that individuals foraged on a different suite of foraging resources when they roosted in major-urban habitat. Chapter 3 was accepted for publication in the journal PLoS ONE on the 19th October 2021.*

In Chapter 4, I report on *P. poliocephalus* preferences for foraging in certain urban land-use categories in the Adelaide region and identify the food plant species visited by foraging individuals. I investigate flowering/fruitle phenology records for each food plant species identified in the preferentially visited land-use categories, to determine whether the food resources available in the Adelaide region collectively, could provide food for *P. poliocephalus* year-round. The findings demonstrated that residential areas are important

foraging areas for the species, and that tracked individuals foraged on a range of locally indigenous, non-indigenous Australian native and non-Australian species that could collectively provide food resources for this species year-round.

In Chapter 5, I present a summary of the results and place my research into the broader context of human-wildlife conflict management and species conservation. I offer potential applications for my research in conservation management of *P. poliocephalus*, and address considerations for future research in this area.

All of the data chapters presented in my thesis were written by me as the primary author, with helpful input from my supervisory panel and Dr John Martin. Tom Hibburt and Dr Wayne Boardman were additional co-authors for the research presented in Chapter 4. Satellite tracking data (Chapter 3), and GPS data (Chapter 4) were previously collected by the supervisory team. Supervisor Dr Jessica Meade assisted greatly with the spatial analyses in Chapter 3. As each data chapter was written as it will appear in a publication, I have retained the use of the collective pronoun throughout.

All references in this thesis have been formatted according to the guidelines for submission to the journal: *Frontiers in Ecology and Evolution*.

* Yabsley, S.H., Meade, J., Martin, J., and Welbergen, J.A. (2021). Human-modified landscapes provide key foraging areas for a threatened flying-mammal: the grey-headed flying-fox. *PLoS ONE*.16(11), e0259395. doi: 10.1371/journal.pone.0259395.

Chapter 3: Human-modified landscapes provide key foraging areas for a threatened flying mammal: the grey-headed flying-fox

3.1 Abstract

Urban expansion is a major threat to natural ecosystems but also creates novel opportunities that adaptable species can exploit. The grey-headed flying-fox (*Pteropus poliocephalus*) is a threatened, highly mobile species of bat that is increasingly found in human-dominated landscapes, leading to many management and conservation challenges. Flying-fox urbanisation is thought to be a result of diminishing natural foraging habitat or increasing urban food resources, or both. However, little is known about landscape utilisation of flying-foxes in human-modified areas, and how this may differ in natural areas. Here we examine positional data from 98 satellite-tracked *P. poliocephalus* for up to 5 years in urban and non-urban environments, in relation to vegetation data and published indices of foraging habitat quality. Our findings indicate that human-modified foraging landscapes sustain a large proportion of the *P. poliocephalus* population year-round. When individuals roosted in non-urban and minor-urban areas, they relied primarily on wet and dry sclerophyll forest, forested wetlands, and rainforest for foraging, and preferentially visited foraging habitat designated as high-quality. However, our results highlight the importance of human-modified foraging habitats throughout the species' range, and particularly for individuals that roosted in major-urban environments. The exact plant species that exist in human-modified habitats are largely undocumented; however, where this information was available, foraging by *P. poliocephalus* was associated with different dominant plant species depending on whether individuals

roosted in ‘urban’ or ‘non-urban’ areas. Overall, our results demonstrate clear differences in urban- and non-urban landscape utilisation by foraging *P. poliocephalus*. However, further research is needed to understand the exact foraging resources used, particularly in human-modified habitats, and hence what attracts flying-foxes to urban areas. Such information could be used to modify the urban foraging landscape, to assist long-term habitat management programs aimed at minimising human-wildlife conflict and maximising resource availability within and outside of urban environments.

3.2 Introduction

Urbanisation and urban expansion are major threats to ecosystems and the services they provide (Marzluff and Ewing, 2001; Shochat et al., 2010; Jung and Threlfall, 2016), due to habitat loss (McKinney, 2002; McDonald et al., 2008) and fragmentation (Marzluff and Ewing, 2001), loss of biodiversity (McKinney, 2002; Sol et al., 2014), and species extinction (Marlow, 1958; McKinney, 2006). While urban growth poses ongoing threats to natural ecosystems, it can also provide new habitats, such as parks and gardens, that provide opportunities for exploitation by adaptable species (McKinney, 2002; Callaghan et al., 2019b). Wildlife urbanisation can be driven by a range of ‘push’ and ‘pull’ factors. Loss of natural habitat and the resulting limitation of resources can ‘push’ animals to search for alternative resting and foraging habitat in urban environments (see Baruch-Mordo et al., 2014). Alternatively, adaptable species can be attracted to urban landscapes by novel food sources (Parris and Hazell, 2005), reduced predation pressure (Eötvös et al., 2018), and lowered interspecific competition for resources (Lill, 2009). However, while the presence of wildlife in urban areas can be perceived as beneficial to human physical and psychological well-being (Fuller et al., 2007; Carrus et al., 2015; Soulsbury and White, 2015), the growing urban human-wildlife interface can result in increased human-wildlife conflict and so poses wildlife management challenges. Understanding what supports the persistence of wildlife in

human-modified landscapes is thus fundamental to developing effective management responses.

In recent years, flying-foxes (*Pteropus* spp.) have become increasingly common in urban areas in Australia (Williams et al., 2006; Plowright et al., 2011; Tait et al., 2014; McCarthy et al., 2021; Timmiss et al., 2021). Traditionally roosts were occupied seasonally, likely reflecting the availability of floral resources in the surrounding landscape (Nelson, 1965). However, many urban roosts are now occupied year-round (Plowright et al., 2011). Flying-fox urbanisation has been hypothesised to be a result of loss of native habitat and urban expansion (Hall and Richards, 2000; Markus and Hall, 2004), and increases in the availability (Markus and Hall, 2004; Williams et al., 2006; Plowright et al., 2011) and temporal stability of urban food resources (Parry-Jones and Augee, 2001; Markus and Hall, 2004; McDonald-Madden et al., 2005; Williams et al., 2006; Plowright et al., 2011) due to planting of native and exotic trees (Gilbert, 2012; Boardman et al., 2021).

Flying-foxes are of critical ecological importance (Aziz et al., 2021) delivering long distance pollination and seed dispersal services that maintain the health and diversity of native habitats, connect forest fragments, and aid in forest regeneration (Fujita and Tuttle, 1991; Trakhtenbrot et al., 2005). Despite this, their presence in urban landscapes has become a prominent management issue (West, 2002; Roberts et al., 2011; Kung et al., 2015). Urban human versus flying-fox conflicts arise from concerns around transfer of zoonotic diseases (Philbey et al., 2008), noise, smell, and faeces (Kung et al., 2015), depredation of fruit crops including backyard fruit trees (Aziz et al., 2016; Oleksy et al., 2018; Tollington et al., 2019), and the defoliation of roosting trees (Vardon et al., 1997). Current management strategies include the removal of roosting trees, dispersal of flying-foxes from their roosts by means of smoke and noise (Roberts et al., 2011; Currey et al., 2018), and even culling (Divljan et al.,

2011; Olival, 2016). However, these methods have had limited success and often inadvertently exacerbate the human-wildlife conflict they aim to resolve. For example, forced dispersals of roosting flying-foxes can lead to the formation of splinter colonies and so proliferate the human-wildlife conflict throughout human communities (Roberts et al., 2011; Roberts et al., 2021) and the stress induced by roost dispersal may increase the prevalence of zoonotic disease and the risk of spillover events (Edson et al., 2015). Culling by direct shooting also raises particular animal welfare concerns, as shooting often results in injuries that cause long-term suffering, and can leave dependent young of shot mothers to die of starvation (e.g. Divljan et al., 2011). Besides raising animal welfare issues, culling of flying-foxes also fails to mitigate drivers of human versus flying-fox conflict including fruit crop predation (e.g. Florens and Baider, 2019). Understanding what foraging resources support flying-foxes in human-modified landscapes throughout time and space will thus help managers make informed decisions regarding humane conflict mitigation and conservation of these ecologically important species.

The grey-headed flying-fox (*Pteropus poliocephalus*) is one of four mainland flying-fox species native to Australia, and is listed as Vulnerable under the IUCN Red List (IUCN, 2021) and Australia's federal legislation (Threatened Species Scientific Committee, 2001). Like other flying-foxes in Australia and elsewhere, this species has become increasingly urbanised (Williams et al., 2006; Plowright et al., 2011; Boardman et al., 2021), and this exposes the species to human-wildlife conflict (Roberts et al., 2011; Currey et al., 2018), along with other anthropogenic threats such as electrocution on power lines and entanglement in fruit tree netting (Tidemann and Nelson, 2011; Scheelings and Frith, 2015; Mo et al., 2020b; Tella et al., 2020). Recent research has indicated that urban roosting *P. poliocephalus* exhibit higher roost fidelity and have shorter foraging distances than where they roost in non-urban habitat, supporting the hypothesis that urban areas provide more favourable foraging

conditions than non-urban areas (Meade et al., 2021). However, at present little is known about how *P. poliocephalus* use the urban landscape for foraging, including how they use foraging sites across time and space, and the composition of their diet in urban areas. As such, we do not know what supports flying-fox urbanisation, which poses serious impediments for the management and conservation of this threatened species (Australian Government, 2021). To investigate whether *P. poliocephalus* foraging landscape utilisation differs between urban and non-urban landscapes, we used satellite tracking data for 98 individuals tracked throughout New South Wales (NSW), Australia, for up to five years. In particular, we examined the foraging preferences of urban and non-urban roosting *P. poliocephalus* according to vegetation type and the likely tree species that foraging individuals visited, and according to a published index of flying-fox foraging habitat quality. We discuss our findings in the context of the management of flying-fox urbanisation.

3.3 Methods

3.3.1 Capture and deployment of transmitters

Pteropus poliocephalus were captured at the Royal Botanic Garden roost (33.8642°S, 151.2166°E), in Sydney, New South Wales (NSW), Australia from 9th-18th May 2012. Capture was conducted pre-dawn as *P. poliocephalus* returned to the roost, using mist nets (12 m x 4.8 m; mesh size 20 mm) suspended by two 15 m aluminum poles. Caught individuals were restrained and untangled immediately after capture. Captured individuals were assessed for sex, age, and body condition, and then placed into individual pillowcases suspended from horizontal poles, for processing that morning. Upon processing, detailed body measurements were taken, and 49 male and 50 female *P. poliocephalus* with no injury/illness and weighing ≥ 650 g were anaesthetised using the inhalation agent Isoflurane (Jonsson et al., 2004) and then fitted with transmitters. The transmitter package consisted of a collar-mounted solar satellite transmitter, attached to a neoprene-lined leather collar, and

fastened by a rivet. Microwave Telemetry 9.5 g transmitters were deployed on females and GeoTrak 12 g transmitters were deployed on males (Welbergen et al., 2020; Meade et al., 2021). The total combined mass of the collar and transmitter was < 15 g which corresponded to < 3 % of the body mass of the lightest individual in the sample (n = 98). Individuals were released at the capture site upon recovery, by midday, after being offered fruit juice for energy and hydration.

Transmitter duty cycles varied; the ‘on’ period was always set to 10 h, but the ‘off’ period was set to a range of values from 50 h to 254 h off, to maximise opportunities for solar recharge. During the ‘on’ periods, locational data was transmitted to orbiting NOAA satellites and sequentially received via ARGOS.

Fieldwork was approved and conducted under the Office of Environment and Heritage Animal Ethics Committee permit 110620/05 and Scientific License 100268.

3.3.2 Data handling and analysis

This study analysed *P. poliocephalus* satellite tracking data collected between 9th May 2012 - 27th April 2017 in NSW. Data were subsetted such that of 100,463 data points, all 51,585 high quality ARGOS location data classes 2 and 3 were initially retained. Positional fixes of these classes are estimated to be accurate to within 250 m and 500 m of the true location, respectively (McKeown and Westcott, 2012). To investigate foraging locations, following Meade et al., (2021), we selected all positional fixes collected during the 10 h ‘on’ periods for which both daytime and night-time location data were available. The daytime fix allowed the roosting colony to be identified, and the night-time fix furthest from the roost site was selected as the assumed foraging location. This resulted in 5,118 paired roosting and foraging locations. Next, we excluded all paired locations (n = 52) where their distance was greater than 50 km, as 99% of foraging takes place within 50 km from a roost (Eby, 1991; Field et

al., 2016; Welbergen et al., 2020) so that greater distances likely represent movements between roosts. Recent research suggests that *P. poliocephalus* individuals travel directly to a foraging site early in the night and then undertake smaller movements between foraging sites before returning to the roost (Boardman et al., 2021). Thus, while we cannot be certain that these locations are ‘foraging locations’ it is likely that the location furthest from the roost site in a night is in an area that an individual was foraging. Finally, we subsetting the data to those animals foraging in NSW to allow for comparison with available data layers (below), resulting in 4,198 paired roosting and foraging locations for 98 of the 99 tracked individuals in this study area.

Data layers: Land-use categories were extracted for each of the foraging locations in NSW (n = 4,198). For this we used a shapefile of Urban Centre and Locality data obtained from the Australian Bureau of Statistics (Australian Bureau of Statistics, 2011b), to classify NSW into three land-use categories. Land was defined as ‘of urban character’ based on dwelling density and population density (Australian Bureau of Statistics, 2011a). ‘Major-urban’ areas were defined as urban centers with a population of > 100,000 (Australian Bureau of Statistics, 2011a). ‘Other-urban’ areas were urban centers with a population of between 1,000 and 99,999 (Australian Bureau of Statistics, 2011a). All other areas were defined as ‘non-urban’. For ease of interpretation, we refer to the ‘other-urban’ land-use category as ‘minor-urban’ throughout.

Vegetation types were extracted for each of the foraging locations in NSW (n = 4,198). For this we used the Vegetation Formations and Classes of NSW (version 3.03 - 200 m Raster) to classify vegetation type in NSW to 16 core classes (Keith and Simpson, 2012). The raster was created and published in 2012 and is thus concurrent with our tracking data. In the Vegetation Formations and Classes of NSW, ‘cleared land’ is defined as land that is not

structurally intact native vegetation (Keith and Simpson, 2008). Thus, cleared land comprises human-modified land including agriculture, parks, gardens, and tree-lined streets. Cleared land may also include small remnant patches of native vegetation up to 2 hectares. For clarity, we refer to ‘cleared land’ as ‘human-modified land’ henceforth.

Flying-fox foraging habitat quality ranks from Eby and Law (2008) were available for 3,757 of the $n = 4,198$ foraging locations in NSW. These habitat quality ranks are based on a complex algorithm incorporating the spatial availability of known *P. poliocephalus* blossom food plant species and indices of productivity and nectar flow, as well as species richness scores of fruit food plant species (Eby and Law, 2008). Here, habitat quality was ranked from 1 (high quality) to 4 (poor quality), and areas were ranked as 0 if neither the dominant nor subdominant species were known *P. poliocephalus* food plant species. We extracted likely food plant species from vegetation shapefiles from Eby and Law (2008). These vegetation shapefiles only contained food plant species in the blossom diet of *P. poliocephalus*, as insufficient data were available on the productivity and reliability of food plant species in the fruit diet (Eby and Law, 2008). Eby and Law’s diet plant list comprised 59 species in the blossom diet including species from the Myrtaceae, Proteaceae, Arecaceae, Fabaceae, and Pittosporaceae families. Only dominant and sub-dominant species (Keith, 2002) were considered resulting in a list of 55 species (see Table 4.1 in Eby and Law, 2008). Habitat quality rank data were split into bi-months to account for seasonal variations in flowering phenology of the food plant species (Eby and Law, 2008); December-January, February-March, April-May, June-July, August-September, October-November. Where more than one dominant or sub-dominant food plant species was available in the bi-month that a foraging fix was recorded, the species that flowered most often and that was most abundant was selected as the most likely food plant species (Eby and Law, 2008). We used a shapefile of *P.*

poliocephalus' range (Currey et al., 2018) and of NSW (Runfola et al., 2020) to clip all data layers.

Analysis: Preliminary analyses revealed that the proportion of foraging fixes in each vegetation type did not differ significantly between study years (the cut-off between years was May 9th as this is when catching began) (Friedman $\chi^2 = 6.79$, df = 4, p = 0.147), bi-month (Friedman $\chi^2 = 2.19$, df = 5, p = 0.823), or between sexes (Friedman $\chi^2 = 0.818$, df = 1, p = 0.366). Similarly, the proportion of foraging fixes in each habitat quality rank did not differ significantly between years (Friedman $\chi^2 = 2.40$, df = 4, p = 0.663), between bi-months (Friedman $\chi^2 = 5.00$, df = 5, p = 0.416), or between sexes (Friedman $\chi^2 = 1.80$, df = 1, p = 0.180). Therefore, the data were analysed as a whole.

To examine whether *P. poliocephalus* exhibited preferences for certain foraging habitats we compared the proportion of foraging fixes in each vegetation type to the proportion that would be expected based on the area of each vegetation type available in *P. poliocephalus*' range inside NSW, using a chi-squared test for given probabilities. To examine whether flying-foxes have a preference for high quality foraging habitat (i.e. ranks 1 and 2; Eby and Law, 2008), this process was repeated for the areas in which a habitat quality rank was available (see Figure 6.7 in Eby and Law, 2008).

Finally, non-urban roosting locations varied in their distance from the nearest urban polygon (Appendix 1). To test for an effect of distance to urban polygons on the relative frequencies of different vegetation types visited by foraging animals, we performed multinomial logistic regression using the 'multinom' function from the R package 'nnet' (Ripley and Venables, 2016).

All analyses were performed in the R environment for statistical computing (R Core Team, 2017).

3.4 Results

Overall, 4,198 foraging fixes were identified from 98 *P. poliocephalus* individuals that roosted at 263 unique roosts within NSW over a period of up to five years. Of the 263 unique roosts, 31 (11.8%) occurred in NSW's major-urban areas, 37 (14.1%) in minor-urban areas, and 195 (74.1%) were located in non-urban areas (Figure 3.1). Of the 98 tracked individuals, 46 roosted in all three land-use categories during their tracking periods (see Appendix 2 for further details).

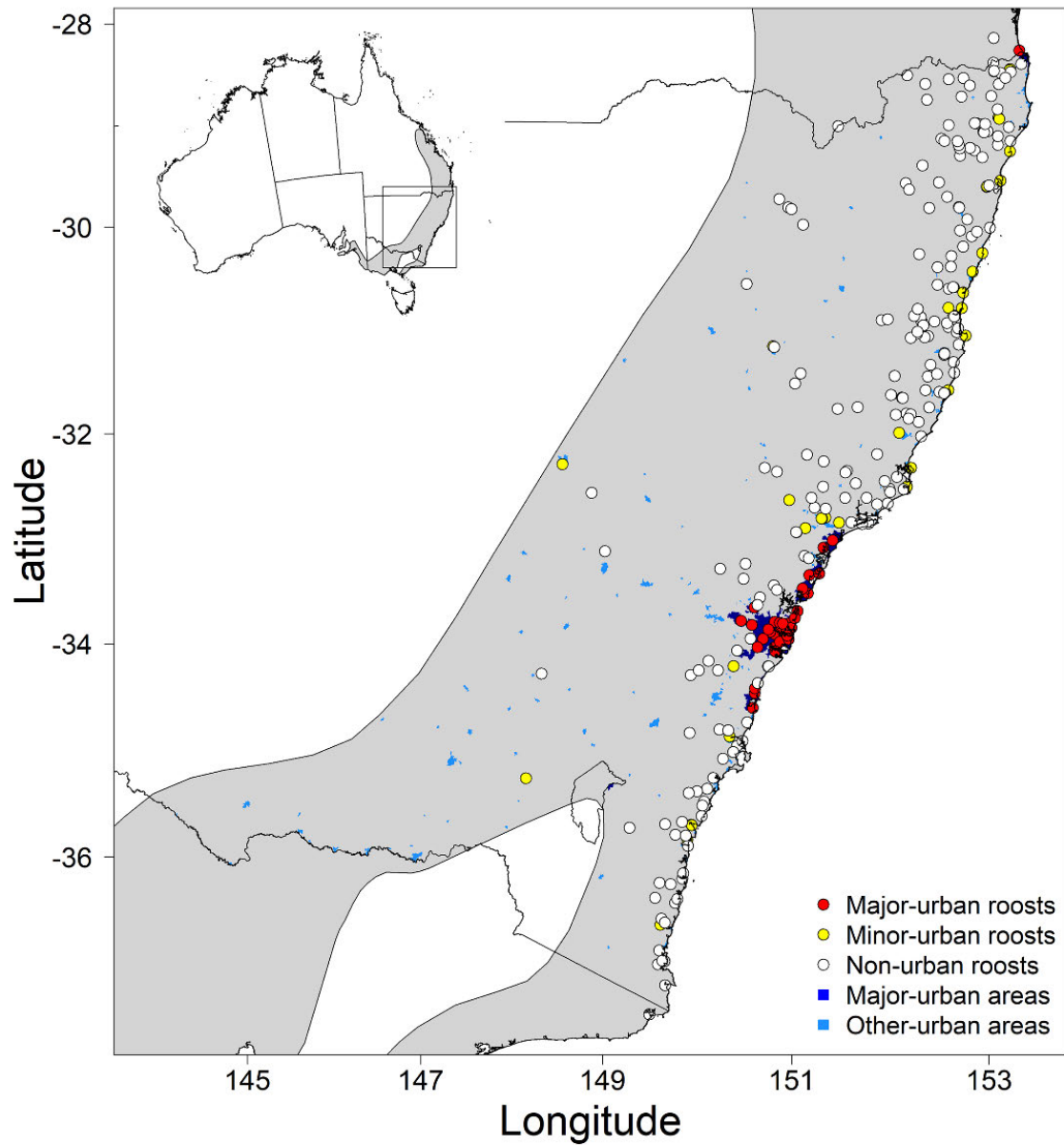


Figure 3.1 Map of *P. poliocephalus* roost sites. Red points indicate the location of roosts in major-urban areas, yellow dots indicate roosts in minor-urban areas, and white dots indicate roosts in non-urban areas. Major-urban areas are indicated by dark blue shading, minor-urban areas are indicated by mid-blue shading. Lines indicate State boundaries. Shaded grey area shows *P. poliocephalus*' range in Australia. Inset, map of Australia with box indicating area used in this study.

3.4.1 Vegetation type preferences

The spatial distribution of foraging fixes ($n = 4,198$) was significantly different to the proportion that would be expected based on the areal extent of available vegetation types overall ($\chi^2 = 1401$, $df = 15$, $p < 0.001$), indicating that individuals preferentially visited certain vegetation types over others (Appendix 3).

The majority of foraging fixes occurred in human-modified land (56%), which was similar to the proportion of human-modified land within *P. poliocephalus*' range in NSW (58%). Tracked individuals exhibited a preference for wet sclerophyll forests (grassy subformation), since this made up 15% of all foraging fixes despite only covering 5% of the study area. However, when foraging locations were divided up based on the land-use category of where the animals were roosting [major-urban: $n = 1,988$ (47.6%); minor-urban: $n = 974$ (23.2%); and non-urban: $n = 1,236$ (29.4%)], the results revealed stark differences between the land-use categories of roosting locations. When roosting in non-urban and minor-urban areas, individuals foraged less in human-modified land than would be expected based on areal availability (26% and 38% of foraging fixes, respectively, vs 58% of area available in NSW; Figure 3.2A-C) and showed a preference for wet sclerophyll forests (grassy subformation) (both 28% of foraging fixes vs 5% of area available in NSW; Figure 3.2A-C). In contrast, when roosting in major-urban areas individuals foraged overwhelmingly in human-modified areas (83% of foraging fixes vs 58% of area available in NSW; Figure 3.2D).

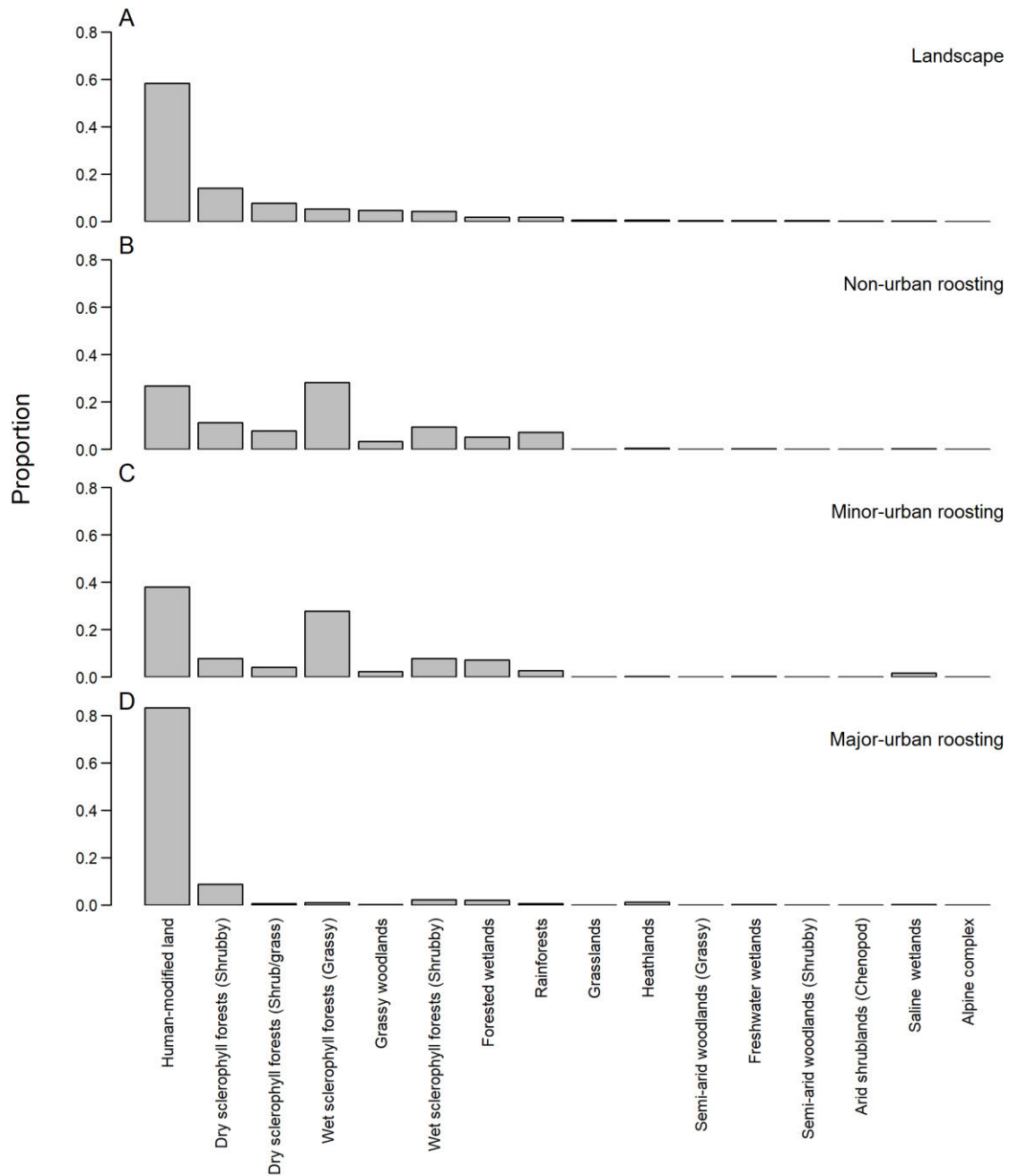


Figure 3.2 Vegetation class preferences. The proportion of (A) each vegetation class in the study area, and (B) of positional fixes ($n = 1,236$) recorded from *P. poliocephalus* roosting in non-urban colonies in each vegetation class, (C) of positional fixes ($n = 974$) recorded from *P. poliocephalus* roosting in minor-urban colonies in each vegetation class, (D) of positional fixes ($n = 1,988$) recorded from *P. poliocephalus* roosting in major-urban colonies in each vegetation class.

We found an effect of distance to the nearest urban polygon on the relative frequency of the vegetation types visited by foraging individuals (AIC of 11988.1 vs AIC of 12538.2 for null model, evidence ratio >1000). As the distance to urban polygons increased, the proportion of human-modified land visited decreased (Figure 3.3A), and the proportion of rainforest area visited increased (Figure 3.3F). The proportion of several vegetation types visited remained consistently low, irrespective of distance to the nearest urban polygon (Figure 3.3D and 3.3E). The proportion of visits to the four types of sclerophyll forests peaked when roost sites were 15-40 km from the nearest urban polygon (Figure 3.3B, C, G, and H) (see Appendix 4 for more details).

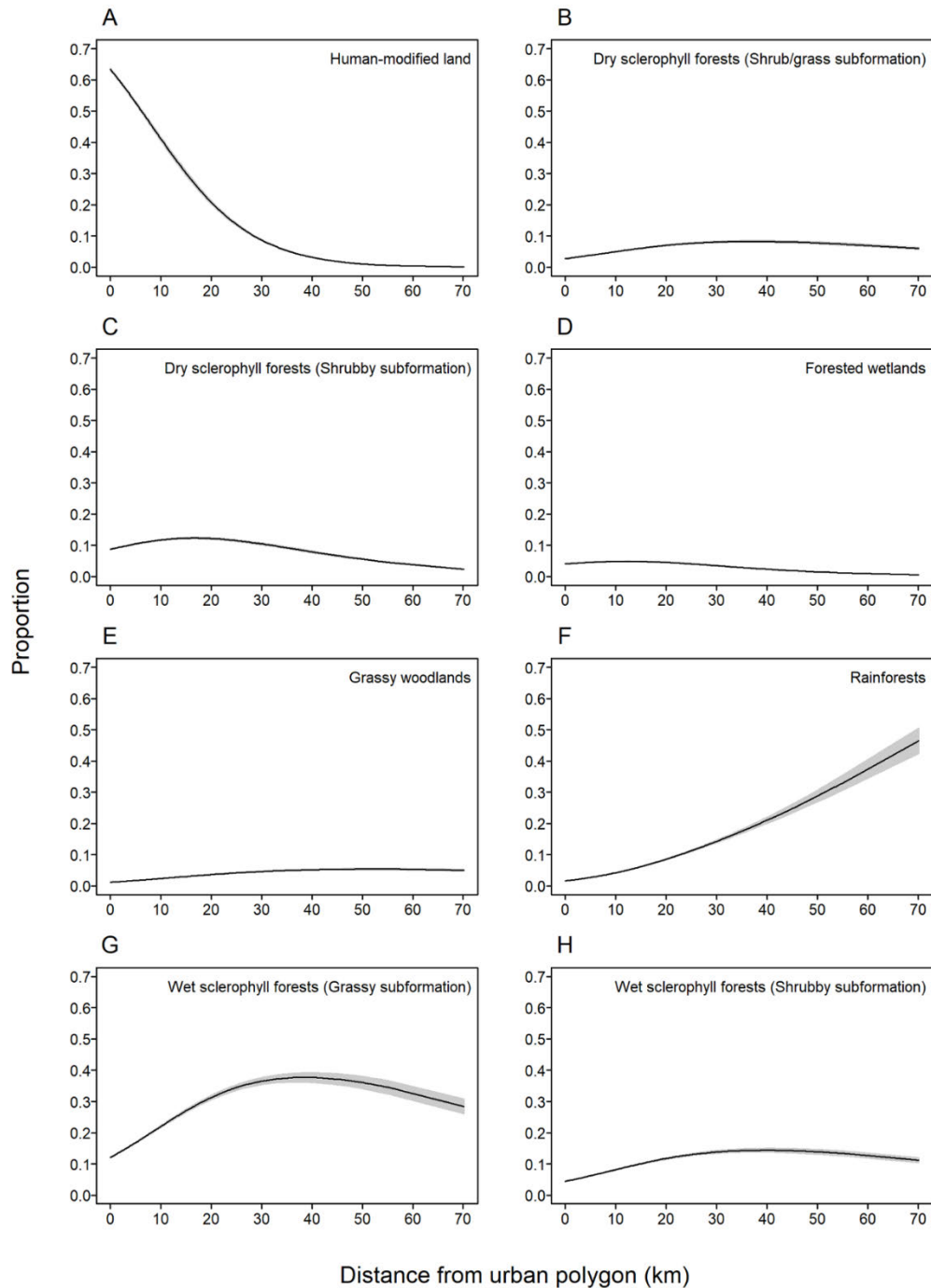


Figure 3.3 Predicted changes in vegetation class preferences with distance from urban areas. The predicted change in proportion of vegetation types visited by foraging *P. poliocephalus* roosting at non-urban colonies as the distance from the roost site to the nearest urban polygon increases. Predictions are taken from a multinomial logistic regression model. Grey polygons indicate 95% confidence intervals. Vegetation types that made up <1% of foraging fixes were excluded from the graph.

3.4.2 Habitat quality rank preferences

The spatial distribution of foraging fixes for which habitat quality ranks were available ($n = 3,757$) was significantly different to the proportion that would be expected based on the areal extent of these habitats ($\chi^2 = 381.1$, $df = 4$, $p < 0.001$; Appendix 5); the main difference being that a greater than expected proportion of foraging fixes occurred in areas where the recorded dominant and subdominant plant species were not part of the *P. poliocephalus* diet. However, when foraging locations were divided up based on the land-use category of where the animals were roosting, results revealed stark differences between land-use categories of roosting locations: individuals roosting in non-urban and minor-urban areas visited a greater proportion of high-quality habitat (rank 1) than was available in the landscape (Figure 3.4A-C; 49% & 48% respectively vs 29% for the sampled area), whereas the vast majority (83%) of foraging fixes of major-urban roosting individuals were in areas where the recorded dominant and subdominant plant species are not part of the *P. poliocephalus* diet (rank 0) (Figure 3.4D).

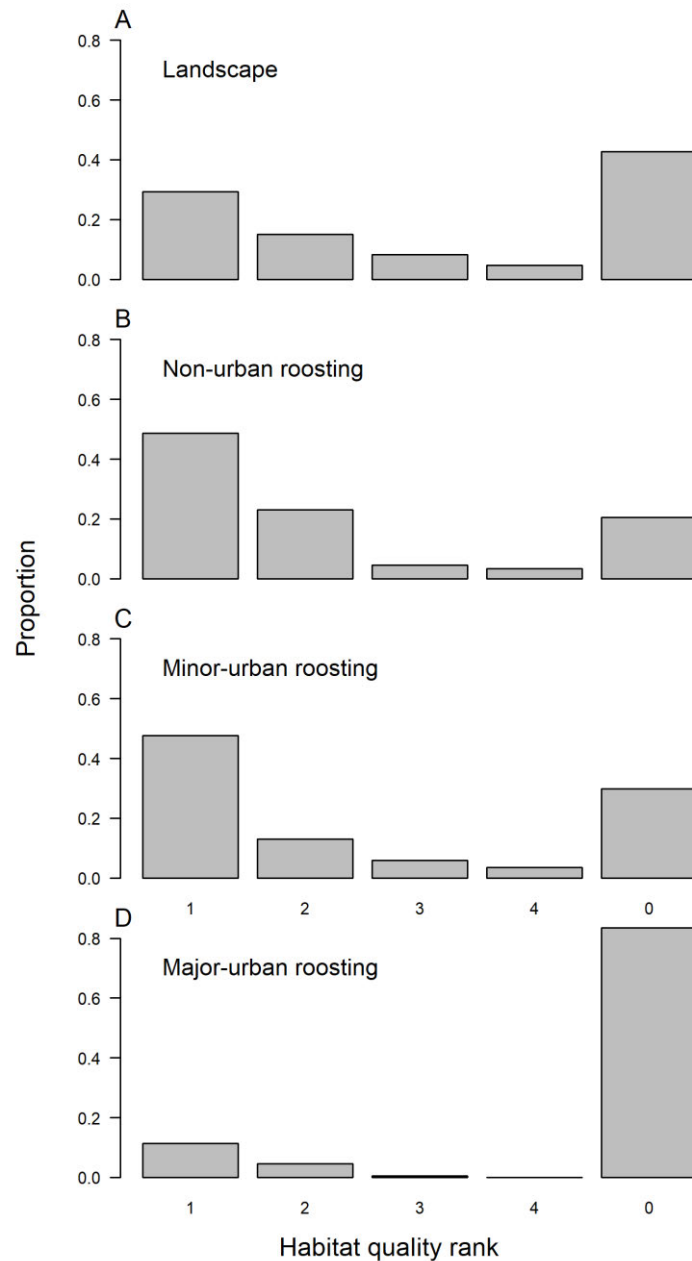


Figure 3.4 Habitat quality preferences. The proportion of (A) each habitat quality rank in the sampled area, (B) of positional fixes ($n = 1031$) recorded from *P. poliocephalus* roosting in non-urban colonies in each habitat quality rank, (C) of positional fixes ($n = 770$) recorded from *P. poliocephalus* roosting in minor-urban colonies in each habitat quality rank, and (D) of positional fixes ($n = 1956$) recorded from *P. poliocephalus* roosting in major-urban colonies in each habitat quality rank. Habitat quality was ranked from 1-4: where rank 1 is good quality foraging habitat, rank 4 is poor quality foraging habitat, and rank 0 is habitat where the recorded dominant and subdominant plant species are not known to be part of the *P. poliocephalus* diet.

3.4.3 Food plant species

We used Eby and Law's (2008) habitat layers to extract likely native, dominant and sub-dominant *P. poliocephalus* food plant species for each foraging fix that was in the sampled area ($n = 3,757$). Of these, 71% were in areas where the dominant and subdominant plant species recorded flowering in the bi-month that the forage fix was observed, were not part of the *P. poliocephalus* diet (major-urban roosting: $n = 1,811$; minor-urban roosting: $n = 376$; non-urban roosting: $n = 471$). Thus, Eby and Law (2008)'s data are limited in urban, particularly major-urban areas.

Examining the food plant species in more detail, tracked individuals appeared to exploit similar plant species when roosting in non-urban and minor-urban habitats (Figure 3.5, Appendix 6 and 7) but different plant species when roosting in major-urban areas (Figure 3.5 and Appendix 6-8). Individuals roosting in major-urban areas foraged on a greater proportion of *Corymbia gummifera*, *Eucalyptus piperita*, and considerably less on *C. maculata* overall, than when roosting in non-urban and minor-urban habitats (Figure 3.5 and Appendix 6-8). However, note that overall, sample sizes were relatively small as only 145 (7%), 394 (51%), and 560 (54%) foraging fixes from major-urban, minor-urban, and non-urban roosting flying-foxes could be assigned a likely food plant species, respectively (Figure 3.5 and Appendix 6-8).

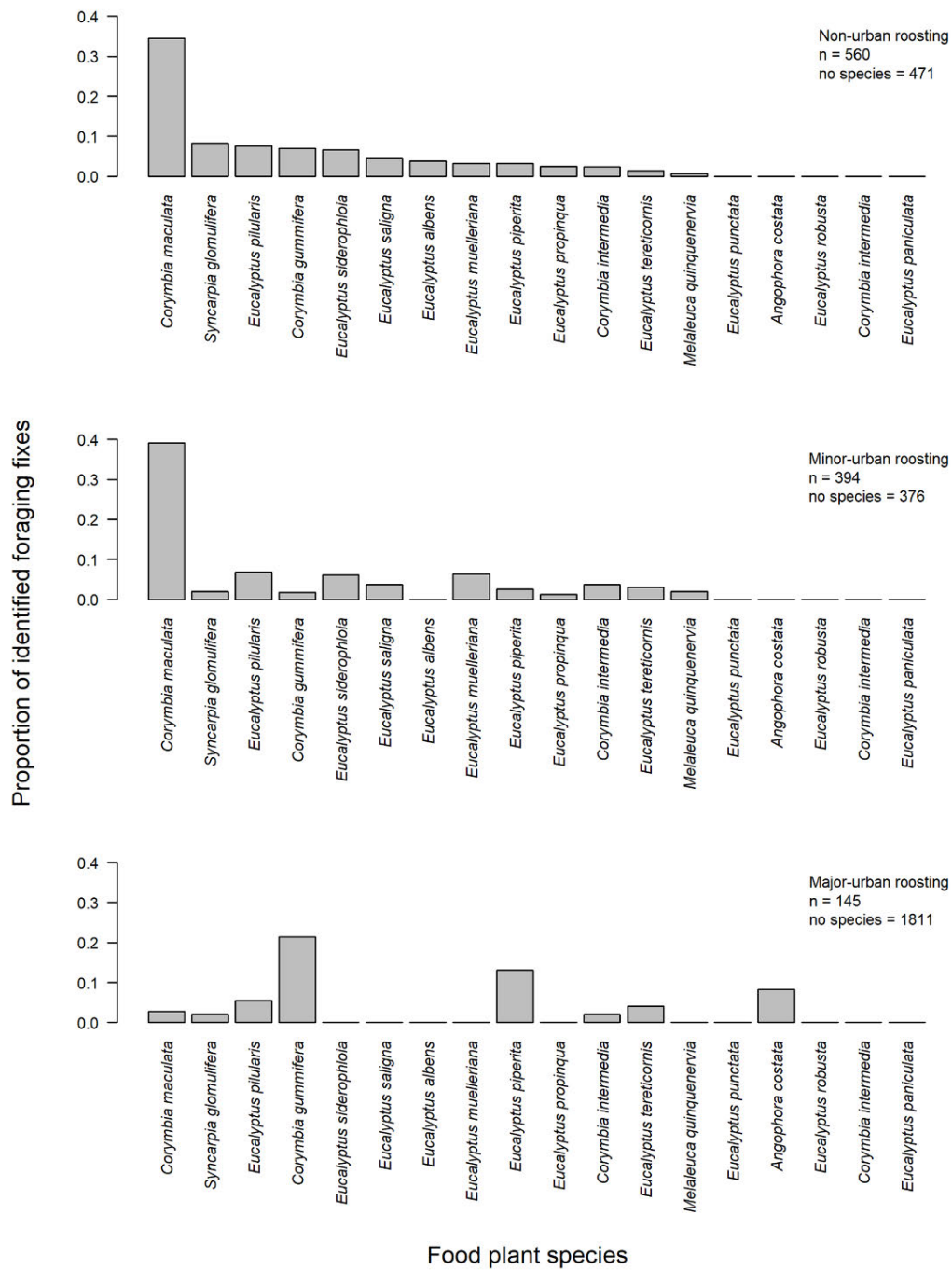


Figure 3.5 Likely food plant species. The identified likely food plant species overall when *P. poliocephalus* roosted in non-urban, minor-urban and major-urban areas. A maximum of 18 different food plant species were included in each graph. n = the number of foraging fixes used to calculate proportions. ‘No species’ indicate additional fixes for the particular bi-month that fell in the sampled area, but for which the recorded dominant and subdominant plant species were not known to be part of the *P. poliocephalus* diet.

The top three likely food plant species assigned to foraging fixes where individuals roosted in non-urban habitat during each bi-month included *E. pilularis* (n = 24, 0.273), *E. piperita* (n = 15; 0.170), and *C. gummifera* (n = 8; 0.091) in December-January; *C. gummifera* (n = 31, 0.223), *E. saligna* (n = 20, 0.144) and *E. muelleriana* (n = 17, 0.122) in February-March, *C. maculata* (n = 57, 0.838); *E. grandis* (n = 6, 0.088) and *E. robusta* (n = 3, 0.044), in April-May; *C. maculata* (n = 63, 0.851), *E. albens* (n = 5, 0.068) and *E. pilularis* (n = 4, 0.054) in June-July; *C. maculata* (n = 67, 0.583), *E. siderophloia* (n = 19, 0.165) and *E. albens* (n = 16, 0.139) in August-September; and *Syncarpia glomulifera* (n = 40, 0.526), *E. siderophloia* (n = 15, 0.197) and *E. planchoniana* (n = 6, 0.079) in October-November (Appendix 6).

The top three likely food plant species assigned to foraging fixes where individuals roosted in minor-urban habitat during each bi-month included *E. paniculata* (n = 20, 0.189), *E. pilularis* (n = 16, 0.151), and *E. muelleriana* (n = 11, 0.104) in December-January; *E. muelleriana* (n = 14, 0.222), *E. paniculata* (n = 10, 0.159), and *E. pilularis* (n = 8, 0.127) in February-March; *C. maculata* (n = 46, 0.807), *Melaleuca quinquenervia* (n = 4, 0.070), and *E. pilularis* (n = 3, 0.053) in April-May; *C. maculata* (n = 87, 0.926), *E. tereticornis* (n = 4, 0.043), and *M. quinquenervia* (n = 3, 0.032) in June-July; *C. maculata* (n = 21, 0.538), *E. siderophloia* (n = 12, 0.308), and *S. glomulifera* (n = 3, 0.077) in August-September; and *E. paniculata* (n = 10, 0.286), *E. siderophloia* (n = 8, 0.229), and *E. tereticornis* (n = 6, 0.171) in October-November (Appendix 7).

The top three likely food plant species where individuals roosted in major urban habitat in each bi-month included *E. punctata* (n = 13, 0.464), *E. piperita* (n = 6, 0.214) and *E. pilularis* (n = 5, 0.179) in December-January; *C. gummifera* (n = 30, 0.380), *E. punctata* (n = 30, 0.380), and *E. piperita* (n = 13, 0.165) in February-March; *E. robusta* (n = 5, 0.556) and

C. maculata (n = 4, 0.444) in April-May, *E. robusta* (n = 5, 1) in June-July; *E. paniculata* (n = 3, 0.75) and *E. tereticornis* (n = 1, 0.25) in August-September; and *Angophora costata* (n = 12, 0.6), *E. tereticornis* (n = 5, 0.25), and *Syncarpia glomulifera* (n = 3, 0.15) in October-November (Appendix 8).

3.5 Discussion

We used a large satellite tracking dataset of 98 individual *P. poliocephalus* over up to 5 years to examine foraging landscape utilisation for animals roosting across 263 roosts in urban and non-urban areas in NSW. The findings demonstrate clear differences in urban- and non-urban landscape utilisation in foraging *P. poliocephalus* individuals, and indicate that human-modified landscapes, including agriculture, parks, gardens, tree-lined streetscapes, and remnant patches of native vegetation, provide important foraging resources for the species, particularly in major-urban areas.

Individuals roosting in non-urban and minor-urban areas visited similar vegetation types, comprising mainly of wet and dry sclerophyll forests, forested wetlands, and rainforest (Figure 3.2), and preferred high-quality foraging habitat (Figure 3.4), in line with known natural foraging preferences of the species (Parry-Jones and Augee, 1991b; Eby, 1998; Eby and Law, 2008). However, while non-urban and minor-urban roosting flying-foxes foraged less in human-modified land than would be expected based on areal availability, human-modified land still encompassed 26% and 38% of their foraging fixes, respectively (Figure 3.2), albeit the relative contribution of human-modified lands for foraging individuals diminished with distance of their roosts to the nearest urban polygon (Figure 3.3). Thus, while the landscape utilisation of non-urban and minor-urban roosting individuals aligned well with the known natural foraging ecology of the species, our findings also highlight the

importance of human-modified foraging areas for individuals roosting outside major-urban areas.

Human-modified foraging landscapes were particularly important for flying-foxes roosting in major-urban areas, with an overwhelming majority of their foraging fixes occurring in human-modified areas. A large proportion of these foraging fixes occurred in habitat rank 0; habitat where the vegetation comprised neither dominant nor subdominant listed *P. poliocephalus* food plant species. For the list of known food plant species used in this study we used the data provided by (Eby and Law, 2008) that includes only native species that *P. poliocephalus* have been recorded feeding on from field observations and/or identified through faecal analysis. However, non-dominant species available in rank 0 habitats may include species on the *P. poliocephalus* diet list, and/or include non-endemic or exotic food plant species of which we currently do not know the importance to the *P. poliocephalus* diet. In addition, in the data provided by (Eby and Law, 2008), food plant species in the fruit diet of *P. poliocephalus* are underrepresented because i) these almost exclusively existed in rainforest which made up just 2% of the study area, and ii) there was insufficient data on the phenology of food plants in the fruit diet of *P. poliocephalus* (Eby and Law, 2008). Nevertheless, previous studies from Melbourne (McDonald-Madden et al., 2005) and Adelaide (Boardman et al., 2021) suggest that *P. poliocephalus* forages on the blossom and fruit of a mixture of native and non-endemic plant genera growing in streetscapes, parks, and gardens, and it has been hypothesised that historical increases in the spatiotemporal availability of these foraging resources have facilitated the expansion of the species into urban areas (Williams et al., 2006). This is supported by recent findings that while *P. poliocephalus* individuals exhibit extreme mobility among roosts throughout the species' range (Welbergen et al., 2020), and forage over shorter distances when roosting in major-urban areas (Meade et al., 2021), implying that urban roosting flying-foxes are

supported by a more stable and abundant supply of local foraging resources. Of the 263 unique roosts visited in our present study, only 11.8% were classified as major-urban (Figure 3.1), yet these were associated with 47.6% of all foraging fixes of which 83% were in human-modified areas (Figure 3.2). Therefore, these results highlight the importance of both urban roosts and associated human-modified foraging areas for supporting a large yet dynamic proportion of the threatened *P. poliocephalus* population.

Though limited, the available data on likely forage species in this study suggested that individuals foraged on different plant species when roosting in major-urban areas versus when roosting in minor-urban and non-urban areas (Figure 3.5). Our results may simply reflect the different plant resources available to this generalist species in urban centers compared to more natural habitat; however, it could also reflect a greater availability of urban nectar, pollen and/or fruit resources due to more regular and intense flowering. Australian plants are notorious for their irregular flowering, some with intervals of up to several years (Law et al., 2000). Interestingly, 60% of the most likely forage species assigned to flying-foxes roosting in major-urban areas during October-November was *A. costata*, while this species was not associated with foraging individuals that roosted outside of major-urban areas. Previous research found that *A. costata* only flowered within street habitats and did not flower at all in remnant and open forests, however this was a short-term study with a small sample size (Davis et al., 2016). The authors proposed, in support with the wider literature (Neil and Wu, 2006), that the urban heat island effect may be responsible for these differences in urban and non-urban phenologies. Other factors associated with urban environments, including higher soil moisture and soils containing higher phosphorus and nitrogen levels as a result of urban runoff of fertilisers and stormwater (Davis et al., 2016) and increased water availability (Hawkins et al., 2018) could affect growth and flowering of urban trees and so increase the spatiotemporal availability of food for flying-foxes in urban

areas (Parris and Hazell, 2005; Williams et al., 2006). However, further research is needed to understand how and why the urban foraging landscape differs from that in non-urban environments, to help explain what attracts flying-foxes to urban areas.

Our results suggest that *P. poliocephalus* may not be attracted to minor-urban roosts because of the availability of urban foraging resources, as foraging landscape utilisation of individuals roosting in minor-urban and natural areas was similar (Figure 3.2). It is possible that minor-urban roosts instead provide more protection from predators (DeStefano and DeGraaf, 2003), including white-bellied sea eagles (*Haliaeetus leucogaster*), wedge-tailed eagles (*Aquila audax*), and powerful owls (*Ninox strenua*). Alternatively, *P. poliocephalus* may roost in small towns due to climate effects (Cai et al., 2018), or proximity to water (Spotswood et al., 2021). It is also possible that minor-urban areas may provide some navigational benefit due to landmarks or lighting (e.g. Boardman et al., 2021). Finally, perhaps roosting in smaller towns is merely an incidental by-product of a learnt association between urban development and increased foraging success experienced by individuals that also forage in major-urban areas. At present, however, the reasons why flying-foxes roost in smaller towns remain unclear (Timmiss et al., 2021) and requires further investigation.

The reliance of *P. poliocephalus* on human-modified areas may have important negative implications for this threatened species. Animals including flying-foxes may be attracted to the increased foraging resource availability in major-urban areas; however, such habitats may act as ‘ecological traps’ (Hale and Swearer, 2016). Major-urban areas present a range of challenges to *P. poliocephalus* including human-wildlife conflict (Currey et al., 2018; Lentini and Welbergen, 2019), and other anthropogenic threats such as electrocution on power lines and entanglement in fruit tree netting in gardens (Tidemann and Nelson, 2011; Scheelings and Frith, 2015; Mo et al., 2020b; Tella et al., 2020). In addition, increasing

frequency and severity of extreme heat events in Australia has caused mass mortality of flying-foxes due to hyperthermia (Welbergen et al., 2008), and urban colonies may be more exposed to the effects of these events due to the urban heat island effect (Khan et al., 2020). Foraging in human-modified land outside of major-urban areas also exposes the species to anthropogenic threats, including increased conflict with fruit growers (Ratcliffe, 1932; Aziz et al., 2016) that can result in culling (Dickman and Fleming, 2002; Divljan et al., 2011), and entanglement in commercial fruit netting and barbed-wire fences (Tidemann and Nelson, 2011; Scheelings and Frith, 2015; Mo et al., 2020b). Flying-foxes have a low natural reproductive ability (McIlwee and Martin, 2002), which renders them particularly vulnerable to population declines from such anthropogenic threats, especially those operating at landscape-scales. Yet, there has been little scope for flying-foxes to adapt to these novel challenges, particularly as flying-fox urbanisation as a biological phenomenon has only been occurring over the last two decades or so (Tait et al., 2014), comprising approximately three flying-fox generations (Divljan et al., 2006). Future research should quantify the impacts on *P. poliocephalus* particularly of threats associated with human-modified landscapes, to inform both conservation management and human-wildlife conflict mitigation.

Further research is clearly needed to identify the exact foraging resources that support flying-foxes, particularly in major-urban areas. High resolution GPS tracking is a good candidate for this since these data are accurate to the scale of an individual tree. In major-urban areas this would reveal which food plant species support the large urban flying-fox populations, and elucidate whether urban populations are supported mainly by exotic trees or by native species that are able to flower or fruit more abundantly and/or for longer due to favourable urban growing conditions (Hawkins et al., 2018). In addition, it could provide targets for government-subsidised exotic tree removal, to minimise foraging in conflict zones and help reduce anthropogenic risks to flying-foxes. However, while exotic tree removal is

considered an effective measure for reducing local human versus flying-fox conflict (Mo et al., 2020a), it would raise serious concerns for the *P. poliocephalus* population as a whole, as it could result in an overall reduction in the foraging resource base for this species, unless local tree removal is offset by targeted plantings of forage trees in natural areas. Clearly, sound, long-term conservation management of *P. poliocephalus* needs to be predicated on better knowledge of its foraging landscape utilisation, to enable more holistic, coordinated habitat management programs that focus on redirecting flying-fox foraging away from urban conflict areas whilst enhancing and restoring resource availability elsewhere for this vulnerable species.

Chapter 4: Grey-headed flying-foxes (*Pteropus poliocephalus*) exhibit greater dietary breadth when feeding within versus outside of urban environments

4.1 Abstract

Flying-foxes are becoming increasingly urbanised, and this is thought to be a result of diminishing natural food resources, increased availability and temporal stability of urban food resources, or a combination of both. Previous research has shown that grey-headed flying-foxes (*Pteropus poliocephalus*) preferentially rely on human-dominated landscapes for foraging when they roost in major-urban areas, and suggests that they feed on different dominant plant species when they roost in major-urban areas versus non-urban areas. However, the plant species that exist in urban areas are largely unsurveyed, and hence the food resources that support flying-foxes in urban areas remains unknown. We used paired GPS and accelerometer data from 9 tracked *P. poliocephalus* roosting at Adelaide Botanic Park, South Australia (SA), between December 2019 and May 2020, to investigate landscape utilisation and identify the exact food plant species visited by individuals in different land-use categories. We found that *P. poliocephalus* have a clear preference for feeding in residential areas, and along linear landscape features including roads. In these land-use categories, tracked individuals visited a high diversity of food resources including species that are locally indigenous (endemic to SA), non-indigenous Australian native (non-endemic to SA but endemic to Australia), and non-Australian (non-endemic to Australia). When combined with information on flowering and fruiting phenology, this strongly suggests that urban environments exhibit greater temporal stability of food resources than surrounding more-natural environments. While we did not actively investigate historical plantings of food resources in cities, the spatiotemporal availability and stability of urban food resources has likely increased in Australian cities over the past few decades as a result of changes in

anthropogenic plantings; planting Australian natives including Eucalypts in urban areas has become popular since the 1970s (Yau, 1982) and these trees will have since matured and likely provide increased flowering than during their immature stages (e.g. Wilson, 2002), in addition to the common use of locally non-indigenous and non-Australian species in urban areas, urban areas likely provide abundant food for flying-foxes throughout the year (Williams et al., 2006). In combination with our findings, this provides support for the hypothesis that increased spatiotemporal availability of food resources, at least in part, has facilitated the increasing prevalence of flying-foxes in urban areas.

4.2 Introduction

Understanding why animals exist where they do, and how and why they move through the habitats they occupy is fundamental to the field of ecology (Ehrlén and Morris, 2015).

Researching animal movement patterns can help us understand interspecies interactions in time and space, and the ecological role a species plays in the ecosystem they inhabit (Jacoby and Freeman, 2016). The study of animal movement can allow us to determine how animals respond to challenges such as habitat fragmentation, and study and model how a species' biogeographic distribution may change in response to environmental or landscape challenges such as climate change and urbanisation (Ancillotto et al., 2016a). Studying the drivers of animal movement in response to such challenges is essential for the development of effective conservation strategies.

Urbanisation is one of the most detrimental processes to organisms and the ecosystem services they provide (McKinney, 2002; Grimm et al., 2008), because it results in the replacement of natural habitat with concrete and buildings interspersed by human-modified 'greenspaces' such as parks and gardens, and the fragmentation of existing natural habitat patches (Marzluff and Ewing, 2001). While urban greenspaces provide novel habitats for adaptable wildlife, they are often distributed patchily throughout the urban landscape

(Callaghan et al., 2019a), making it difficult for poorly mobile species to exploit (Öckinger et al., 2010; Concepción et al., 2015; Jung and Threlfall, 2018). Additionally, urban clearing promotes the establishment of disturbance tolerant, ‘weedy’ non-native plants, and these processes influence the biotic homogenisation of urban habitat (McKinney, 2002). However, the occurrence of remnant native trees and the active planting of aesthetically pleasing non-indigenous Australian native and non-Australian species in urban greenspaces (Kendal et al., 2012), can provide a wide range of foraging opportunities for highly mobile nectivorous and frugivorous species including birds (e.g. Evans et al., 2012) and bats (e.g. Meade et al., 2021). Increased temperatures associated with the urban heat island effect (Magee et al., 1999), artificial watering systems and the use of fertilisers may enhance the growth and productivity of urban plants (Williams et al., 2003; Neil and Wu, 2006; Davis et al., 2016; Zhao et al., 2016). Taken together, the planting of non-indigenous and non-Australian species as well as increased local temperatures, supplemental watering and fertilisation in urban areas may result in more temporally reliable food supplies in urban areas. Urban greenspaces can therefore attract adaptable species, often exhibiting generalist diets (Callaghan et al., 2019b) and high mobility (Öckinger et al., 2010). Thus, urbanisation can influence changes in the distribution of species; however, there is often little empirical understanding of the factors that drive such distributional changes. Gaining sufficient understanding of the ecological drivers of wildlife urbanisation is critical to balance conservation, and to manage potential urban human-wildlife conflicts.

In Australia, flying-fox (*Pteropus* spp.) movement patterns are changing as a response to urbanisation, they are more likely to roost near urban settlements than expected by chance (Tait et al., 2014); preferentially visit urban roosts; and stay longer in urban roosts than in natural areas (Meade et al., 2021). The documented increase in flying-fox urbanisation has exacerbated human-wildlife conflict, largely surrounding a fear of zoonotic disease

transmission (Kung et al., 2015) and loss of social amenity as a result of objectionable noise and smell (Currey et al., 2018). Such conflict has often resulted in imbalanced management approaches, including vegetation removal and flying-fox dispersal; however, these techniques often have limited success in conflict reduction (Roberts et al., 2011; Roberts et al., 2012; Roberts and Eby, 2013; Roberts et al., 2021), due to the highly mobile, nomadic behaviour of these species (Welbergen et al., 2020). In addition, the spectacled flying-fox (*Pteropus conspicillatus*) is currently listed as an endangered species and the grey-headed flying-fox (*P. poliocephalus*) is listed as vulnerable, under federal legislation (Threatened Species Scientific Committee, 2001; 2019) and the IUCN Red List of Threatened Species (IUCN, 2021). The listing of these species as threatened with extinction further complicates management actions as strategies must balance human-wildlife conflict mitigation with conservation support for these species. Furthermore, flying-foxes provide essential ecosystem services, maintaining the health and diversity of native forests through long distance pollination and seed dispersal (Fujita and Tuttle, 1991; Aziz et al., 2021). In order to develop strategies that support the conservation of flying-fox species, the ecosystems they service, and reduce urban conflicts with humans, it is important to understand the underlying drivers of flying-fox urbanisation (Meade et al., 2021; Yabsley et al., 2021).

Flying-foxes are highly mobile, nomadic species that commute long distances (Welbergen et al., 2020), likely in response to the availability of floral resources (Eby, 1991; Parry-Jones and Augee, 1992). Flying-foxes forage during the night and rest during the day in communal arboreal roosts (Hall and Richards, 2000) that exist as a network of highly connected ‘staging posts’ throughout their range (Welbergen et al., 2020). In Australia, roosts were traditionally occupied on a seasonal basis, a likely result of both climatic variables and the irregular, asynchronous flowering of many native diet species across space (Nelson, 1965). However, many urban flying-fox roosts are now occupied year-round, and multiple

new roosts have been established in urban areas (Plowright et al., 2011). For example, in 1986 a permanently occupied *P. poliocephalus* roost was established in Melbourne CBD, at the Royal Botanic Gardens (Aston, 1987; McDonald-Madden et al., 2005) and more recently, in 2011, this species has established a roost in Adelaide Botanic Park, an area well-outside their previously recorded range (Boardman et al., 2021).

The drivers behind flying-fox urbanisation are currently unknown; however, it has been hypothesised to be a response to the year-round availability and stability of urban food resources (Williams et al., 2006; Tait et al., 2014; Meade et al., 2021; Yabsley et al., 2021). In addition, habitat loss may increase the foraging distance required in natural habitats to access high energy food plant species, and hence urban food plant resources (where resources are presumed to be more plentiful) may be less energetically demanding (Páez et al., 2018). Preliminary research on the foraging habitat preferences of *P. poliocephalus* has indicated that individuals roosting in major-urban areas forage preferentially in human-modified landscapes, that may include agriculture, parks, gardens, tree-lined streets and small patches of remnant vegetation (Yabsley et al., 2021). The exact plant species that occur in human-modified landscapes are largely undocumented; however, where those data were available, the study suggested that *P. poliocephalus* utilises different food plant species when they roost in major-urban and non-urban areas. These findings suggest that an ‘attraction’ to urban food plant resources is likely a driving force for increasing flying-fox urbanisation (Yabsley et al., 2021). A study on food plant resource use of *P. poliocephalus* in Adelaide during spring, found that the most common foraging sites occurred in residential areas, and that common food plant species included species not indigenous to the region such as lemon-scented gum and Port Jackson fig (Boardman et al., 2021). These findings suggest that the urban plantings of non-indigenous species provide spatiotemporally stable food resources to *P. poliocephalus*. While there is little detailed documented information to indicate that the

spatiotemporal availability and stability of food plant resources has increased in Australian cities in recent decades, Australian native trees have become increasingly popular as candidates for street trees, and as a result, many locally indigenous and non-indigenous Australian native diet plant species (e.g., Eucalypts, Corymbias, and Angophoras of the Myrtaceae family) have been planted since the 1970's (Yau, 1982). These plants will have since matured, and as such have likely increased the availability of food to flying-foxes in urban areas as mature individuals produce more flowers, flower more frequently, and flower for longer than younger individuals (see Wilson, 2002). The increase in abundance of airborne Myrtaceous pollen in Melbourne since the 1960s indicates increasing flowering; this has been attributed to the maturation of planted eucalypts (Williams et al., 2006). In addition to pollen and nectar, the availability of fruit for flying-foxes has increased in urban areas with plantings of non-indigenous Australian native fruit-bearing trees including *Ficus macrophylla* and *Acmena smithii* in streets and parks, and the cultivation of non-Australian species such as apples, plums, and figs (Williams et al., 2006). Furthermore, plantings of non-indigenous Australian native and non-Australian species may increase the period of time food is available for flying-foxes roosting in urban areas as these species may flower or fruit at different times of the year compared to locally indigenous species (e.g., Williams et al., 2006), thus potentially extending the temporal availability of food. In combination, this suggests that the spatiotemporal availability and stability of urban food resources for flying-foxes has increased since the 1980s and this has likely supports their almost year-round persistence in many urban areas.

While it is now clear that human-modified landscapes support a large proportion of the *P. poliocephalus* population, and that it is likely a response to increased spatiotemporal availability and stability of urban food plant resources, we do not know exactly how *P. poliocephalus* utilise the urban foraging landscape, and in particular, the exact food plant

resources that support this species in cities and towns (Yabsley et al., 2021). This study aims to investigate whether *P. poliocephalus* exhibit a preference for feeding in certain urban land-use categories, and to identify the food plant species visited by *P. poliocephalus* residing at a recently established roost in Adelaide Botanic Park, South Australia, using paired GPS tracking and accelerometer data. We investigated flowering and fruiting phenology records to examine the timing and duration of availability of identified *P. poliocephalus* food plant species in the Adelaide region. We predicted that *P. poliocephalus* would preferentially feed on plants in highly urban areas including residential areas, and that food plant species in these habitats would comprise a wide range of locally indigenous, non-indigenous Australian native, and non-Australian species. We also predicted that flowering/fruiting phenology records would indicate that *P. poliocephalus* food plants collectively, provide year-round availability of food resources. We discuss our findings in the context of flying-fox conservation management.

4.3 Methods

4.3.1 Study area

The focal flying-fox roost used for this study (Adelaide Botanic Park; -34.916, 138.607) represents the furthest south-west documented colony of *P. poliocephalus*. The Adelaide Botanic Park colony was established in 2011, and the roost is now occupied year-round (Boardman et al., 2021).

Adelaide is an isolated city located in South Australia, bordered by a range of hills to the East and the Australian coastline to the west (Tait et al., 2005). Adelaide has a Mediterranean climate exhibiting cool, wet winters and hot, dry summers (Tait et al., 2005; Milazzo et al., 2016). The dominant land-use for the Adelaide region is cropping and pasture, followed closely by urban habitat (Tait et al., 2005). Other land-uses include remnant

vegetation, orchards, irrigated areas, water bodies, quarries, swamp, hardwood and pine plantations (Tait et al., 2005). Residential areas in the Adelaide region are largely characterised by front and back gardens; the metropolitan area has a range of parks and gardens that support a wide range of vegetation types; of locally indigenous, non-indigenous Australian native, and non-Australian species.

It is at present unclear what factors influenced the relatively recent *P. poliocephalus* colonisation of the Adelaide region, an area outside the former range for this species (Boardman et al., 2021). The Adelaide Botanic Park roost thus offers an ideal opportunity to investigate flying-fox urbanisation due to its locality within an urban centre, and the relative isolation of this roost with respect to other identified roost sites (Figure 4.1; National flying-fox monitoring program, Australian Government); making it more likely that individuals will stay at this roost site for extended periods of time, and that the resources within the Adelaide region exclusively support *P. poliocephalus* when they roost there.



Figure 4.1 The distribution of grey-headed flying-fox (*P. poliocephalus*) roosts in Australia. Image extracted from the National flying-fox monitoring viewer; Australian Government: Department of Agriculture, Water and the Environment. The size of the markers represents an estimate of colony size in terms of the number of individuals recorded there.

4.3.2 Capture and deployment of transmitters

Pteropus poliocephalus individuals were captured at the Adelaide Botanic Gardens between the 10th and 11th of December, 2019. Inbound flying-foxes were captured using two double banked mist nets (18m×5m and 12m×5m, 38mm mesh, Ecotone Telemetry, Poland) suspended 15 m high in the canopy of the colony. Nets were run on pulley systems that were continuously monitored by volunteers and 2 or 3 trained and immunised (Australian Bat Lyssavirus) researchers. Each flying-fox was removed from the net by researchers and

placed into a pillowcase that was suspended on a horizontal pole while other flying-foxes were captured. Females that were lactating, pregnant or carrying a pup were immediately released.

Captured individuals were transported to Adelaide Zoo where they were processed. Individuals were anaesthetised under 5% vaporised isoflurane via facemask and maintained at 2% isoflurane until processing was complete. While anaesthetised, morphometrics were taken and all bats were banded (ABBBS banding scheme; Dr. J. Martin, license number 9180). Ten *P. poliocephalus* (five adult males and five adult females) were fitted with a collar supporting a GPS and accelerometry unit (hereafter: transmitter) (CREX GPS Logger, Ecotone Telemetry, Poland). The five females had a mass of 724.8 ± 93.1 (568.0 - 806.0) and the five males had a body mass of 818.2 ± 127.0 (685.0 - 954.0). The transmitter and collar weighed 14.0 g and 4.0 g, respectively, giving a total weight of 18.0 g and representing no more than 5% of individual body mass. After animals recovered from the anesthesia, they were placed in animal holding facilities at the Adelaide Zoo for recovery. The $n = 5$ male flying-foxes required surgery to implant thermo-sensitive radio transmitters (SB-2T, 3.8 g, battery life: 5 months; Holohil) as part of another study (Walker et al., unpublished). Individuals that did not require surgery ($n = 5$ females) were released back into the colony within 6 hours of capture, and the $n = 5$ males that were surgically implanted with thermo-sensitive radio transmitters were released back into the colony the next morning following an assessment by a wildlife veterinarian (Dr Wayne Boardman).

4.3.3 Data collection

Accelerometer and GPS data were collected from December 13th, 2019 - May 23rd, 2020 (Austral Summer to Winter). Accelerometer data were recorded on 3 orthogonal axes and GPS data were collected as latitude and longitude fixes, and were used to identify fixes associated with feeding, as opposed to other behaviours such as flying (see below).

Transmitters were programmed to collect accelerometer data in 3 bursts types: 12 sec at 5 Hz every 15 mins, 2 sec at 30 Hz every 30 mins, and 3 sec at 10 Hz every 30 mins depending on battery voltage (solar recharge). The transmitters are capable of recording GPS data every 15 minutes when fully charged, and short bursts of up to 1 minute every 1 hour via GPRS, with an accuracy of <5 m. In this study, duty cycles were highly variable; transmitters were set to recorded GPS data via GPRS every 30 minutes during the night when there was sufficient solar recharge (GPS data collection was linked with accelerometer data collection). The duty cycles of the transmitters were monitored and changed remotely via Global System for Mobile (GSM) network using the web-panel depending upon the solar recharge of the batteries. Transmitters were set to ECO mode for the duration of the study, whereby 80% of the fixes were within 20 m of the true position of the flying-fox.

Data were collected via an Ultra High Frequency (UHF) link to 3G enabled mobile phone towers that then reported the data to a File Transfer Protocol (FTP) server, accessed through the NGA Analyser GPS data processing software package (Ecotone Telemetry, Poland).

Some of the collared individuals left the Adelaide region (defined as ≥ 75 km from the center of the Adelaide Botanic Garden roost) during our study (Table 4.1). Individual FFOX05 left Adelaide before the transmitter began collecting data and hence her data was excluded from analyses herein ($n = 5$ males and 4 females). Individual FFOX02 left Adelaide on the 18th January, 2020, and returned on the 2nd April, 2020. Individual FFOX07 and FFOX09 left Adelaide on the 31st December, 2019, and the 19th March, 2020, respectively, and did not return to the region for the duration of the study. We removed GPS fixes associated with travel outside of the Adelaide region, by calculating the distance from the colony and GPS fix using the 'distHaversine' function from the 'geosphere' package in R. GPS fixes less than 500 m from the center of the colony were removed as flying-foxes are

known to return to the colony to rest (and may not forage there) during the night. GPS fixes greater than 75 km from the colony were also removed to account for any travel between roosts. GPS fixes recorded on the day of departure or day of arrival were also excluded as food resources at these sites were likely supporting the individual's journey rather than their stay in Adelaide.

Table 4.1 The number of *P. poliocephalus* feeding fixes, and the duration each transmitter recorded GPS and accelerometer data for each individual (n = 9). Individual FFOX05 left the study area (within a 75 km radius from the center of the Adelaide Botanic Park roost; -34.916, 138.607) before the transmitter began collecting data and hence this individual produced no usable data.

ID	Date of first fix	Date of last fix	Duration (days)	N fixes
Female				N = 392
FFOX01	15/12/2019	27/03/2020	104	150
FFOX02	18/12/2019	21/04/2020	126	68
FFOX03	22/12/2019	23/05/2020	154	70
FFOX04	16/12/2019	28/04/2020	135	104
FFOX05	NA	NA	NA	NA
Male				N = 97
FFOX06	20/12/2019	12/02/2020	55	28
FFOX07	21/12/2019	26/12/2019	6	14
FFOX08	21/12/2019	23/12/2019	3	3
FFOX09	21/12/2019	15/03/2020	86	46
FFOX010	20/12/2019	25/01/2020	37	6
Total				489

4.3.4 Data sub-setting

Feeding activity was assigned according to activity derived from acceleration forces. To determine each level of activity, we applied a principal components analysis (PCA) to the 3 axes of acceleration in order to maximise the amount of variation caused by movement that is expressed in a single vector (i.e. principal component 1 = 0.4). We did this using the 'prcomp' function from the 'stats' package in R. A PCA was run partly to account for variation among individuals in the spatial orientation of the transmitter, which could have influenced the distribution of acceleration forces caused by activities across the 3 axes. The standard deviations (SD) of the PC1 scores of each burst for each individual were plotted as a histogram to identify peaks and troughs in the data. Three peaks were identified in this first histogram which were broadly interpreted as levels of low, moderate, and high activity. We calculated an interpeak frequency minimum (IPFM) between the second and third peak; data above IPFM-1 was assigned 'high activity', and data below IPFM-1 was assigned 'other'. We ran a second PCA on the 'other' data (PC1 = 0.4), and created a second histogram of SD; this histogram contained two peaks. We calculated IPFM-2; data above IPFM-2 was assigned 'moderate activity', and data below IPFM-2 was assigned as 'low activity'. We inferred that high activity pertains to flight, moderate activity pertains to moderate tree-based movements including feeding (i.e. the behaviour of eating a dietary component and any associated movement within a foraging tree), and low activity pertains to minimal tree-based movement such as rest.

4.3.5 Identifying feeding fixes

Date-time stamps associated with assigned levels of activity were rounded to the nearest second. We then aligned the closest activity date-time stamps to the GPS date-time stamp. To minimise the possibility of misinterpreting the level of activity at each GPS coordinate, we calculated the time discrepancy between each pair of activity and GPS data, using the

‘difftime’ function from the ‘lubridate’ package in R. We subsetting the data to include data pairs that were within a +/- 60 sec discrepancy buffer. We used the ‘suncalc’ package in R to calculate local sunrise and sunset times and define night (after sunset and before sunrise); to increase the certainty that we were capturing feeding behaviour and not roosting behaviour, we subsetting paired activity and GPS data for the moderate level of activity during the night only. Data sub-setting was carried out by Melissa Walker in R v. 3.6.1.

4.3.6 Identifying food plant species

Fixes pertaining to moderate levels of activity at night were read into Google Earth Pro. To further discriminate feeding fixes from non-feeding fixes, we checked the location of fixes in Google Earth Pro and removed fixes that were not within trees (where flying-foxes feed) (n = 489).

A random subset of the total 489 feeding fixes was generated (n = 325) and the GPS location of each feeding fixes was visited in person by Thomas Hibburt (Student, University of Adelaide; n = 125), and author SY (n = 200). Where fixes were within private property, we attempted to obtain permission for access. However, 35 food plants were inaccessible due to dangerous terrain, restricted access due to water catchment areas and/or we unable to obtain access to private property (Appendix 9). Of the 35 inaccessible food plants, 60% were in residential areas, 20% in reserves, 9% in agricultural areas, 6% in mining and road/river areas, and 3% in utilities (Appendix 9). Thus, exclusion of these fixes from the dataset is unlikely to bias the results.

For each tree that the flying-foxes visited for which we had access (n = 290), photographs were captured, and samples of bark, leaves, buds, flowers and fruit were taken where possible to aid in species identification. Author SY used an Olympus EM5 MkII with Panasonic 100-400mm telephoto lens to obtain close-up photographs of plant characteristics,

particularly where samples were unable to be obtained (see Figure 4.2). Where samples could be obtained, they were photographed next to a ruler so that size estimates could be made. Tree characteristics including details on the bark, leaves, buds, fruits and inflorescences were recorded for each tree following the EUCLID key and an attempt at identifying the species was made using tree identification guides (Nicolle, 2013; Centre for Australian National Biodiversity Research, 2015; Brooker and Kleinig, 2016; Lucid, 2016). South Australian eucalypt expert Dr Dean Nicolle provided confirmations on each food plant species from photographs and detailed field notes. Of the 290 food plants photographed, 22 were of poor quality and thus could not be confidently identified. Additionally, 3 of the food plants were surveyed by both author SY and TH; for each of the duplicated food plants, the set of highest quality images were used to in the identification process. Therefore, a total of $n = 265$ food plants were identified.

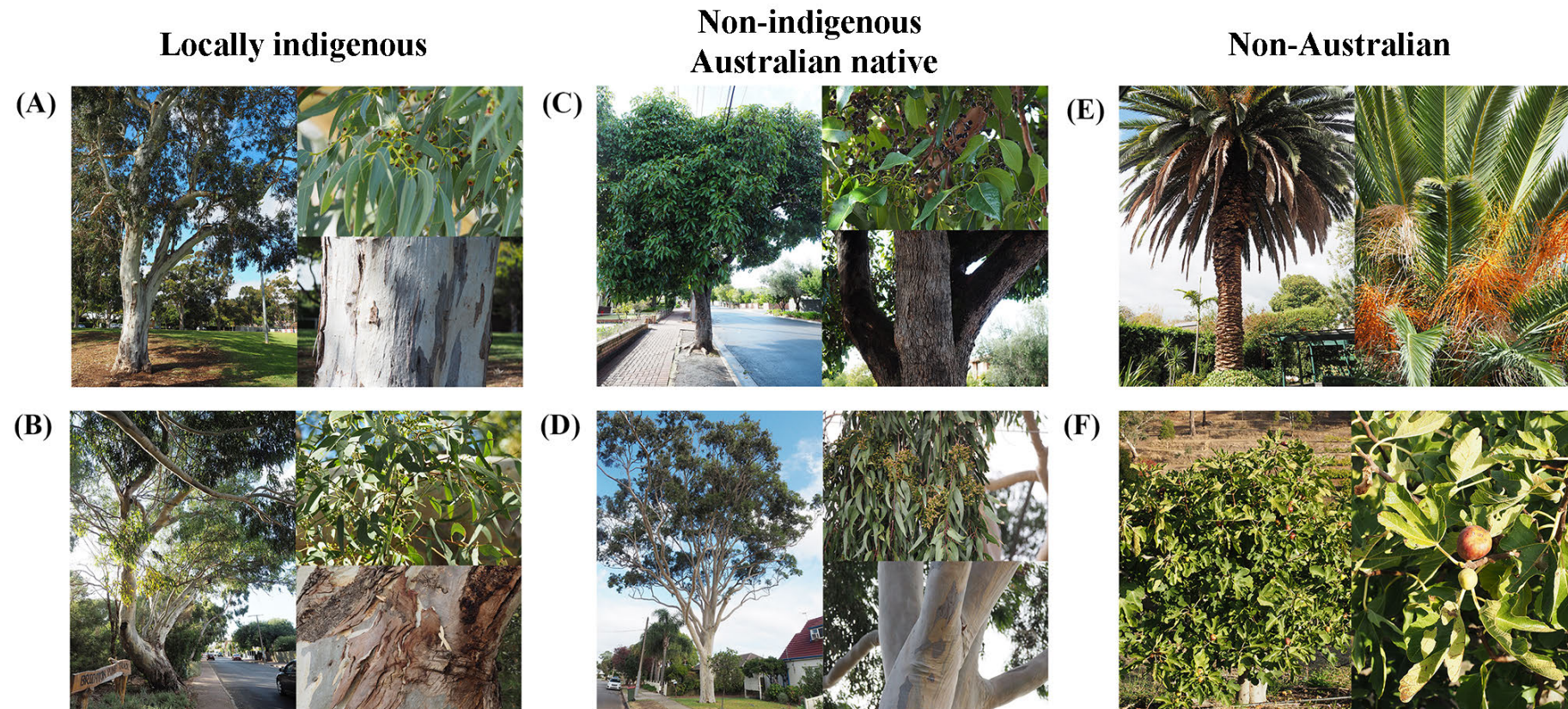


Figure 4.2 Example photographs taken of locally indigenous, non-indigenous Australian native (non-endemic to South Australia but endemic to Australia), and non-Australian food plant species visited by $n = 9$ GPS tracked *P. poliocephalus* roosting in Adelaide, South Australia. A) *Eucalyptus leucoxylon*, B) *E. camaldulensis*, C) *Lophostemon confertus*, D) *Corymbia citriodora*, E) *Phoenix canariensis*, and F) *Ficus carica*.

4.3.7 Data analysis

All analyses were performed in the R environment for statistical computing (R Core Team, 2017).

Land-use data layers: To investigate whether *P. poliocephalus* exhibited a preference for feeding in certain urban land-use categories, we used the South Australian Government’s “Generalised Land Use 2020” shapefile of the land-use categories of South Australia (Government of South Government of South Australia, 2020). Land-use classes were grouped into 10 categories; primary production (i.e. areas that are used for agriculture, horticulture, forestry, and livestock), residential area (i.e. urban and rural residential, hotel/motel accommodation, and institutional accommodation), reserve (i.e. national park, median strips, and road reserves), vacant (i.e. urban and non-urban vacant land, and steep/rocky land), utilities (i.e. gas, electricity, water/sewage/waste disposal, public transportation, and telecommunications), institution (i.e. government, and education), mining (i.e. mines, open workings, wells, and quarries), recreation (i.e. ovals, golf courses, camping grounds, and stadiums), commercial (i.e. wholesale trade, retail, and finance), and industrial (i.e. food manufacture). The shapefile has gaps between polygons that pertain to linear landscape features including roads and rivers and thus, we assigned these areas a new land-use category called ‘road/river’.

The shapefile was clipped by a circle with a 75 km radius (as flying-fox GPS fixes beyond 75 km in the present study were excluded; Figure 4.3), and a geoBoundaries shapefile of Australia (Runfola et al., 2020), using the function ‘st_buffer’ in the R package ‘st’, to obtain the total area where *P. poliocephalus* foraging could have occurred.



Figure 4.3 Study area; the Adelaide region. Feeding fixes are represented by yellow markers. All feeding fixes are 500m - 75km from the center of the roost; -34.916, 138.607, depicted by the red circle. Image created in ArcGIS.

Land-use categories were then extracted for the total $n = 489$ feeding fixes in the study area. The areal extent of each land-use category within the study area was then calculated. To calculate the area pertaining to the 'road/river' land-use category, the sum of the area of all the land-use categories was subtracted from the clipped study area.

Feeding habitat preferences: To examine whether *P. poliocephalus* exhibited a preference for feeding in certain land-use classes, we compared the proportion of feeding fixes in each land-

use category to the proportion that would be expected based on the area of each land-use category in the study area, using a Chi squared test for given probabilities.

Identifying food plant species visited by P. poliocephalus: The food plant species visited by *P. poliocephalus* in each land-use category was then examined, for the n = 265 subsample. We then assessed whether each tree species was locally indigenous (endemic to South Australia), non-indigenous Australian native (non-endemic to South Australia but endemic to Australia) or non-Australian (non-endemic to Australia). Herein, we refer use the terms ‘locally indigenous’, ‘non-indigenous Australian native’, or ‘non-Australian’ to describe the geographic origin of each food plant species. Geographic origin was assessed by studying the native distribution of species in identification guides (Nicolle, 2013; Centre for Australian National Biodiversity Research, 2015; Brooker and Kleinig, 2016; Lucid, 2016).

Plant species flowering/fruiting phenologies: Phenology tables were constructed by compiling flowering and fruiting data collected from a range of published articles, online databases, and apiary flowering records (Australian Native Plants Society; Botanic Gardens of South Australia; Brisbane City Council; Innis, 1989; Burgess and Griffin, 1991; Parry-Jones and Augee, 1991b; Sallabanks, 1992; Gilman and Watson, 1993; Song and Bangerth, 1996; Somerville, 1999; Gleadow and Woodrow, 2000; Law et al., 2000; Brien and Hardy, 2002; McDonald et al., 2003; Ryan et al., 2003; Starr et al., 2003a; b; Paton et al., 2004; Birtchnell and Gibson, 2006; Stover et al., 2007; Eby and Law, 2008; Jia et al., 2008; Scariot and Gullino, 2008; Culley and Hardiman, 2009; Edwards, 2012; Guitton et al., 2012; Nicolle, 2013; Centre for Australian National Biodiversity Research, 2015; Mo and Waterhouse, 2015; Brooker and Kleinig, 2016; Lucid, 2016; Upadhaya et al., 2018; Walther et al., 2018; Prakash et al., 2019; Spennemann, 2019; Fichtner and Wissemann, 2021; Flora of North America Association, 2021; The Royal Horticultural Society, 2021). Where records from the Northern Hemisphere were used, flowering/fruiting phenology was standardised by stating

which season flowering was recorded (Table 4.2). Where data were available, the peak time of flowering/fruitle, duration of flowering/fruitle in months, and annual reliability of flowering/fruitle, were recorded and standardised. For example, Eby and Law 2008 express annual reliability as the proportion of years in which flowering occurs, while other papers express annual reliability as the number of years between flowering events (e.g. Law et al., 2000). To standardise these records, where data were given as a percentage of years where flowering occurs, they were expressed as a proportion of years that flowering occurred, and where records were expressed as the number of years between flowering, the proportion was calculated by dividing 1 by the number of years between flowering events. For example, where flowering occurred once every 2 years, the proportion was calculated: $1 / 2 = 0.5$.

4.4 Results

4.4.1 Land-use preferences

The spatial distribution of feeding fixes ($n = 489$) was significantly different to the proportion that would be expected based on the areal extent of available land-use types overall ($\chi^2 = 726.33$, $df = 10$, $p < 0.001$), indicating that individuals preferentially visited certain land-use categories over others (Figure 4.4A and B).

Tracked individuals visited residential areas most frequently and at a higher rate than would be expected based on the area available (39.7% vs 19.6% areal availability; Figure 4.4A and B). Of the 489 feeding fixes, 68 (13.9%) were in linear landscape features (including roads: $n = 66$ fixes, and watercourses: $n = 2$ fixes), which was notably higher than expected from the areal extent of these features (6.3%; Figure 4.4A and B). Tracked individuals also visited ‘reserve’ (13.3% vs 3.3% areal availability), ‘utilities’ (7.6% vs 1.7% of areal availability), ‘recreation’ (4.9 vs 0.8% areal availability), and ‘vacant’ (3.8% vs 1.8% areal availability) land-use categories more than expected based on areal availability (Figure

4.4A and B). Individuals visited remarkably less food plant species in the ‘primary production’ land-use category than expected based on areal availability (12.7% vs 64.0%; Figure 4.4A, B).

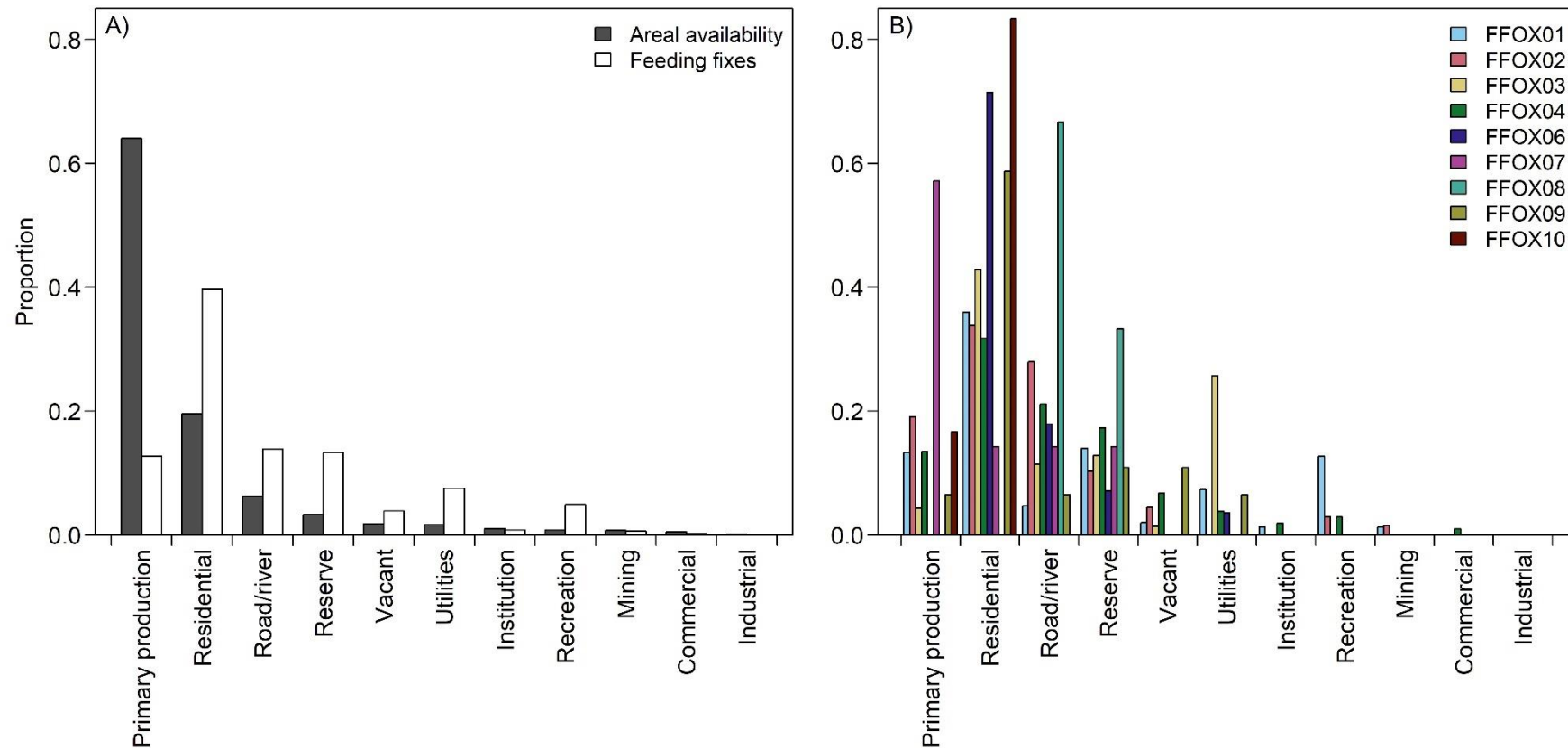


Figure 4.4 A) the expected proportion of *P. poliocephalus* feeding fixes in each land-use category based on areal availability (grey bars), and the observed proportion of feeding fixes in each land-use category overall (white bars), and B) the observed proportion of feeding fixes in each land-use category shown for each of the 9 individuals. Data (n = 489) were obtained from GPS tracked *P. poliocephalus* collected between December 2019 and May 2020.

4.4.2 Food plant species

Tracked *P. poliocephalus* visited a total of 49 unique plant species in the study period.

Individuals visited a greater diversity of species ($n = 28$), in residential areas than any other land-use category, and visited locally indigenous ($n = 8$), non-indigenous Australian native ($n = 10$), and non-Australian ($n = 10$) species (Figure 4.5). Tracked individuals also visited a high diversity of species in linear landscape features ($n = 20$), including roads (97% of fixes in this category) and rivers (0.3% of fixes in this category), and included locally indigenous ($n = 6$), non-indigenous Australian native ($n = 5$), and non-Australian species ($n = 8$; Figure 4.5). Individuals visited between 1-10 food plant species in other land-use categories (Figure 4.5).

The majority of the $n = 265$ surveyed feeding fixes included plant species that were locally indigenous to South Australia, (63%; Figure 4.5). However, 18% of total visitations occurred in non-indigenous Australian native plant species, 16% in non-Australian plant species, and 3% occurred in species with unknown geographic origin (Figure 4.5). The two most visited plant species were *Eucalyptus leucoxylon* (35% of all visitations) and *E. camaldulensis* (16% of all visitations), both of which are locally indigenous to South Australia (Figure 4.5; Table 4.2).

Of the $n = 265$ subsample of feeding fixes surveyed, $n = 90$ occurred in residential areas, where tracked individuals visited the highest number of non-Australian food plants overall (63% of all non-Australian species visitations; Figure 4.5). In residential areas, 30% of food plant species visitations were non-Australian species, 23% were non-indigenous Australian native species and 47% were locally indigenous species (Figure 4.5). Species visited by *P. poliocephalus* in residential areas included members of the Myrtaceae, Moraceae, Arecaceae, Platanaceae, Rosaceae, Salicaceae, Theaceae, Oleaceae, Pittosporaceae

and Magnoliaceae families (Figure 4.5). The most common species visited in residential areas were *E. leucoxylon*, *E. camaldulensis* and *Ficus carica* (Figure 4.5).

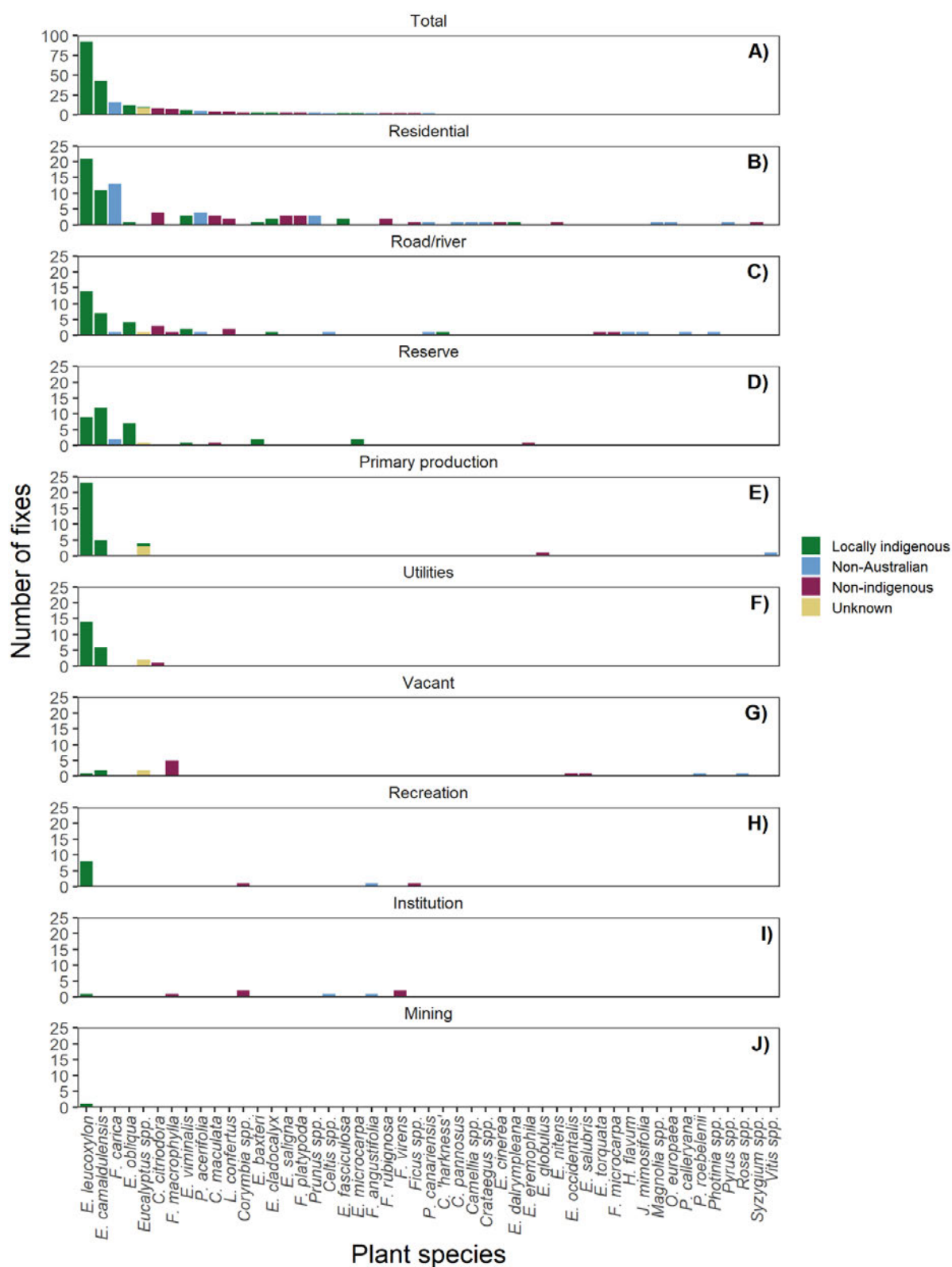


Figure 4.5 The number of plant species visitations (n = 265) by *Pteropus poliocephalus*. The top panel (A) shows the total number of plant species visitation across all land-use categories. The following panels show the number of visits in each land-use category separately: (B) residential (n = 90), (C) road/river (n = 46), (D) reserve (n = 38), (E) primary production (n = 34), (F) utilities (n = 23), (G) vacant (n = 14), (H) recreation (n = 11), (I) institution (n = 8), (J) mining (n = 1). Plant species are listed in order of most feeding visitations overall. Locally indigenous plant species are shown in green, non-indigenous Australian native species are shown in blue, non-Australian species are shown in pink, and those with unknown geographic origin are shown in yellow. Data were obtained from 9 GPS tracked *P. poliocephalus* roosting in the Adelaide region (-34.916, 138.607) from December 2019 – May 2020.

4.4.3 Phenology of food plant species

Collectively, the plant species visited by *P. poliocephalus* in the current study provide feeding resources throughout the year (Table 4.2). All of the locally indigenous food plant species visited by *P. poliocephalus* were species of the Myrtaceae family and known to contribute to the *P. poliocephalus* blossom diet (Table 4.2). The majority of these locally indigenous food plant species had been recorded to provide floral resources during summer – autumn (Table 4.2). In addition, 7 of the 10 non-indigenous Australian native food plant species were members of the Myrtaceae family and are known to contribute to the *P. poliocephalus* blossom diet (Table 4.2). While recurrent periods of natural food shortage during winter and spring have been recorded elsewhere in the *P. poliocephalus* range (Eby, 1991; Parry-Jones and Augee, 2001), tree species including *C. citriodora* and *C. maculata* had been recorded to provide floral resources during winter in the Adelaide region (Table 4.2). Non-indigenous Australian native food plant species also comprised fruiting Australian *Ficus* species including *F. rubiginosa*, *F. platypoda*, *F. macrophylla* and *F. microcarpa* (Table 4.2). Many species of *Ficus* exhibit asynchronous fruiting and thus can produce fruits at any time of the year (Innis, 1989). However, ripening is often documented during summer-

winter (Table 4.2). Almost all of the non-Australian food plant species visited by *P. poliocephalus* in this study were species that are known to contribute to the fruit diet of *P. poliocephalus*, many of which are cultivated (Table 4.2). Several of the non-Australian fruiting food plant species have been recorded to provide food resources during winter and/or spring, and include cultivated *Prunus* spp (stone fruits), and other species including date palm species (Table 4.2). One of the non-Australian food plant species visited (*P. acerifolia*) does not produce prominent flowers or fleshy fruit, although *P. poliocephalus* is known to consume the leaves and/or bark of species including *Populus* spp. (Parry-Jones and Augee, 1991b; Table 4.2). However, leaves and bark are not considered primary dietary components and are generally consumed during shortages of blossom and fruits (Eby and Law, 2008). This species is thus considered leave/bark food plant species and may provide minor supplementary resources year-round (Table 4.2).

The annual reliability of food plant species is highly variable between species (Table 4.2). Where annual reliability data were available, the findings indicated that many locally indigenous and non-indigenous Australian native plant species contributing to the blossom diet do not flower every year; flowering occurs every 1-4 years (Table 4.2). However, most of the non-Australian food plant species exhibit more regular flowering/fruiting (higher annual reliability) with some species including *Ficus* spp. producing two crops every year (Table 4.2).

Table 4.2 The flowering and fruiting phenology of the food plant species visited by *P. poliocephalus* in residential areas, and linear landscape features including road-side trees. Boxes are coloured to indicate months in which plant species have ever been recorded to flower/fruit. Dark shading represents periods of likely peak flowering or occurrence of ripe fruit, and moderate shading represents moderate flowering/fruiting. Blank spaces represent months in which food plant species have not been recorded to flower/fruit and hence are unlikely to contribute to the *P. poliocephalus* diet during these times. Asterisks represent species that are not known food plant species to *P. poliocephalus*. Colours indicate geographic origin; green indicates locally indigenous species, blue indicates non-indigenous Australian native species, and red represents non-Australian species. Where data were available, the flowering/fruiting duration is shown in months and annual reliability of flowering/fruiting is shown as a proportion of years when flowering occurs.

Family	Species	Summer			Autumn			Winter			Spring			Average duration	Annual reliability
		Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov		
	<u>Blossom</u>														
Myrtaceae	<i>Callistemon 'Harkness'</i>														
	<i>Corymbia citriodora</i>													≥3	0.3
	<i>C. maculata</i>													≥3	0.3
	<i>Eucalyptus baxteri</i>														0.5
	<i>E. camaldulensis</i>													2	0.25-0.5
	<i>E. cinerea</i>														
	<i>E. cladocalyx</i>														1
	<i>E. dalrympleana</i>														
	<i>E. fasciculosa</i>														0.5
	<i>E. leucoxylon</i>													7.1-9.7	0.5
	<i>E. nitens</i>														
	<i>E. obliqua</i>														0.5
	<i>E. saligna</i>													1	0.3
	<i>E. torquata</i>														
	<i>E. viminalis</i>														0.25-0.3
	<i>Lophostemon confertus</i>												1	0.5-0.3	
Magnoliaceae	<i>Magnolia</i> spp.*														
Rosaceae	<i>Crataegus monogyna</i> *														
Theaceae	<i>Camellia</i> spp.*														
Pittosporaceae	<i>Hymenosporum flavum</i>														
Bignoniaceae	<i>Jacaranda mimosifolia</i>														
	<u>Fruit</u>														
Myrtaceae	<i>Syzygium</i> spp.														
Moraceae	<i>Ficus carica</i>														2
	<i>F. macrophylla</i>														
	<i>F. microcarpa</i>														
	<i>F. platypoda</i>														
	<i>F. rubiginosa</i>														
	<i>Cotoneaster pannosus</i>														
Rosaceae	<i>Crataegus</i> spp.*														
	<i>Prunus</i> spp.														0.5
	<i>Pyrus</i> spp.														0.5
	<i>P. calleryana</i>														
	<i>Photinia</i> spp.														
	<i>Phoenix canariensis</i>													1	
Arecaceae	<i>P. roebelenii</i>														
	<i>Olea europaea</i>														
Oleaceae	<i>Celtis</i> spp.														
	<u>Leaves/bark</u>														
Platanaceae	<i>Platanus acerifolia</i> *														

4.5 Discussion

We investigated the foraging landscape utilisation, and plant species visitations of 9 GPS tracked individual *P. poliocephalus* in the urban landscape of Adelaide, South Australia. We found that *P. poliocephalus* most frequently visit residential areas for feeding, and visit residential and linear landscape features including roads and rivers for feeding more often than expected based on areal availability. Tracked individuals utilised a relatively wide range of food plant species in these two land-use categories, including locally indigenous, non-indigenous Australian native, and non-Australian species. Thus, our findings suggest that *P. poliocephalus* have a greater dietary breadth in highly urbanised habitats including residential areas compared to more natural environments such as nature reserves. Furthermore, flowering and fruiting phenology records of food plant species indicated that residential areas and road-side trees provide temporal stability of food plant resources for *P. poliocephalus* in the Adelaide region. While we did not study historical urban plantings in Adelaide, the spatiotemporal availability and stability of urban food resources for flying-foxes has likely increased in Australian cities over the last few decades as a result of changes in anthropogenic plantings (e.g., Williams et al., 2006); native Australian species became popular candidates for street trees in the 1970s (Yau, 1982), and these individuals will have since matured and likely exhibit increased flowering (e.g. Wilson, 2002). Increased availability of locally indigenous food resources in urban areas along with the availability of non-indigenous Australian native and non-Australian species likely extend the time that food is available for flying-foxes in Adelaide. In combination with our results, this may help to explain, why *P. poliocephalus* are increasingly prevalent in urban environments.

A large proportion of the food plants visited by *P. poliocephalus* included locally indigenous species, including *E. leucoxylon* and *E. camaldulensis*, and these species were visited by individuals in most of the land-use categories; primary production, reserve,

utilities, residential areas and road/river habitats. All of the locally indigenous, food plant species visited by flying-foxes belonged to the Myrtaceae family and are known to contribute to the *P. poliocephalus* blossom diet. This supports previous research that shows that *P. poliocephalus* preferentially and primarily feed on the nectar and pollen from a wide range of Myrtaceous plants (Parry-Jones and Augee, 1991b). Many Myrtaceous plants are notorious for their irregular and intermittent flowering (Law et al., 2000), and thus, each species may not provide floral resources for flying-foxes every year. Our findings indicated that peak flowering of the locally indigenous food plant species visited by *P. poliocephalus* in residential areas occurred most often during summer and autumn, with an annual reliability of flowering between 1-4 years. Thus, natural food plant resources alone are not likely able to support individuals roosting in Adelaide year-round. However, urban areas are often characteristic of increased temperatures as a result of the urban heat island effect (Magee et al., 1999), and increased soil moisture and soil nutrients, resulting from irrigation and the use of fertilisers (Sukopp, 2004; Neil and Wu, 2006). These factors have been shown to promote more regular and intense flowering (Williams et al., 2003; Neil and Wu, 2006; Davis et al., 2016). Locally indigenous and non-indigenous Australian native species that exist in urban areas may thus on average exhibit enhanced growth (e.g. Zhao et al., 2016), higher annual reliability of flowering, and produce more flowers per flowering event than individuals in native habitats (e.g. Davis et al., 2016), thereby improving the spatiotemporal availability and stability of urban, floral resources.

Our findings indicated that *P. poliocephalus* roosting in Adelaide not only fed on locally indigenous species, but also on a range of non-indigenous Australian native and non-Australian plant species. Many of the non-indigenous Australian native plant species visited by individuals were also known blossom diet species in the Myrtaceae family (see Table 4.2; Parry-Jones and Augee, 1991b; Eby and Law, 2008). Phenological records indicated that

non-indigenous Australian native species including lemon-scented gum (*C. citriodora*) and spotted gum (*C. maculata*), may provide floral resources for *P. poliocephalus* during winter when other species endemic to the Adelaide region are less likely and/or have not been recorded to flower (Table 4.2). Additionally, many of the listed non-indigenous flowering species visited by *P. poliocephalus* including *C. citriodora*, *C. maculata*, *E. saligna* and *L. confertus*, have now become naturalised in South Australia (Hosking et al., 2011; Centre for Australian National Biodiversity Research, 2015; Lucid, 2016). Thus, non-indigenous Australian native and non-Australian flowering species in Adelaide likely contribute to the spatiotemporal stability of food plant resources in this Australian city.

Our findings suggest that anthropogenic planting of fruit-bearing plants including tropical *Ficus* species (i.e. *F. macrophylla*, *F. microcarpa*, *F. platypoda* and *F. rubiginosa*) as well as widely cultivated non-Australian fruits including the common fig (*F. carica*), pear (*Pyrus* spp.), stone fruits (*Prunus* spp.), and date palm (*P. canariensis*), may increase the availability of fruit as a resource to *P. poliocephalus* in urban areas, particularly in residential areas and road-side habitats. Some of these non-Australian species including *F. carica* (Hosking et al., 2011), and *P. canariensis* (Brodie and Reynolds, 2012; Spennemann, 2018) have now become naturalised in South Australia. Fruiting phenology records suggested that many of the non-Australian, fruit-bearing food plant species visited by *P. poliocephalus* in residential area provide food resources for *P. poliocephalus* at different stages of the year, that both overlap with and extend the overall availability of food (Table 4.2). Previous research has shown that native food plant species in the fruit diet primarily exist in rainforest in which constitutes only a small proportion of the *P. poliocephalus* range (Eby and Law, 2008), and models have predicted that *P. poliocephalus* feed on less fruit than other *Pteropus* species including black flying-foxes (*P. alecto*) with more tropical distributions (Griffith et al., 2020). Additionally, previous research from New South Wales has indicated that *P.*

poliocephalus appear to feed on cultivated fruit only during natural food shortages (Parry-Jones and Augee, 1991b). While it is known that fruits are an important constituent of the *P. poliocephalus* diet (Eby, 1998), they generally exhibit a preference for nectar and blossom, particularly of the Myrtaceae family (Parry-Jones and Augee, 1991b), possibly a result of a limitation of fruit as a resource throughout the natural range of this species. However, anthropogenic plantings of fruit-bearing food plant species may locally increase the availability of fruit as a resource to individuals roosting in urban habitats including Adelaide. Furthermore, our data suggest residential areas and road-side habitats in the Adelaide region exhibit a range of locally indigenous, non-indigenous Australian native, and non-Australian species that in combination, provide year-round food plant resources for *P. poliocephalus* (Table 4.2). It is likely that the spatiotemporal availability and stability of urban foraging resources has increased over the last few decades owing to changes in urban plantings (e.g., Williams et al., 2006), and taken together with our findings, it could help to explain the increasing prevalence of *P. poliocephalus* in Adelaide metropolitan area, and by extension the increased prevalence of the species in urban areas in Australia more generally (Meade et al., 2021; Chapter 3; Yabsley et al., 2021).

Our results also indicated that tracked individuals visited a number of non-Australian plant species that are not known food plant species for *P. poliocephalus*, including *magnolia* spp., *Camelia* spp., *Crataegus* spp., and *P. acerifolia* (Table 4.2). The majority of these tree species were only associated with one feeding fix, with the exception of *P. acerifolia*. Identification of these tree species as food plant species may be a result of sampling error. Although methods to obtain ‘feeding fixes’ were conservative, the GPS and accelerometry data were paired within a +/- 60 second buffer, and hence it is possible that some of the *P. poliocephalus* feeding fixes were misidentified as ‘feeding’ if individuals moved between trees within the 60 second discrepancy buffer. Alternatively, *P. poliocephalus* could have

visited these tree species to rest in-between feeding, or perhaps carried fruit from a different tree species and consumed it in the tree species recorded, as behaviour described in other *Pteropus* spp. (Richards, 1990). Multiple feeding fixes were associated with *Platanus acerifolia*, a deciduous hybrid cross between American sycamore and oriental plane tree, that produces insignificant flowers that turn into non-fleshy, spherical fruiting balls (Missouri Botanical Gardens, 2021). For these reasons, it is unlikely that *P. poliocephalus* rely on this plant species for flowers or fruit. Of the four feeding fixes associated with this plant species, three were along a private road on Glen Ewin Estate fig (*F. carica*) orchard; multiple *P. poliocephalus* feeding fixes were also associated with cultivated *F. carica* at this locality. Flying-fox species often carry fruits away from the tree they were selected from before consumption (Marshall, 1985; Richards, 1990), and thus, the majority of fixes associated with *P. acerifolia* likely instead, pertain to the consumption of *F. carica*. To conclude whether these tree species are in fact consumed by *P. poliocephalus* in the Adelaide region or pertain to sampling error, future research should focus on analysis of scats and ejecta.

The preference of *P. poliocephalus* for feeding in human-modified areas including residential habitat is likely to have important implications in human-wildlife conflict management and the conservation of this vulnerable species. In particular, the attraction of *P. poliocephalus* to cultivated fruits such as the common fig (*F. carica*) is likely to cause conflict with residents growing backyard fruit crops (see Aziz et al., 2016), and with orchardists. Previous research has shown the effectiveness of protecting cultivated fruits from flying-fox depredation including lychees using exclusion netting (Tollington et al., 2019). However, without the appropriate use of fruit nets, flying-foxes can become entangled and potentially suffer from life-threatening injuries (Scheelings and Frith, 2015). Thus, government subsidised wildlife-safe exclusion netting could be used to mitigate conflict between *P. poliocephalus* and fruit growers in the Adelaide region (Mo et al., 2020a). Other

urban threats to flying-foxes including electrocution on powerlines (see Tella et al., 2020) may be increased by their reliance on plants grown in residential area and road-side habitats in the Adelaide region. Government subsidised exotic tree removal schemes have been considered an effective measure for reducing urban conflict (Mo et al., 2020a), and our data could be used to inform which species to target. Our findings also provide information on species that could be planted in natural habitats to increase the availability of food plant resources away from conflict zones, which could be seen by governments as supporting the conservation of this vulnerable species.

We now know that a large proportion of the *P. poliocephalus* population is reliant on human-modified landscapes (Yabsley et al., 2021), and that in residential areas and road-side habitats *P. poliocephalus* visit a wider range of food plant species than in more-natural habitats including nature reserves and remnant patches of native vegetation; thus appearing to exhibit greater dietary breadth in urban vs non-urban habitats. While we did not investigate historical urban plantings, the spatiotemporal availability and stability of food resources in Australian cities has likely increased in the last few decades as a result of changes in urban plantings (e.g., Williams et al., 2006). Together these findings provide support for the hypothesis that the increasing prevalence of *P. poliocephalus* in urban areas is at least in part, driven by increased availability and stability of urban food plant resources. However, further research is needed to quantify exactly how the composition and density of urban plantings has changed over time and whether this translates to increased spatiotemporal availability of food resources for flying-foxes. Furthermore, longer-term GPS tracking of individuals throughout their range, and better mapping of urban plantings will allow managers to predict when and where human versus flying-fox conflicts are likely to occur; develop ethical, conservation-management strategies that focus on redistribution of food plant resources; and encourage integration of these management strategies across jurisdictional boundaries.

Chapter 5: Conclusion

5.1 Main Findings

Flying-foxes (*Pteropus* spp.) are becoming increasingly urbanised, for reasons that are not yet fully understood (Tait et al., 2014). Recent research has indicated grey-headed flying-foxes (*Pteropus poliocephalus*) are more likely to stay for longer, and exhibit shorter foraging distances, in urban areas (Meade et al., 2021). These findings are in keeping with the hypothesis that an increased prevalence of flying-foxes in cities and towns is supported by the availability and temporal stability of urban food plant resources. This thesis aimed to better understand foraging resource availability as a driver of *P. poliocephalus* urbanisation by investigating the long-term foraging habitat use of satellite tracked individuals roosting in major-, minor- and non-urban roosts along the east coast of New South Wales; and by investigating the finer scale foraging landscape utilisation and food plant species of GPS tracked individuals roosting in a major city - Adelaide.

Analysis of long-term satellite tracking data suggested that *P. poliocephalus* utilised different foraging landscapes when they roosted in major-urban areas versus when they roosted in smaller urban centres and in non-urban areas (Chapter 3). In particular, tracked individuals preferentially visited wet and dry sclerophyll forest for foraging when they roosted in minor-urban and non-urban areas, but were overwhelmingly supported by ‘human-modified’ habitat for foraging, particularly when roosting in major-urban areas. The data presented in Chapter 3 indicated that human-modified landscapes provide important foraging resources for *P. poliocephalus* throughout a large proportion of their range. However, it also highlighted a key knowledge gap; that we do not know precisely how *P. poliocephalus* utilise the urban foraging landscape, or what exact foraging resources support the persistence of this species in cities and towns.

In Chapter 4, high resolution tracking (GPS) was used to investigate how *P. poliocephalus* utilise the urban foraging landscape; to determine whether individuals exhibit a preference for certain urban land-use categories, and to identify particular food resources that support this species in a major Australian city, Adelaide. The findings presented in Chapter 4 indicated that *P. poliocephalus* most frequently fed in residential areas and road-side habitats and at a higher rate than expected based on the availability of these habitats, and that individuals visited a relatively high diversity of plant species in these habitats compared to other, more natural land-use categories including nature reserves. The food plant species visited by individuals in residential areas included locally indigenous, non-indigenous Australian native, and non-Australian species, and the fruiting/flowering phenology of these food plant species suggest that the foraging landscape in the Adelaide region may provide food plant resources for *P. poliocephalus* year-round.

5.2 Drivers of flying-fox urbanisation, and implications for flying-fox management and conservation

While we did not investigate historical urban plantings in Adelaide, the spatiotemporal availability and stability of urban foraging resources for flying-foxes in Australian cities has likely increased in the past few decades owing to changes in anthropogenic plantings (e.g., Williams et al., 2006). Native Australian plants including Eucalypts, gained popularity as candidates for street trees in the 1970s (Yau, 1982), and these trees will have since matured and likely experience increased flowering (e.g., Wilson, 2002). In addition to the common use of non-indigenous Australian native and non-Australian species in urban areas, this anthropogenic mixture likely provides increased spatiotemporal availability of food. In combination with the findings presented in the current thesis, this provides support for the hypothesis that *P. poliocephalus* urbanisation is, at least in part, driven by an attraction to an increased availability and spatiotemporal stability of food plant resources.

Many factors, including the loss of natural foraging habitat as a result of urban expansion (Páez et al., 2018), and environmental disturbances including the devastating 2019-2020 bushfires in Australia (Baranowski et al., 2021) are likely to increase the reliance of *P. poliocephalus* on urban areas. Previous research has suggested that flying-fox roost occupancy is partially dependent on the availability of winter foraging habitat (Baranowski et al., 2021). The megafires of 2019-2020 are thought to have burned approximately 34% of the total *P. poliocephalus* foraging habitat, including almost 42% of the species' critical winter habitat (Baranowski et al., 2021). These impacts are likely to have devastating impacts on species including *P. poliocephalus*, that are known to experience food resource bottlenecks during the winter-spring (Eby et al., 1999; Parry-Jones and Augee, 2001). Furthermore, periods of limited winter resources have already shown to be linked to high mortality rates in adults, and low rates of reproduction in this species (Hall et al., 1991).

We now know that a large proportion of the vulnerable *P. poliocephalus* population are reliant on human-modified landscapes for roosting and foraging (Chapter 3; Meade et al., 2021; Timmiss et al., 2021). Flying-fox urbanisation has implications for human-wildlife conflict, and species conservation, and thus it requires precarious balancing of community and conservation concerns. Furthermore, the extreme mobility and nomadic behaviour displayed by this species; frequently travelling within and between jurisdictional boundaries, can further complicate the success of conservation management actions (Welbergen et al., 2020). For example, adverse actions employed by one government agency can consequently negate or weaken the conservation attempts of another (Welbergen et al., 2020). Thus, local government conservation management approaches would be most effective if coordinated on a national scale.

5.2.1 Urban areas as ‘ecological traps’

The overwhelming dependence of *P. poliocephalus* on major-urban areas, as highlighted in Chapter 3, is likely to have important negative implications for this threatened species.

Firstly, *P. poliocephalus* may be exposed to a range of urban related anthropogenic threats including electrocution on power lines and entanglement in fruit tree netting in gardens (Tidemann and Nelson, 2011; Scheelings and Frith, 2015; Mo et al., 2020b; Tella et al., 2020). In addition, the increase in frequency and severity of extreme heat events in Australia has caused mass mortality of flying-foxes due to hyperthermia (Welbergen et al., 2008), and urban colonies may be more exposed to the effects of these events due to the urban heat island effect (Khan et al., 2020). Thus, the documented increasing prevalence of flying-foxes in urban areas could be detrimental to their conservation.

5.2.2 Increased human-wildlife conflict

Increasing *P. poliocephalus* urbanisation is likely to have profound implications for the management of human versus flying-fox conflicts, particularly as flying-foxes have been shown to preferentially visit food plant species in residential areas (Chapter 4). Urban human versus flying-fox conflicts include the noise, smell and soiling associated with nightly foraging visits (Kung et al., 2015), depredation of backyard fruit trees (Aziz et al., 2016; Oleksy et al., 2018; Tollington et al., 2019), defoliation of roosting trees (Vardon et al., 1997), and concerns around the transfer of zoonotic diseases (Philbey et al., 2008). Previous attempts to evict flying-foxes from urban roosts have proven difficult and largely unsuccessful (Roberts et al., 2011; Roberts et al., 2021), due to the extreme mobility and nomadic behaviour of these species (Welbergen et al., 2020). Human versus flying-fox conflict is likely to worsen if flying-fox urbanisation continues to increase, thereby increasing the pressure on wildlife managers to develop balanced strategies that mitigate these conflicts while supporting the conservation of this nationally important species.

5.2.3 Ecosystem services provided by flying-foxes

Flying-foxes, including *P. poliocephalus*, perform an essential role in maintaining the health and genetic diversity of native forests, connecting fragmented habitat patches and urban areas, through long distance pollination and seed dispersal (Fujita and Tuttle, 1991; Nyhagen et al., 2005; Trakhtenbrot et al., 2005; Kunz et al., 2011; Aziz et al., 2021). They also aid in the regeneration of native forest in cleared habitat patches where other species seldom visit (Fujita and Tuttle, 1991); some research suggests that flying-fox species are responsible for up to 98% of the first seeds deposited in man-made clearings (Thomas, 1982). Furthermore, although plant species such as figs are consumed by several species not limited to flying-foxes, flying-foxes are often the primary dispersal agents (Fujita and Tuttle, 1991; Aziz et al., 2021). Thus, flying-foxes are central to the ecology of native ecosystems globally. However, as flying-foxes become increasingly urbanised, spend more time in urban areas, and exhibit shorter foraging distances in urban areas (Meade et al., 2021), a large proportion of flying-fox populations is likely no longer engaging in long-distance pollination and seed dispersal services. Therefore, flying-fox urbanisation may have unexpected indirect impacts on forest connectivity, long-term genetic diversity, regeneration of native forest ecosystems, with cascading effects on forest biodiversity.

Flying-foxes also have the potential to facilitate dispersal of alien species throughout urban landscapes and native vegetation (Voigt et al., 2011), due to the consumption of a number of non-indigenous Australian native and non-Australian species (see Chapter 4). Some research suggests that flying-foxes can disperse larger seeds than many species of bird due to their capacity to carry whole fruits away from the forage tree (Richards, 1990), and in some cases, can enhance the germination process (Jordaan et al., 2012). This could have serious ecological consequences for native ecosystems including loss of biodiversity via the spread of plant pathogens (Rai and Singh, 2020).

5.3 Potential application of results and future research directions

Chapter 3 demonstrated that large-scale and long-term satellite tracking is useful to infer trends in foraging habitat use in the *P. poliocephalus* population at large. Furthermore, the research presented in the Chapter 4 has demonstrated the effectiveness of using GPS tracking to identify food plant species visited by *P. poliocephalus*; however, we only tracked a small number of individuals over up to six months of the year. Future research should focus on longer-term GPS tracking to investigate seasonal and annual feeding patterns in this species.

The findings presented in the current thesis could be used to assist wildlife managers in the development of balanced and ethical management practices for *P. poliocephalus* in the Adelaide region and suggests research methods to investigate the drivers of *P. poliocephalus* urbanisation in other cities and towns throughout their range. Firstly, the findings presented in Chapter 3 have indicated that human-dominated landscapes are now overwhelmingly important for *P. poliocephalus* roosting and foraging in major-urban areas and that this trend is consistent throughout time and space. These findings imply that redistribution of foraging resources in urban areas could effectively reduce foraging in conflict areas. However, we also identified a key knowledge gap; that mapping of major-urban plantings is largely under-surveyed in Australia resulting in a limited ability to infer likely food plant species in these areas. Nevertheless, high-resolution GPS tracking used in Chapter 4, allowed for finer scale inferences of land-use preferences and the identification of tree species visited by *P. poliocephalus* in the Adelaide region. If this information is used alongside flowering/fruitlet phenology records, and better mapping of urban tree plantings, it could be used to predict where and when human versus flying-fox conflict is likely to arise. It could also be used to target tree species for government-subsidised exotic tree removal and/or species in which to endorse wildlife-safe exclusion netting as conflict mitigation strategies (Mo et al., 2020a).

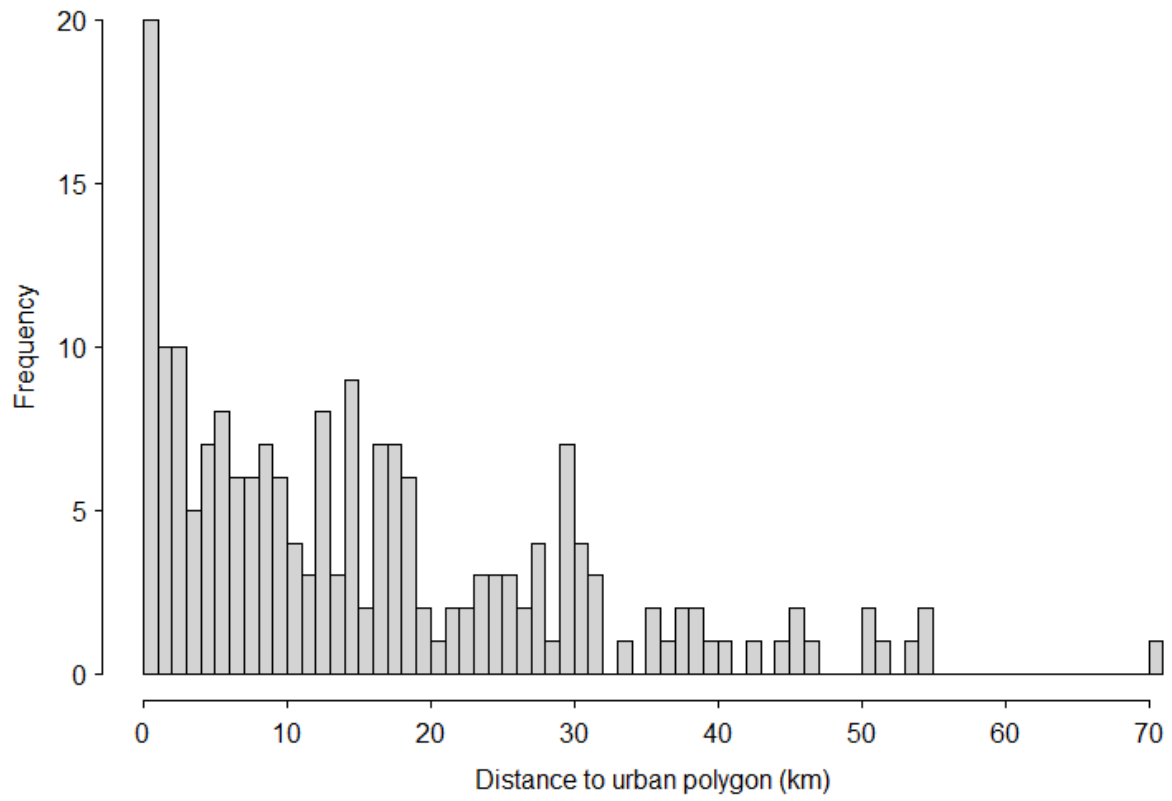
Reducing the availability of urban food plant resources (at least in terms of non-indigenous and non-Australian plant species), through targeted tree removal and/or the use of wildlife-safe exclusion netting could reduce the attractiveness of residential areas and road-side trees to *P. poliocephalus*; thereby, not only reducing conflict with humans, but also reducing urban anthropogenic risks to flying-foxes including electrocution on powerlines. However, without simultaneously improving the availability of food plant resources for *P. poliocephalus* in natural areas, this strategy may be detrimental to the overall conservation of this species. As discussed in section 5.2, effective, well-balanced conservation management of urban flying-foxes is reliant on evidence-based approaches that are co-ordinated beyond jurisdictional boundaries, throughout the entire range of this species.

In Chapter 3, we identified that while *P. poliocephalus* preferentially visit human-modified landscapes for foraging when they roost in major-urban areas; they exhibit an overall preference for foraging in wet and dry sclerophyll forest habitats when they roost in minor-urban and non-urban areas. Thus, these findings could inform managers of the most suitable habitats in which tree planting schemes could be implemented to improve the availability of food resources in natural foraging landscapes for this species. In Chapter 4, we identified food plant species visited by *P. poliocephalus* roosting in the Adelaide region. Food plant species included a combination of species endemic to South Australia, and non-endemic to South Australia however endemic to other regions in the *P. poliocephalus* range. In combination with the results presented in Chapter 3, this information could be used to inform managers in the Adelaide region, and perhaps other regions including NSW and Queensland, of suitable habitats and species to target for tree planting schemes (Law et al., 2002). This strategy could be used to support the conservation of this vulnerable species. Additionally, our methods could be used to further investigate the food plant resources sustaining *P. poliocephalus* in other cities throughout their range, and to investigate

population trends at large. This information would further inform wildlife managers in multiple jurisdictions and local government areas, in the development and integration of effective and ethical, coordinated conservation-management strategies for *P. poliocephalus* at large.

Appendices

Appendix 1. Distribution of non-urban roosts in relation to the distance to the nearest urban polygon.

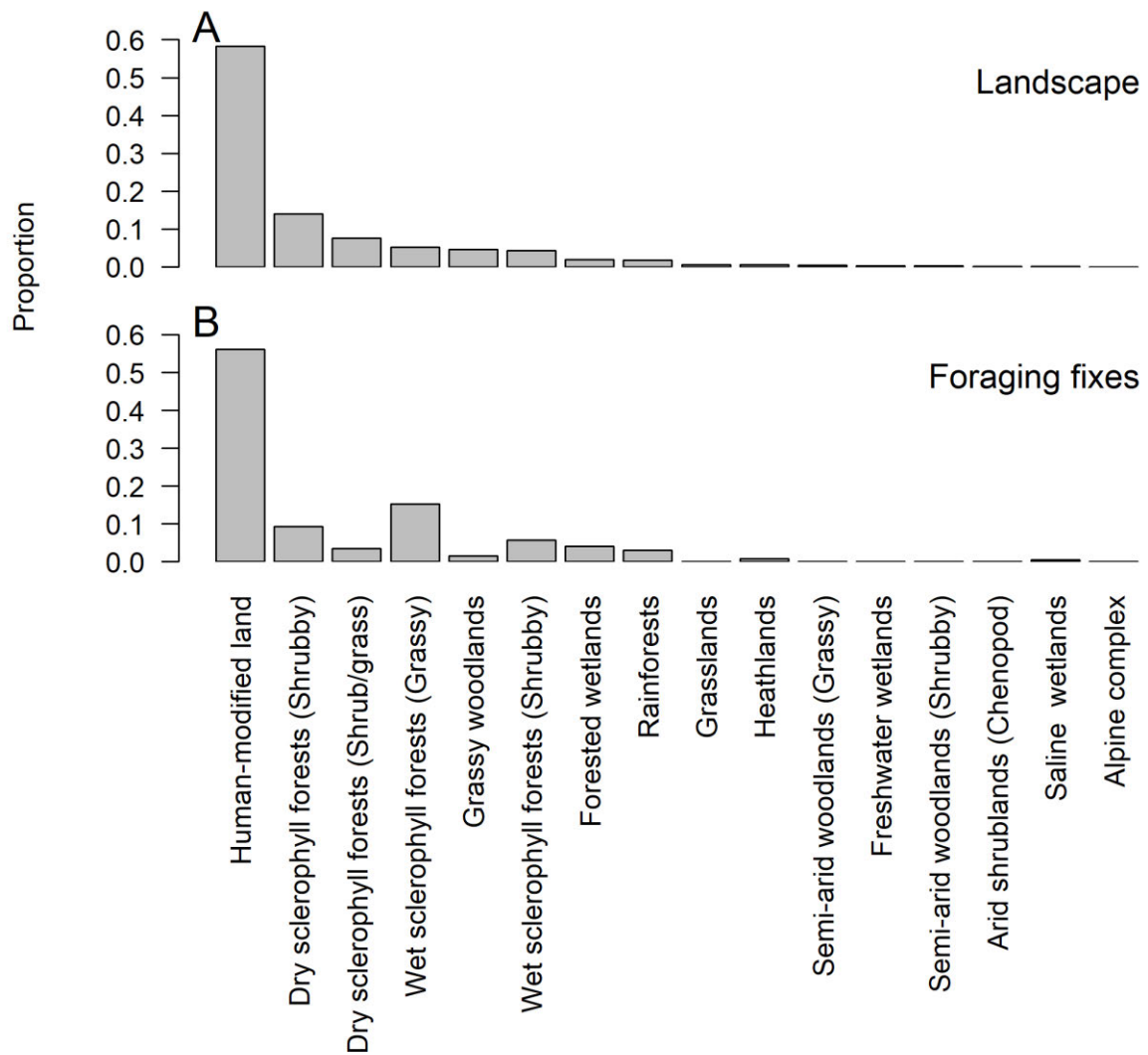


Appendix 2. The numbers of visiting individuals for all combinations of roost types ($N_{\text{total}} = 98$ individuals, satellite tracked over up to 5 years between 2012-2017).

Roost type	Number of individuals
Major-urban only	17
Minor-urban only	3
Non-urban only	2
Major- and minor-urban	4
Major- and non-urban	10
Minor- and non-urban	16
All types	46

Appendix 3. The proportion of (A) each vegetation class in the study area, and (B) of *P.*

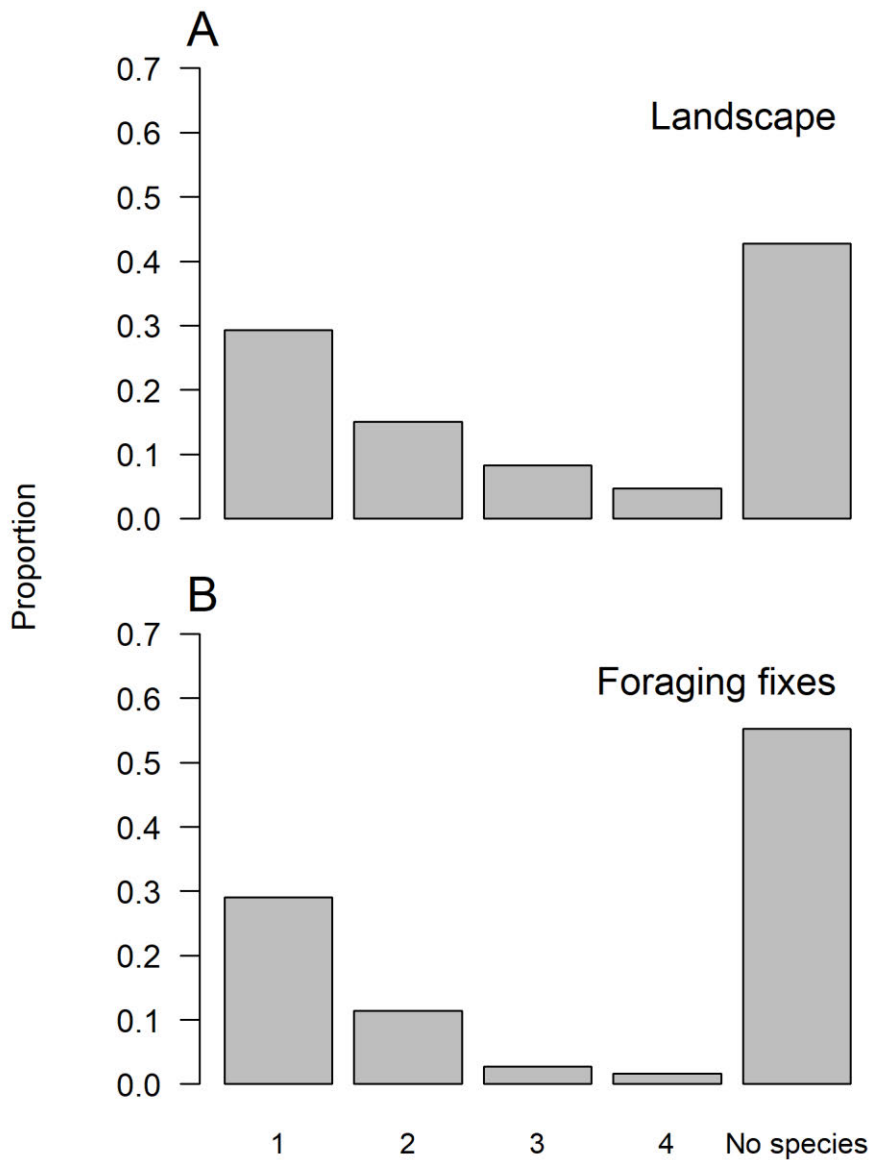
poliocephalus foraging positional fixes (n = 4,233) recorded in each vegetation class. Satellite tracking data were collected between 2012-2017 and is representative of 98 individuals.



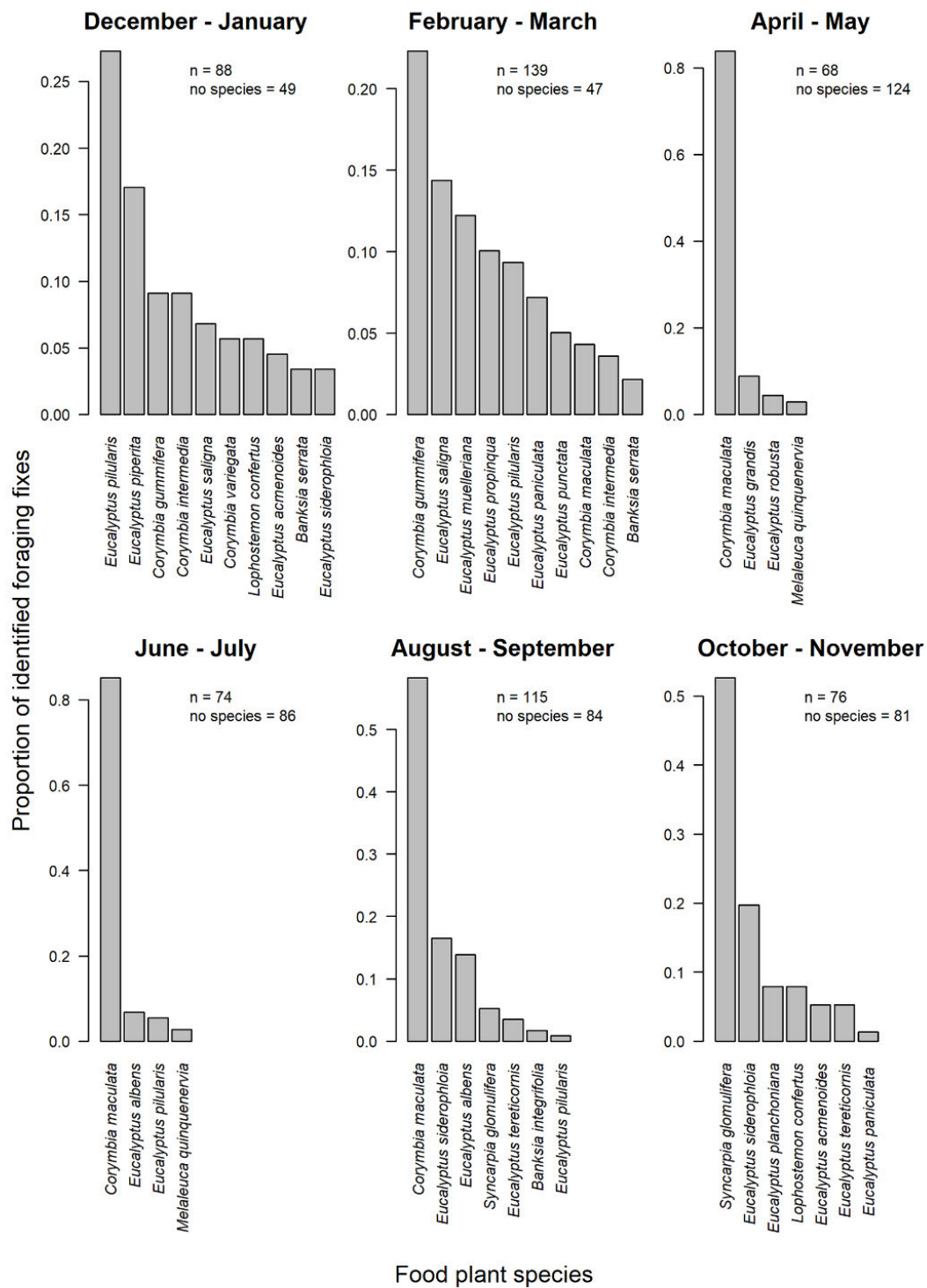
Appendix 4. Estimated regression parameters, standard errors, z values, and p-values for the best fitting multinomial logistic regression. Cleared land is the reference category.

Parameter	Estimate \pm	SE	Z value	P-value
Intercept				
Dry sclerophyll forests (shrub/grass subformation)	-1.341 \pm	0.167	-8.025	0.000
Dry sclerophyll forests (shrubby subformation)	-1.041 \pm	0.147	-7.103	0.000
Forested wetlands	-1.613 \pm	0.195	-8.269	0.000
Freshwater wetlands	-5.120 \pm	1.013	-5.054	0.000
Grassy woodlands	-2.501 \pm	0.248	-10.094	0.000
Heathlands	-3.078 \pm	0.550	-5.593	0.000
Rainforests	-2.342 \pm	0.197	-11.874	0.000
Saline wetlands	-3.924 \pm	0.662	-5.927	0.000
Wet sclerophyll forests (grassy subformation)	-0.291 \pm	0.113	-2.582	0.010
Wet sclerophyll forests (shrubby subformation)	-1.534 \pm	0.162	-9.463	0.000
Distance to urban polygon				
Dry sclerophyll forests	0.010 \pm	0.011	0.881	0.379
Dry sclerophyll forests	0.016 \pm	0.009	1.684	0.092
Forested wetlands	-0.005 \pm	0.014	-0.327	0.744
Freshwater wetlands	0.001 \pm	0.070	0.016	0.987
Grassy woodlands	0.034 \pm	0.013	2.554	0.011
Heathlands	-0.254 \pm	0.164	-1.549	0.121
Rainforests	0.068 \pm	0.009	7.674	0.000
Saline wetlands	-0.064 \pm	0.074	-0.866	0.387
Wet sclerophyll forests (grassy subformation)	0.029 \pm	0.007	4.102	0.000
Wet sclerophyll forests (shrubby subformation)	0.039 \pm	0.009	4.416	0.000

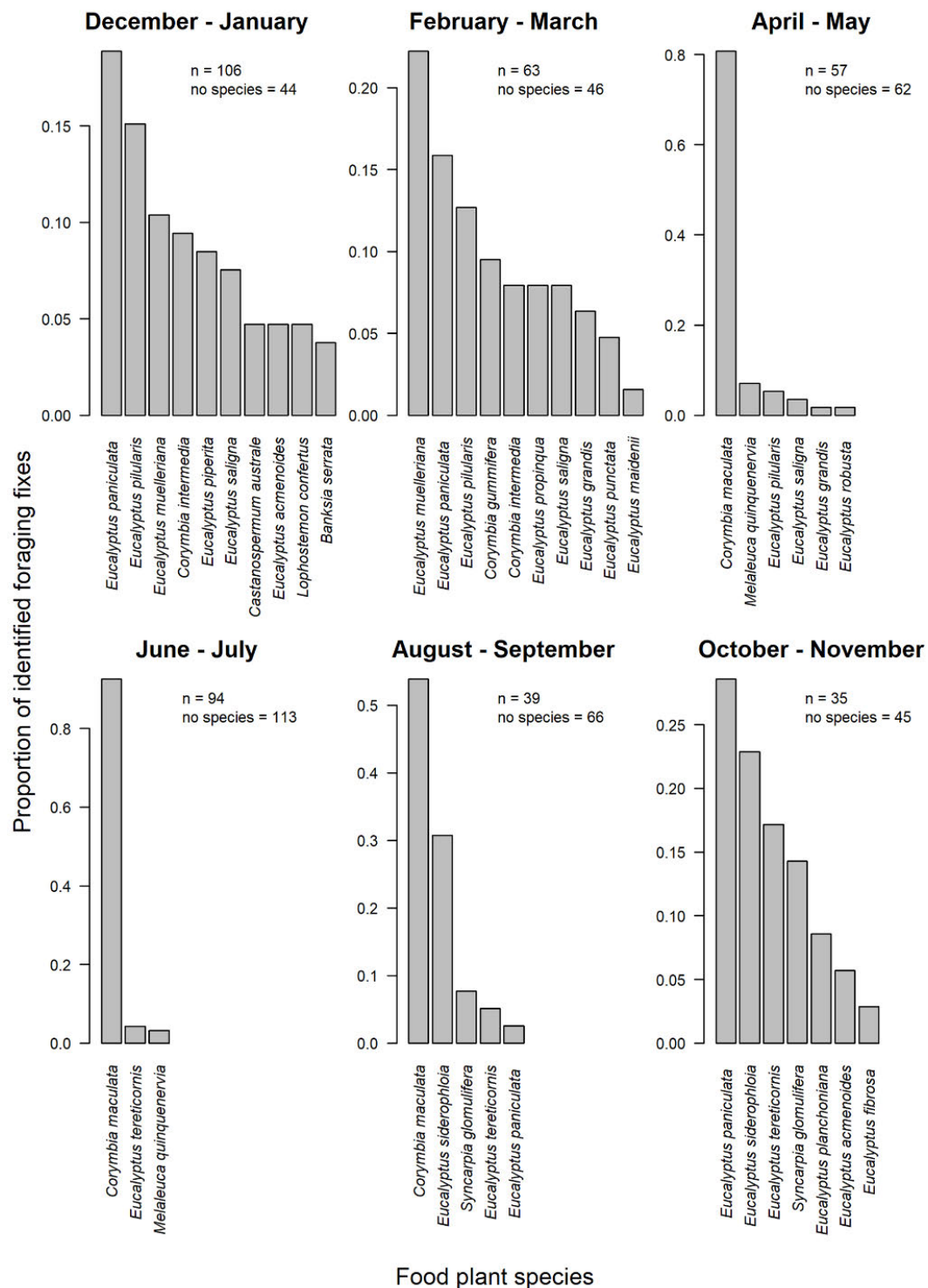
Appendix 5. The proportion of (A) each habitat quality rank in the area sampled, and (B) of foraging positional fixes (n = 3,773) recorded in each habitat quality rank. Habitat quality was ranked from 1-4: where 1 is good quality foraging habitat, rank 4 is poor quality foraging habitat, and 'No species' is habitat where the recorded dominant and subdominant plant species were not known to be part of the *P. poliocephalus* diet.



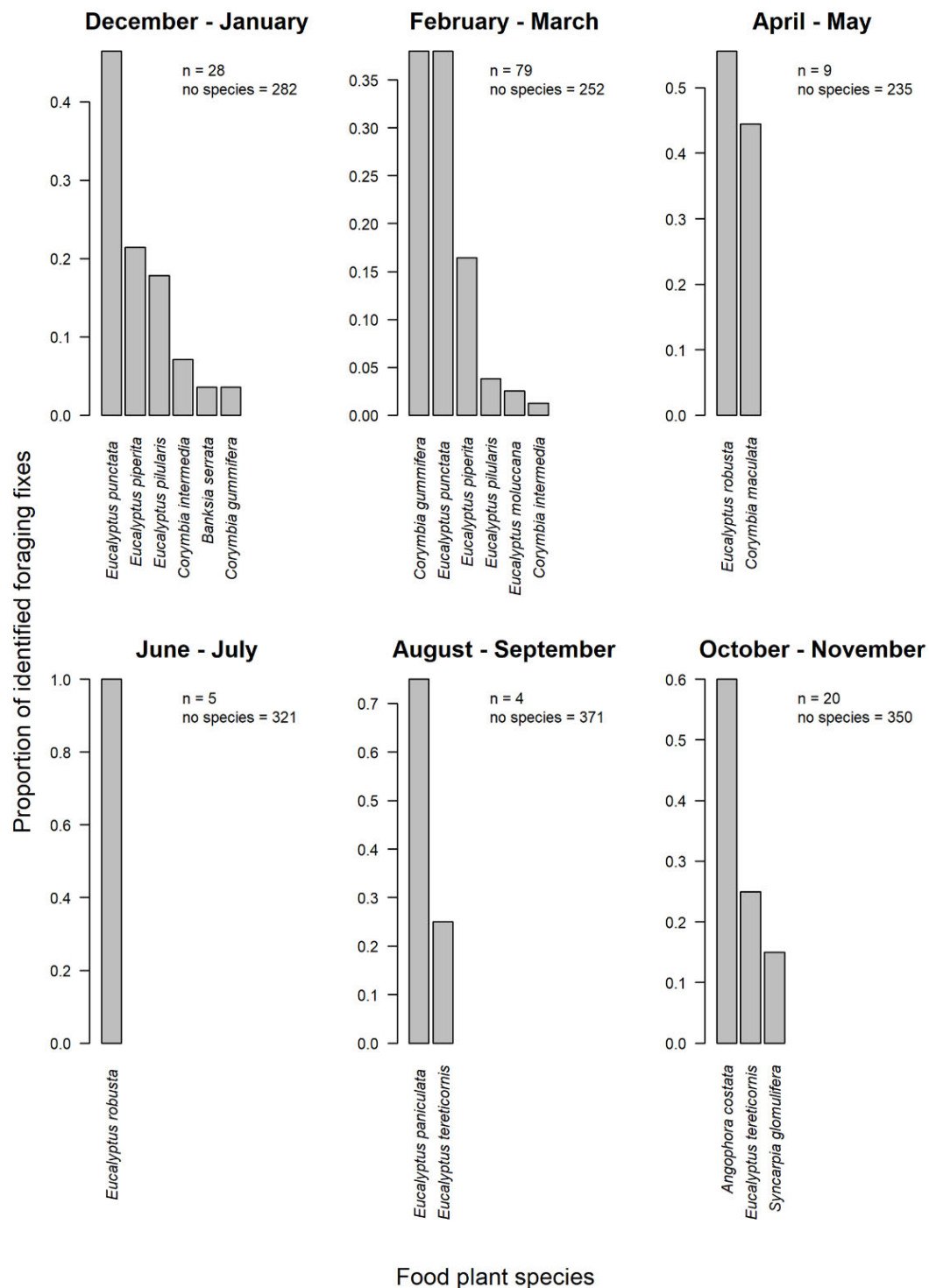
Appendix 6. Likely *P. poliocephalus* food plant species in each bi-month where individuals roosted in non-urban areas. A maximum of 10 different food plant species were included in each graph. n = the number of foraging fixes used to calculate proportions. ‘No species’ indicate additional fixes for the particular bi-month that fell in the sampled area, but for which the recorded dominant and subdominant plant species were not known to be part of the *P. poliocephalus* diet.



Appendix 7. Likely *P. poliocephalus* food plant species in each bi-month where individuals roosted in minor-urban areas. A maximum of 10 different food plant species were included in each graph. n = the number of foraging fixes used to calculate proportions. ‘No species’ indicate additional fixes for the particular bi-month that fell in the sampled area, but for which the recorded dominant and subdominant plant species were not known to be part of the *P. poliocephalus* diet.



Appendix 8. Likely *P. poliocephalus* food plant species in each bi-month where individuals roosted in major-urban areas. A maximum of 10 different food plant species were included in each graph. n = the number of foraging fixes used to calculate proportions. ‘No species’ indicate additional fixes for the particular bi-month that fell in the sampled area, but for which the recorded dominant and subdominant plant species were not known to be part of the *P. poliocephalus* diet.



Appendix 9. Inaccessible GPS feeding fixes (n = 35), the land-use categories they pertain to and the reason for inaccessibility.

Foraging fix ID	Individual	Land-use category	Reason for inaccessibility
<i>F3_040</i>	3	Agriculture	Private property
<i>F3_055</i>	3	Agriculture	Private property
<i>F4_002</i>	4	Agriculture	Private property
<i>F1_145</i>	1	Mining	Dangerous/steep terrain
<i>F1_148</i>	1	Reserve	Dangerous/steep terrain
<i>F3_028</i>	3	Reserve	Restricted access – water catchment area
<i>F3_029</i>	3	Reserve	Restricted access – water catchment area
<i>F3_037</i>	3	Reserve	Restricted access – water catchment area
<i>F4_077</i>	4	Reserve	Dangerous/steep terrain
<i>F1_058</i>	1	Reserve	Could not get close enough to distinguish between 2 trees
<i>F1_086</i>	1	Reserve	Could not get close enough to distinguish between 2 trees
<i>F1_092</i>	1	Residential	Dangerous/steep terrain
<i>F1_132</i>	1	Residential	Private property, no one home
<i>F10_005</i>	10	Residential	Private property, no one home
<i>F3_001</i>	3	Residential	Private road – no access signage
<i>F3_013</i>	3	Residential	Dangerous/steep terrain
<i>F3_020</i>	3	Residential	Private property, no one home
<i>F3_032</i>	3	Residential	Rural residential private property
<i>F3_058</i>	3	Residential	Private property, no one home
<i>F3_069</i>	3	Residential	Private property, no one home
<i>F4_082</i>	4	Residential	Private property, no one home
<i>F4_086</i>	4	Residential	No tree at location
<i>F4_103</i>	4	Residential	Private property with signage
<i>F6_003</i>	6	Residential	Private property, no one home
<i>F6_005</i>	6	Residential	Dangerous/steep terrain
<i>F6_006</i>	6	Residential	Dangerous/steep terrain
<i>F6_008</i>	6	Residential	Dangerous/steep terrain
<i>F6_020</i>	6	Residential	Private property, no one home
<i>F6_021</i>	6	Residential	Private property, no one home
<i>F6_025</i>	6	Residential	Private property, no one home
<i>F2_059</i>	2	Residential	Private property, no one home
<i>F2_067</i>	2	Residential	Dangerous/steep terrain
<i>F1_127</i>	1	Road/river	Private property, no one home
<i>F7_006</i>	7	Road/river	Within locked fence on golf course
<i>F3_014</i>	3	Utilities	Restricted access – Kangaroo Creek reservoir

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