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JAMES COOK
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Studying mobile species in spatially complex ecosystems:
Australian flying-foxes as a case study

by

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BSc (hons) James Cook University, 2006.

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Doctor of Philosophy

in the discipline of Zoology and Tropical Ecology

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ABSTRACT

The high degree of environmental heterogeneity present in Australia has resulted in species possessing specific traits that ensure their survival, one such trait is a high degree of mobility. Some species will migrate or travel long distances in order to track seasonally available resources. This makes the monitoring of mobile species difficult and as climate change continues to affect the timing and availability of these resources, understanding the response of these species is more important than ever. Here I use flying-foxes (*Pteropus* spp.) as a study group as they are highly mobile, the influence of climate change on their distribution is yet to be investigated, they have complex management issues and they are widely distributed across coastal Australia. I identify methods of monitoring highly mobile flying-foxes on a variety of spatial and temporal scales. I then apply the ecological information collected to a specific management issue: bat strikes in the aviation industry.

I develop a new method of monitoring flying-foxes at camps that are difficult to access: aerial photography. This technique produces results comparable to traditional census methods, and the remote capture allows access to information on camps that were impossible to access before. My results from North Queensland show that camp use is highly variable and that patterns shown at a regional level are not necessarily reflected at all camps. This technique can be applied across large areas and could be the key to a national monitoring strategy for Australian flying-foxes.

I then develop climate models for all four Australian mainland flying-foxes on a national scale and find that parameters associated with precipitation are the single most important climatic factor contributing to flying-fox camp location. This could be due to the importance of precipitation for the fruiting and flowering phenology of flying-fox food trees. When modeling the changes in climatic space for these four species with global climate data from 2030, 2050 and 2070. I find that three species (*Pteropus alecto, P. conspicillatus* and *P. scapulatus*) should experience an increase in mean area and abundance at

each time slice and that one species shows a decrease (*P. poliocephalus*). With variable future projections for precipitation in future global climate models and the absence of finer scale data, this should be interpreted with caution. Changes in distribution have been identified for all four species already and a camp has been located that now contains all four species, when previously only two were known to co-roost at this location. The climate at this location is suitable for the two newly recorded species but marginally so for one (*P. conspicillatus*). Evidence suggests that *P. poliocephalus* has historically occurred at this location but that *P. conspicillatus* has more recently occurred in this region, possibly as a result of climate change.

To explore the ecological factors influencing behaviour at a local scale, emergence timing at a flying-fox camp in tropical North Queensland was investigated. This also allowed me to determine if the factors influencing emergence timing in the tropics differed from other areas. I found that a linear relationship with the time of civil twilight explains most of the variation in emergence time, but that significant effects of weather, month and year also exist. Many of these factors also related to light levels, with cloud cover and heavy rainfall, delaying emergence. There was also a possible influence from increased anthropogenic lighting over the seven years of the study as I found that yearly variation in emergence time is correlated with increased activity from a nearby port, possibly reflecting increased light pollution. On a monthly basis, emergence timing was influenced by seasonal variation in roost occupancy, suggesting that foraging competition may also influence this behaviour. At a finer scale again, I investigated roost tree usage within camps and found high variability on a variety of time scales with seasonal changes in abundance overlain on highly variable day-to-day patterns of roost use.

To apply this information to a current management problem, I next investigate flying-fox movements and strikes at a local airport and on a national scale. To identify movement patterns at an airport, I develop motion-detecting infra-red camera technology to detect nocturnal wildlife movements. I found that flying-foxes dominate the nocturnal wildlife activity at this airport and that there are seasonal peaks of activity in the periods preceding and following the wet

season. These peaks of activity correspond with flowering peaks of food trees in the region and a nightly peak of activity after sunset corresponded with the emergence time of flying-foxes in the region. Flying-foxes and birds had opposing directional movements with flying-foxes moving toward the urban centre in the evening whilst diurnally active birds were leaving the area. The pattern reversed in the morning when flying-foxes returned to the camp. This can be explained by the different activity patterns of these groups with both going to forage at different times. Infra-red cameras can provide an efficient and inexpensive monitoring tool for aviation managers and the similarity of local studies to national patterns provides evidence that nocturnal monitoring of wildlife can provide an excellent mitigation strategy. Data on a national scale showed that flying-fox strikes are increasing, are greatest in tropical regions, and are more likely during early evening and while an aircraft is landing rather than departing. These studies show that movements and patterns of aircraft strike differ for flying-foxes and birds and highlight the importance of taxon-specific studies.

I have shown that good baseline ecological data from a variety of spatial and temporal scales can provide important information for the management of flying-foxes at a local airport. I have also provided an overview of many monitoring methods that can be translated to other regions and to other highly mobile species.

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ACKNOWLEDGEMENT OF THE CONTRIBUTION OF OTHERS

Chapter #	Role	Co-authors
2	Writing	Parsons.
	Data collection	Parsons
	Development of technique	Parsons, Robson.
	Analysis	Parsons, Robson.
3	Writing	Parsons, Robson, Shilton.
	Data collection	Parsons
	Model development	Parsons, VanDerWal.
	Analysis	Parsons, VanDerWal.
4	Writing	Parsons
	Data collection	Parsons
	Analysis	Parsons, Jones, Robson.
5	Writing	Parsons
	Data collection	Parsons
	Analysis	Parsons, Robson.
6	Writing	Parsons, Robson.
	Data collection	Parsons
	Development of technology	Parsons.
	Analysis	Parsons, Jha, Burns.
7	Writing	Parsons, Robson, Luly, Blair.
	Data collection	Parsons
	Analysis	Parsons, Robson.

RESEARCH OUTPUTS ARISING FROM THIS THESIS

Peer Reviewed Journal Articles

1. **Parsons, J.G.**, VandDerWal, J., Robson, S.K.A. and Shilton, L.A.(2010) The implications of sympatry in the spectacled and grey headed flying-fox, *Pteropus conspicillatus and P. poliocephalus* (Chiroptera: Pteropodidae). *Acta Chiropterologica*:.

2. **Parsons, J.G**., Blair, D., Luly, J. and Robson, S.K.A. (2009). Bat strikes in the Australian aviation industry. *Journal of Wildlife Management*: **73(4):** 526 - 529.

3. **Parsons, J.G.**, Blair, D., Luly, J. and Robson, S.K.A. (2008). Flying-fox (Megachiroptera: Pteropodidae) flight altitudes determined via an unusual sampling method: aircraft strikes in Australia. *Acta Chiropterologica* **10(2)**: 377-379.

Peer Reviewed Book Chapters

4. Luly, J.G., Blair, D., **Parsons, J.G.**, Fox, S. and VanDerWal, J. (2010). Chapter 6: Last Glacial Maximum habitat change and its effects on the grey headed flying- fox (*Pteropus poliocephalus* Temminck 1825). In Simon G. Haberle, Janelle Stevenson & Matthew Prebble (editors), *Altered Ecologies: Fire, Climate and Human Influence on Terrestrial Landscapes,* Terra Australis 32. ANU E-Press, Canberra, The Australian National University.

5. **Parsons, J.G**., Robson, S.K.A. and Shilton, L.A. (2010). Roost fidelity in spectacled flying-foxes (*Pteropus conspicillatus*): Implications for conservation and management. *Proceedings of the Symposium on the Biology and Conservation of Australasian Bats.* in press

Reports to Industry

6. Robson, S.K.A., Blair, D. Luly, J. and **Parsons, J.G.** Annual Report for Townsville Airport (August 2007 – July 2008). Minimising the risk of flying-fox strikes to Australian aircraft.

7. Robson, S.K.A., Blair, D. Luly, J. and **Parsons, J.G.** Annual Report for Townsville Airport (August 2006 – July 2007). Minimising the risk of flying-fox strikes to Australian aircraft.

8. Robson, S.K.A. and **Parsons, J.G.** Towards a National Aviation Policy Statement: Issues Paper April 2008. Minimising the risk of bat strikes in the airline industry: a new threat to Australian aircraft.

Conference/Workshop Presentations

9. **Parsons, J.G.** *Studying mobile species in spatially complex ecosystems: flying-foxes as a case study.* James Cook University. 14th July 2009.

10. **Parsons, J.G.**, VanDerWal, J., Robson, S.K.A. and Shilton, L.A. *Micro and macro scale sensing of flying-fox camps in Australia.* 1st International Symposium on Bat Migration. Berlin, Germany. 16-18 January, 2009.

11. **Parsons, J.G.**, Blair, D., Luly, J. and Robson, S.K.A. *Bat strikes in the Australian aviation industry.* 1st International Symposium on Bat Migration, Berlin, Germany, 16-18 January 2009.

12. **Parsons, J.G.**, Robson, S.K.A., Blair, D., Shilton, L.A. and Luly, J. Australian Aviation Wildlife Hazard Group – Education and Information Sharing Forum. Sydney International Airport, Sydney. *Understanding bat strikes in the Australian Aviation Industry.* 11th August, 2008. **Invited speaker.**

13. **Parsons, J.G**., Robson, S.K.A., Blair, D. and Luly, J. *Flying-fox strikes in the Australian aviation industry.* International Bird Strike Conference, Kingston, Canada. 10 – 13 September 2007.

14. **Parsons, J.G**., Robson, S.K.A., Blair, D. and Luly, J. *Aerial photography and digital image analysis: New techniques for monitoring problematic flying-fox camps.* 14th International Bat Research Conference, Merida, Mexico. 19 – 23 August 2007.

15. **Parsons, J.G.**, Robson, S.K.A., Blair, D., Shilton, L.A. and Luly, J. *A preliminary analysis of aircraft bat strikes in Australia.* Symposium on the Biology and Conservation of Australasian Bats, Sydney. 12-14th April 2007.

16. **Parsons, J.G.**, Robson, S.K.A., Blair, D., Shilton, L.A. and Luly, J. *Aerial photography and digital image analysis: New techniques for monitoring problematic flying-fox camps.* Symposium on the Biology and Conservation of Australasian Bats, Sydney. 12-14th April 2007.

17. **Parsons, J.G.**, Robson, S.K.A., Blair, D., Shilton, L.A. and Luly, J. *The foraging ecology, diet and movement of Australian Pteropodids: Implications for aircraft strike.* Botanists and Zoologists of North Queensland Conference, Cairns. 18-19th November 2006.

18. **Parsons, J.G.**, Robson, S.K.A., Blair, D., Shilton, L.A. and Luly, J. *When bats and planes meet: Minimising the risk of bat strike to the Australian Aviation Industry.* Australian Aviation Bird and Animal Hazard Working Group – Education and Information Sharing Forum. Sydney Airport,

Sydney. 27th September, 2006. ***Invited speaker***.

19. Robson, S.K.A., **Parsons, J.G.**, Blair, D. and Luly, J. *When bats and planes meet: Minimising the risk of bat strike to the Australian Aviation Industry.* 12th Australasian Bat Society Conference, Auckland, New Zealand. 19 -21st April, 2006.

Chapter 1 - General Introduction

The use of heterogenous landscapes by mobile species

Heterogeneity refers to the complexity and/or variability of a system property in space and/or time (Li and Reynolds, 1995). Environmental heterogeneity influences species density (Chamberlain et al., 1999) and diversity and it plays an important role in population stability (Oliver et al., 2010, Kindvall, 1996, Kareiva, 1990). The strength of this relationship is influenced by the mobility of the species (Öckinger et al., 2009) and the manner in which animals search for resources is critical to their success (Fritz et al., 2003). When resources are variable in space and time, an increased ability to track them can be very beneficial (Roshier et al., 2008). As a result, mobile species feature prominently in landscapes that have highly variable patterns of resource availability or that are resource-poor (Roshier et al., 2008).

For some mobile species, seasonal patterns of resource availability are predictable. Migration is a strategy that can be used by species responding to patchily distributed resources that are seasonally predictable and this is expressed by a strongly directional, regular seasonal movement to more favourable areas (Dingle and Drake, 2007) that correspond with resource availability (Boyle and Conway, 2007). Migration is commonly encountered in temperate species that experience predictable seasons, leading to predictable fluctuations in resource availability. For example, western north Atlantic right whales *Eubalaena glacialis*, undertake predictable long distance seasonal movements for foraging (Kenney et al., 2001). Other species have to employ different strategies if patterns of resource availability are irregular or unpredictable. Nomadism is a strategy used by species that follow the irregular availability of food items. These species show little site tenacity and no quantifiable directional component but will move long distances to track food resources, (Andersson, 1980) (Roshier et al., 2008). Nomadic behaviour is more prevalent in nectarivorous birds relying on irregular flowering in Australia (Woinarski, 2006) and in granivorous birds with fluctuating resources in semi-arid, South Africa (Dean, 1997). While these strategies have been

successful in the past, all species are now facing environmental change at an increasing rate and the influence of this change on mobile species and the way they track resources is unclear.

Mobile species in a changing environment

Ecosystems are spatially and temporally dynamic but at no time in recorded history has environmental change occurred at a more rapid rate than the present (Laurance, 1997, Hughes, 2003). This accelerated change is a result of human modification of ecosystems through agriculture, development and the over-exploitation of resources (Krummel et al., 1987, Manning et al., 2009). Additionally, anthropogenically driven climate change is having continuing impacts on ecosystem health and biodiversity (Root et al., 2003, Walther et al., 2002). One of the consequences of this accelerated change is an increase in environmental heterogeneity and a reduction in the size and spatial extent of vegetation fragments (leading to patchily distributed resources). As previously mentioned, these processes have a major effect on species persistence and their population dynamics (Kareiva, 1990).

There is already compelling evidence that global climate change is affecting the distribution, abundance and behaviour of species worldwide (Walther et al., 2002, Root et al., 2003). The impacts of these changes vary greatly between species and taxonomic groups. For example, the geographic range of the silver-spotted skipper butterfly (*Hesperia comma*) and the brown argus butterfly (*Aricia agestis*) in South-east England has expanded as a result of recent warming events (Thomas et al., 2001). Contrasting this, significant population declines of high altitude vertebrates at Monte Verde, Costa Rica, have occurred in the past 20 years as a result of climate change (Pounds et al., 1999). Many species traits have been identified as predictors of persistence in the face of climate change and one important trait identified for persistence is mobility or dispersal ability (Meynecke, 2004). It is predicted that mobile species will have greater adaptability to climate change as they will have a greater ability to move to more suitable habitats (Meynecke, 2004). British butterfly species have responded differently to warming in the last 30

years and it has been demonstrated that generalist species with greater mobility have a greater likelihood of survival (Warren et al., 2001).

Climate change has had vastly different effects on different regions For example, increases in precipitation have been recorded since the 1900's in Northern Europe, parts of Asia and north-west Australia (CSIRO, 2007) and declines have been observed in Central and Southern Africa, the Mediterranean and south-western Australia (CSIRO, 2007). Australia is a continent of extreme climatic variability, which provides challenging environments for species and has led to various survival strategies, including a high degree of mobility (Fleming and Eby, 2003). While temperature in Australia has risen consistent with global trends (0.74°C rise in Australia in the last 100 years compared with + 0.9°C worldwide since 1950), there has been increased variability in rainfall (Knapp et al., 2008) and increased incidence and intensity of extreme weather events (e.g. floods and storms) (CSIRO). As these environmental factors continue to change, the monitoring and management of mobile species will become increasingly difficult

Monitoring and management of mobile species

An important challenge for the management of mobile species is to identify areas of key habitat and to understand the environmental variables influencing their distribution (Roshier et al., 2008). This information is necessary to make targeted and effective management decisions (Roshier et al., 2008). Mobile species will often cross local, state or national boundaries (Mannert-Maschke, 2008) and many require connectivity of patches to persist (Mannert-Maschke, 2008). Various cross-institutional organisations and specialist legislation have been developed to conserve and manage migratory species that cross international boundaries as many species continue to decline (Kirby et al., 2008). An example of this is the convention on migratory species, an intergovernmental treaty developed through the United Nations Environment Program (UNEP) to conserve migratory species and their habitats on a global scale. This organization has developed agreements and memorandums of understanding in many regions for the conservation of

migratory species including European bats, dugongs, marine turtles and many migratory birds (Mannert-Maschke, 2008).

Mobile species are notoriously difficult to study but understanding their population dynamics, resource use and movement patterns, at a variety of scales, is important for ensuring their persistence in the future (Roshier et al., 2008). New methods and technology are now being used that allow researchers to track and monitor mobile species more effectively. The use of citizen science is one method used to address this problem (Cooper et al., 2007, Lee et al., 2006). Researchers train a group of interested volunteers across large geographical regions to gather important ecological data. This method does provide a cost-effective solution; however, there has been some criticism of the data reliability (Cohn, 2008). Despite this, important studies and discoveries have resulted from data collected by trained volunteers e.g. (Reif et al., 2008, Beaumont et al., 2006, Losey et al., 2007).

The increasing accuracy of satellite imagery and power of computing software means that some species' habitats can be located and monitored remotely. Vegetation containing Asian migratory locust egg pods can now be successfully identified in Uzbekistan using high resolution Landsat imagery (Sivanpillai and Latchininsky, 2008) and the abundance of ungulates in Africa can also be determined by measures of vegetative health extrapolated from NOAA images (Pettorelli et al., 2009) . Other new technology including: camera traps, night-vision equipment, thermal imaging and infra-red cameras and videos are also being used to monitor species that have been notoriously difficult to observe in the past (e.g. (Brown et al., 2005, Snyder et al., 2001, Laliberte and Ripple, 2003, Magome et al., 2007). Also, online resources have made databases of historical data more accessible (e.g. from museums, government agencies and special interest groups), allowing researchers access to important distribution data for habitat suitability modeling. These resources are particularly useful for the monitoring of biodiversity in response to climate change, (Lepetz et al., 2009) and many important examples of this exist (La Sorte and Thompson, 2007, Koleček et al., Parsons et al., 2010, Beaumont and Hughes, 2002, Townsend Peterson et al., 2001).

Many mobile species use the aerosphere for movement, to migrate, disperse or forage, yet little is known about the many organisms that spend substantial time using this space and the influence of human interference (e.g. buildings, pollution, aircraft) on them (Kunz et al., 2008). Species that spend significant time using this space are challenging to monitor and therefore difficult to manage (Kunz et al., 2008). A new discipline has emerged, 'aeroecology', with the aim of resolving this knowledge gap (Kunz et al., 2008). Aeroecology focuses on the natural phenomena and anthropogenic factors that influence the aerospere (Kunz et al., 2008).

Flying-fox movement and roost use

Flying-foxes (*Pteropus* spp., Pteropodidae) are large phytophagous bats that are capable of flying long distances for foraging (Hall and Richards, 2000). They are distributed throughout the paleotropics and many are restricted to islands (Hall and Richards, 2000). In Australia there are four species of *Pteropus* present on the mainland, the black flying-fox (*Pteropus alecto*), the spectacled flying-fox (*P. conspicillatus*), the grey headed flying-fox (*P. poliocephalus*) and the little red flying-fox (*P. scapulatus*). Each of these species has a primarily coastal distribution with little red flying-foxes covering a much greater area than the others, and ranging much farther inland (Hall and Richards, 2000, Churchill, 2008).

Substantial resource fluctuation is a conspicuous feature of the Australian flying-foxes environment and bats relying on fruit and floral resources have to adapt to these fluctuations (Fleming and Eby, 2003). In order to maximize exposure to these resources, flying-foxes will travel short and long distances between roosts (commonly referred to as camps). Both the little red and grey headed flying-fox undertake long distance migrations following the patchy flowering of food trees. A single movement of 1600 kms was recorded when a little red flying-fox was found in New Zealand (Daniel, 1975), however more regular seasonal movements of this species from inland Australia to coastal

areas throughout the year have also been documented (Churchill, 2008, Sinclair et al., 1996). Grey headed flying-foxes have been recorded undertaking round trips of over 2000 km within a year using satellite telemetry (Tidemann and Nelson, 2004) and a distance of greater than 500 km in a month, detected with radio telemetry (Eby, 1991). A high degree of temporal fluctuation in flying-fox numbers in camps of all of four Australian mainland flying-fox species has been recorded (Spencer et al., 1991, Shilton et al., 2008, Parsons et al., 2006, Markus and Hall, 2004, Tidemann et al., 1999, Parry-Jones and Augee, 1992) indicating local movement between camps in their known range. These movements in black (*P. alecto*) and spectacled (*P. conspicallatus*) flying-foxes are more indicative of nomadic behaviour as long-distance migration in these species has not been recorded.

Australian flying-foxes are nocturnal and they commonly camp in vegetation patches by day in large numbers (Ratcliffe, 1932, Hall and Richards, 2000, Churchill, 2008, Nelson, 1965). These camps can contain hundreds to hundreds of thousands of flying-foxes (Churchill, 2008, Hall and Richards, 2000) and can consist of single or multiple species if their range overlaps (Nelson, 1965, Ratcliffe, 1932, Hall and Richards, 2000). Individuals hang exposed on tree branches usually wrapping their wings around them for protection (Ratcliffe, 1932, Churchill, 2008). Camps are present in a variety of vegetation types including: mangroves, riparian vegetation, urban parks, Eucalyptus woodlands and rainforest (Ratcliffe, 1932, Churchill, 2008). Camps may be occupied either permanently or seasonally and abundance at camps will also fluctuate seasonally, attributed to the availability of dietary resources (Churchill, 2008, Parsons et al., 2006, Parry-Jones and Augee, 2001, Markus and Hall, 2004).

Flying-fox monitoring and management

In order to monitor these large bats, a variety of methods have been used to estimate camp and population numbers. These have ranged from rough estimates based on observation of camps and the night-time emergence of

bats (Garnett et al., 1999, Ratcliffe, 1932, Eby et al., 1999, Vardon and Tidemann, 1999), to quantitative estimates of high precision and accuracy using modern video recording equipment (Westcott and McKeown, 2004, Forsyth et al., 2006). Belt transects are also used to count bats and estimate occupancy of roost trees e.g.(Garnett et al., 1999). Audio recordings were used in one study to infer camp size through the analysis of flying-fox vocalizations (Parry-Jones and Augee, 1992) but this method has not been used since. All of these techniques require access to the vicinity of the camp, this is problematic, particularly when the camp is located in a remote, impenetrable area or if it is located in mangroves known to be occupied by estuarine crocodiles.

All four Australian mainland flying-fox species present difficult management and conservation challenges. All species are regarded as a threat to orchard crops (Loebel, 1985, Tidemann et al., 1997) and commonly encounter conflict with humans in urban settings due to noise, smell, defoliation of roost trees and the concern of disease transmission (Tidemann, 2003, Thiriet, 2005, Thomson, 2007). However, each of these species provides important ecosystem services such as pollination, the dispersal of seed (Richards, 1990b, Parry-Jones and Augee, 1991, Parsons et al., 2006) and other vegetative propagules (Parsons et al., 2007); and two species (*P. conspicillatus* and *P. poliocephalus*) are now considered vulnerable in Australia (EPBC, 1999). For these reasons, being able to successfully monitor populations is critical to both their management and conservation.

Flying-foxes and air strikes as a study system

The mobile behaviour of flying-foxes also brings them into conflict with other elements of the aerosphere (Parsons et al., 2008).Damage to aircraft by wildlife is responsible for the loss of billions of dollars to commercial aviation authorities and operators worldwide due to damage, lost revenue and litigation (Allan and Orosz, 2001, Anon., 2001). There is also the potential for wildlife strike to lead to the loss of aircraft, resulting in injuries and the loss of

life (Wright, 2010). Because of the implementation of successful bird strike management programs, flying-foxes now represent a significant proportion of aircraft strikes in Australia (Christidis et al., 2006, ATSB, 2002, ATSB, 2010). In part, this reflects their relatively large body size (up to 1kg), nocturnal habits, and tendency to form large aggregations both in trees and in the air (Hall and Richards, 2000, Churchill, 2008). Flying-fox camps near tropical and subtropical Australian airports containing large numbers of roosting bats and their frequent foraging movements bring them into conflict with aircraft in this region (Parsons et al., 2008).

Successful bird strike management in Australia has been a result of targeted environmental modification at the airport (ATSB, 2002). This type of mitigation strategy uses the control of grass height, lights, surrounding vegetation and land use in conjunction with scaring techniques such as bird fright to reduce the number of bird using the airport environment and surrounds (ATSB, 2002). Flying-foxes provide a challenge for airport managers because in most cases they are not attracted to the airport environment *per se* but are simply commuting between foraging and roosting habitats (Parsons et al., 2008). This project has been designed to identify spatial and temporal information on the roosting and commuting behaviour of flying-foxes for bat strike mitigation.

Aims of the study

In this thesis I report a variety of methods to examine spatial and temporal patterns of roost use by highly mobile flying-foxes (*Pteropus spp.*) and uses an applied scenario (bat strikes in the aviation industry) in order to direct management decisions based on sound ecological knowledge. The primary aims of my work are as follows:

- Expand ecological knowledge of Australian flying-foxes on local and regional scales
- Develop and explore new techniques for locating and monitoring mobile animals in spatially heterogenous landscapes

- Predict the geographic distribution of flying-fox camps and the variables that contribute to this distribution
- Explore the dynamics of spatial and temporal resource use and how this influences movement and distribution
- Apply this information to a specific management scenario as a case study: flying-foxes and aircraft strikes

Thesis structure

This thesis is produced as a conceptually cohesive unit but each chapter is presented as a stand-alone publication. The overall thesis structure, context and spatial scale of each chapter are shown in Figure 1. Several chapters have already been published, see research outputs from this thesis (page iv) for details. For published chapters, I have followed the format of the publication with minor adjustments for this thesis. A combined reference list follows all chapters in order to minimise repetition and save space.

The organisation of my chapters and a short description is presented here:

Chapter 1: Introduces the subject of the thesis by outlining the spatial heterogeneity present in Australia, how mobile species have succeeded in this environment, outlining the difficulties in studying mobile species and introducing the study species and applied scenario that I will investigate.

Chapter 2: Trials the use of aerial photography as a new technique for monitoring flying-foxes at camps in the dry tropics of North-eastern Queensland. This new technique is successfully used to determine seasonal trends in roost use, producing comparable results to traditional counting methods. It also provides a safe and cost-effective method of detecting seasonal patterns that may be implemented on a regional scale.

Chapter 3: Uses historical data on a national scale to explore the climatic determinants of flying-fox distribution and the possible effects of global climate change on this distribution in the future. This chapter shows a marked increase in global climate space for three species of Australian flying-fox and a reduction for one. This chapter explores the other factors that may also contribute to the persistence of Australian flying-foxes with impending climate change.

Chapter 4: Expanding on the climatic model developed in chapter 3, I explore the implications of expanding ranges at a local scale. To do this, I examine the climatic suitability of a newly discovered camp containing all four species of Australian flying-fox and I discuss the implications of sympatry in two species previously thought to be allopatric.

Chapter 5: Uses a long-term data set (citizen science) to look for temporal patterns of roost usage by black (*P. alecto*) and little red (*P. scapulatus*) flying-foxes at a mangrove roost in the dry tropics region. This local study shows how light levels influence the emergence timing of flying-foxes and discusses the possible effects of light pollution and foraging competition on this behaviour.

Chapter 6: Here I use traditional observation methods to examine roost tree fidelity in spectacled flying-foxes (*P. conspicillatus*) within camps and how this varies over a wet season in the Australian Wet Tropics bioregion. I find high day-to-day variability in roost tree usage within these camps during this study, highlighting the importance of roost use knowledge for management and conservation.

Chapter 7: In this chapter I use novel infra-red camera technology at Townsville airport to monitor the movement of nocturnal animals over an eighteen month period. This local study shows that flying-foxes dominate nocturnal movements at this airport and that they have different movement patterns to birds. The factor contributing most to flying-fox movements at this airport is food resource availability.

Chapter 8: Here, I use historical data from an aviation regulatory body to determine temporal patterns of bat strike on a national scale and establish how these strikes relate to environmental variables. I find that most strikes occur in the tropics and that flying-foxes have patterns that differ from birds. In this national study, food resource availability is also reflected in patterns of flying-fox strike.

Chapter 9: Includes a summary of my major findings, the synthesis of my results on local and national scales, the implications for management and directions for future research.
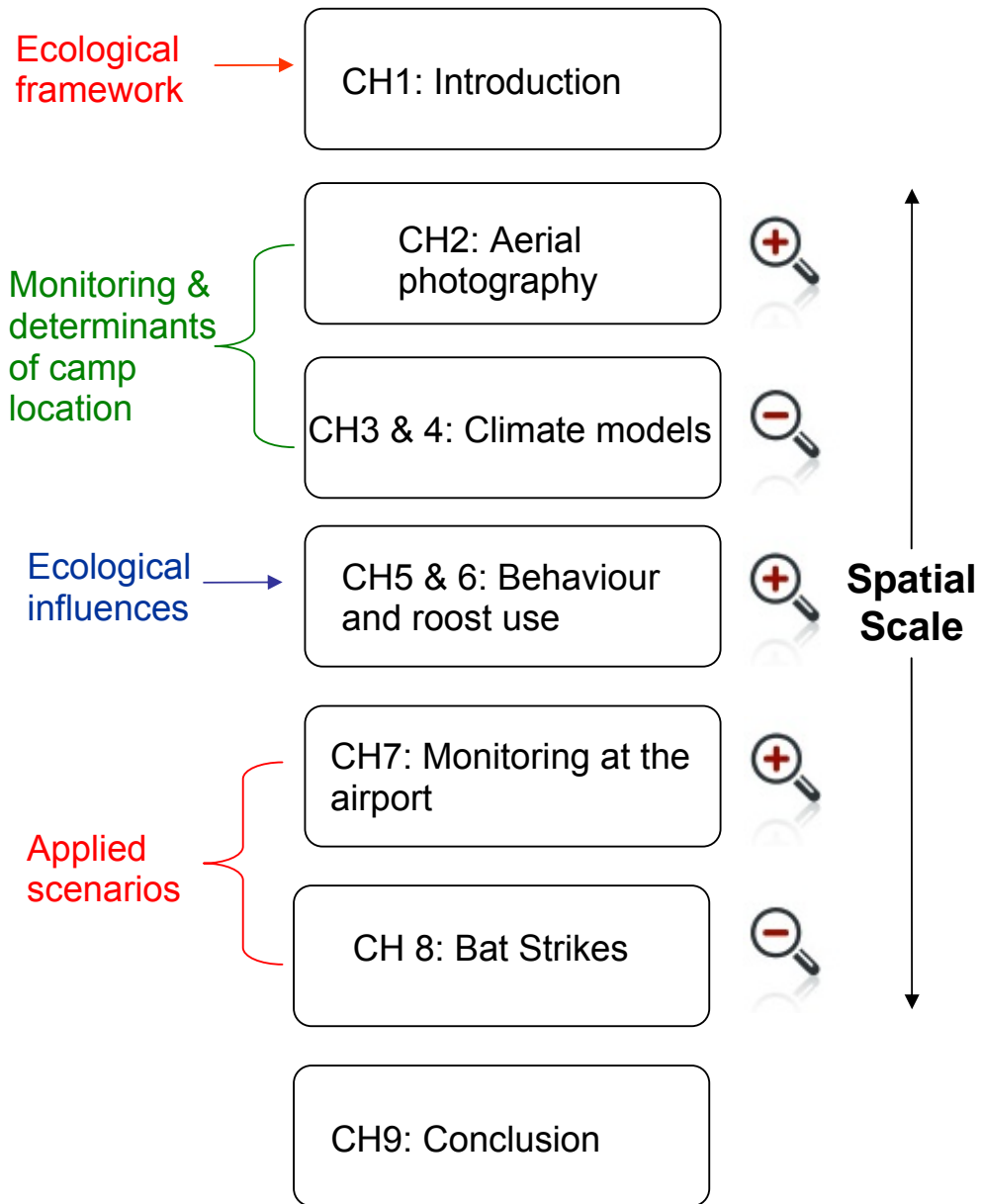
Figure 1: Overall thesis structure, showing the context and spatial scale of each chapter.

Chapter 2 - Monitoring flying-fox camps using aerial photography.

Abstract

Here we describe a photographic digital technique for the counting of flying-foxes from aerial photographs of day roosts (camps) in North-eastern Queensland. We compare this method with the traditional monitoring techniques of fly-out and transect counts. We find that the use of aerial photography produces accurate estimates of camp size, reduces the effort required and increases the safety of the observer. This method will be of great use in areas that are historically difficult to sample due to their remote location or because of safety concerns. As technology improves, aerial and satellite photography may also provide a useful tool for locating new camps. Our results show that roost use in this region is variable in individual camps and that patterns shown at a regional level are not necessarily reflected at all camps. We recommend the monitoring of individual camps for improved conservation and management outcomes.

Introduction

A detailed understanding of the seasonal movement patterns of a species is important for conservation prioritisation and the development of management strategies. However, this information can be difficult to obtain in highly mobile or cryptic species (McClelland, 2009). Aerial photography is a technique that has been successfully used to monitor a variety of populations for several decades, this has included; water birds (Brown et al., 2005), sea lion pups (Snyder et al., 2001, Hiby et al., 1987), jellyfish (Magome et al., 2007) and penguins (Trathan, 2004). While early use of aerial photographs required the manual counting of individuals from these images which is time and labour intensive, the recent availability and development of automated counting software has now emerged as a more accurate and time-efficient technique (Laliberte and Ripple, 2003).

In eastern and northern Australia, flying-foxes (*Pteropus* spp.) roost in day camps that can contain >100 000 individuals. Population census of flying-foxes is difficult as individuals can move between camps (Shilton et al., 2008, Markus and Hall, 2004) and undertake long-distance seasonal movements, such as those that have been documented in grey headed and little red flying-foxes (Tidemann and Nelson, 2004, Sinclair et al., 1996). Traditional techniques for flying-fox census include fly-out counts from the camp perimeter (Westcott and McKeown, 2004) and transect counts from within a camp (Shilton et al., 2008, Vardon et al., 2001) . Fly-out counts are most commonly used and this technique requires the perimeter of the camp to be surrounded by human counters or video recording equipment. Transect counts are conducted by individuals entering the camp, counting the number of bats in a representative number of trees, counting trees and then multiplication. In both of these methods, recorders need to be physically present at the camp.

Flying-fox population studies in Australia have been heavily focused on urban camps, presumably as many of these camps are situated in parks or reserves

in metropolitan areas and are easily accessible. While this work has added great value to our knowledge of flying-fox ecology, there are few studies located in areas that are remote or difficult to access. This is understandable as flying-fox population monitoring in some areas can be very complicated due to the species' highly mobile habits and their roosts being located in thick, inaccessible vegetation in potentially dangerous areas. An exception to this is important flying-fox research undertaken in the Northern Territory, where on many occasions researchers accessed camps by foot (Tidemann et al., 1999, Palmer and Woinarski, 1999).

Flying-fox camps in Northern Australia are typically located in thick mangrove forests or adjoining riparian vegetation (Vardon et al., 2001). This makes the use of traditional census techniques extremely difficult and dangerous due to impenetrable mangrove thickets, thick mud and the presence of estuarine crocodiles and wild pigs. Here we trial a new method of monitoring these camps remotely using high-resolution aerial photography and counting software and compare this technique to traditional census methods of fly outs and transect counts. We use this to identify a new technique for safely monitoring flying-foxes in remote regions and apply this technique to flying-fox camps in Townsville, North Queensland.

Methods

Eight flying-fox camps (day roosts) were monitored from October 2006 – May 2009 in Townsville, north-eastern Queensland. Four camps were counted quarterly (Bushland Beach, Magnetic Island-Arcadia, Mystic Sands and Ross River) and another four were monitored opportunistically (Billabong Sanctuary, Bohle, Magnetic Island-West Point and Kelso).

Predicting the number of bats in camps involved obtaining high-resolution digital aerial photographs of camps, calibrating image selection and counting procedures using the programs Adobe Photoshop and ImageJ, and then using these optimized procedures to count the number of bats in the camp as a whole.

Digital photographs were obtained using a12.4 mega pixel Canon 1D MK III with a 30mm lens. Images were taken from a Cessna light aircraft in the morning (from 08:00 – 10:00) at a height of 600 ft AGL (182.88 m). Photographs were taken of camps regardless of occupancy to ensure an reliable representation of occupancy was obtained over the two year census period.

The numbers of bats was estimated from digital photographs by importing the image into Adobe Photoshop, magnifying a portion of the total image, selecting a randomly chosen individual bat with the 'magic wand' tool (contiguous option unselected and tolerance level = 16) and saving this selection to a new layer as a .tiff image. This created a digital image only containing pixels from the entire image with a similar colour to those selected with the magic wand tool. This image was then imported into the program ImageJ (Abramoff et al., 2004), converted to an 8–bit binary format, and the number of individual particles counted automatically using the Analyse – Analyse Particles function.

Prior to counting bats, the tolerance levels within Adobe Photoshop were first optimized. We define tolerance level as the level that determines how similar pixels elsewhere in the image must be to those selected with the magic wand. One quarter of a complete image from a single camp was selected, printed at magnification and the number of bats counted in order to estimate the absolute number of bats visible in the photograph. Five bats were then randomly selected from this image at a tolerance level of 12 and the number of bats in each image counted using the method described in the previous paragraph. This procedure was repeated with the tolerance level incrementing by 2, up until a level of 24. A scatterplot of the relationship between the number of bats predicted in this image and the tolerance levels used during the Photoshop selection process was then used to optimise the tolerance selection procedure.

A pilot study initially tested for differences between transects and fly-out counts in order to find the best method for comparing traditional techniques to aerial photography. We conducted both traditional methods on the same day on six occasions at three easily accessible sites (Billabong Sanctuary, Ross River and Magnetic Island-Arcadia). Transects were marked and bats counted in trees along this transect, tree numbers at the camp were then estimated and the mean number of bats were multiplied by the number of trees. Then, at twilight, we used video equipment (SONY digital video camera recorder, Model No. DCR-SR100E on the 'NightShot plus' setting) to record the evening fly-out, cameras and/or observers were placed to capture all emerging streams of bats from the perimeter of the camp.

We used Pearson's correlation to compare counting techniques and all analysis was performed using S-Plus 8 for windows.

Results

A high resolution digital photograph was chosen from images taken at the Ross River camp on the 31st December 2006 (Figure 1). When manually counting flying-foxes in an enlarged quarter of the image, 753 bats were located. This image was then analysed in Photoshop and Image J using the methods described above (Figure 2). The calibration process indicated that a tolerance level of 16 best represented the number of bats manually counted in the image, at which Image J counted 700 bat shapes (Figure 3).

Our comparison of fly-out counts with transect counts showed a strong positive correlation (R^2=0.906, p= 0.003, n=6, Figure 4) between results obtained by each of the methods. Transect counts were then chosen to represent traditional methods, as this technique was the least resource intensive and produced similar results. When we then compared traditional methods to aerial photography from October 2006 – May 2009 and found that there was a strong positive correlation (R^2= 0.89, p<0.001, n = 23, Figure 5), with numbers at camps ranging from 0 – 46 521.
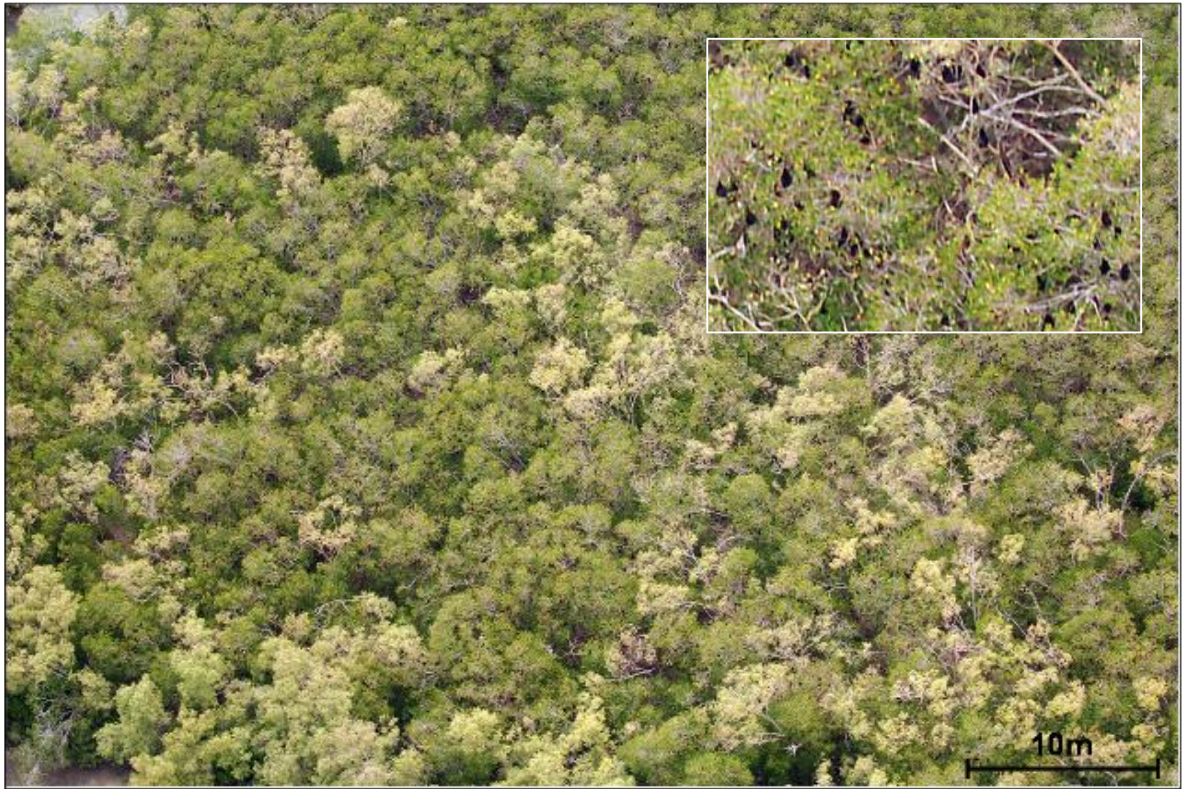
Figure 1: Digital image of Ross River flying-fox camp located in mangrove forest, Townsville northeastern Queensland. Image taken at 600 ft AGL (182.88 m)(182.88m) on 31/12/06 at 09:15 am. Inset is enlarged section of total image flying-foxes visible.
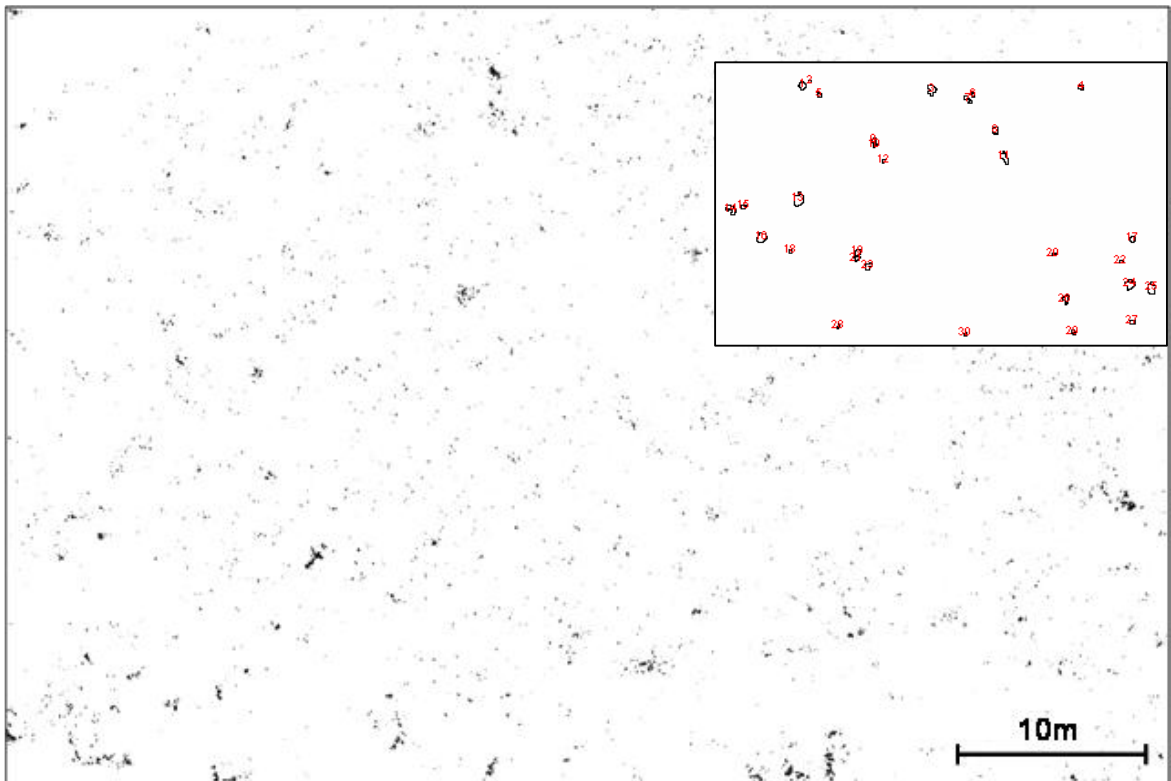
Figure 2: Digital image with 'bats' selected in Adobe Photoshop under a tolerance level of 16, inset image shows 'bats' being counted in Image J.
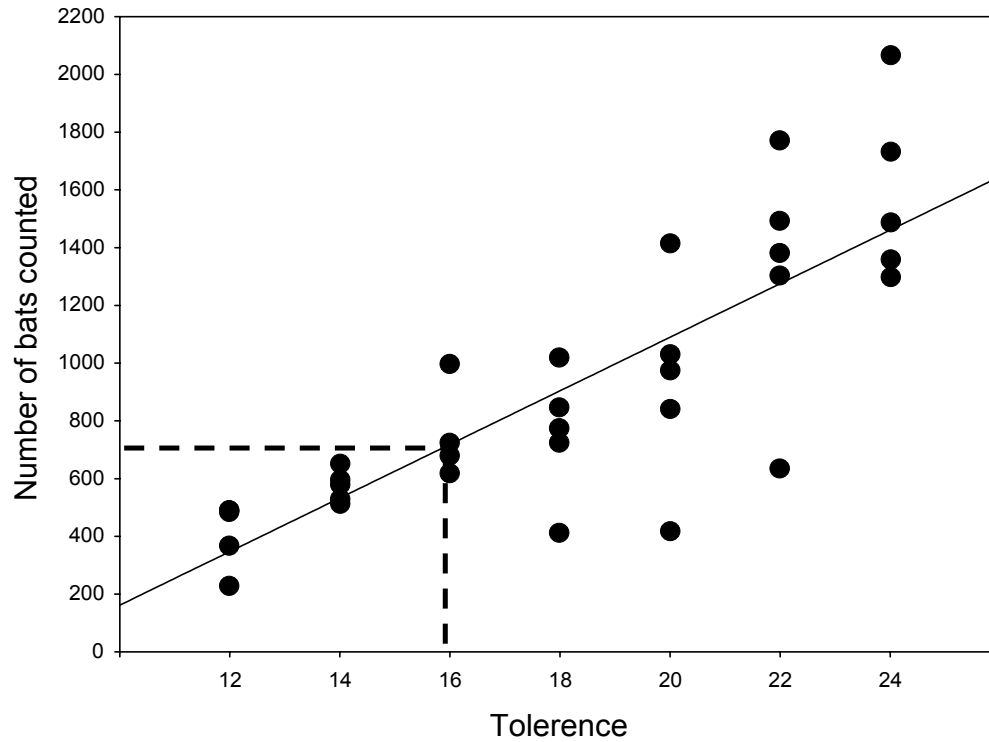
Figure 3: Optimising tolerance selection criteria. Dashed line indicates the tolerance level (16) that best predicts the observed number of bats in the sample image (753 bats) in our example.
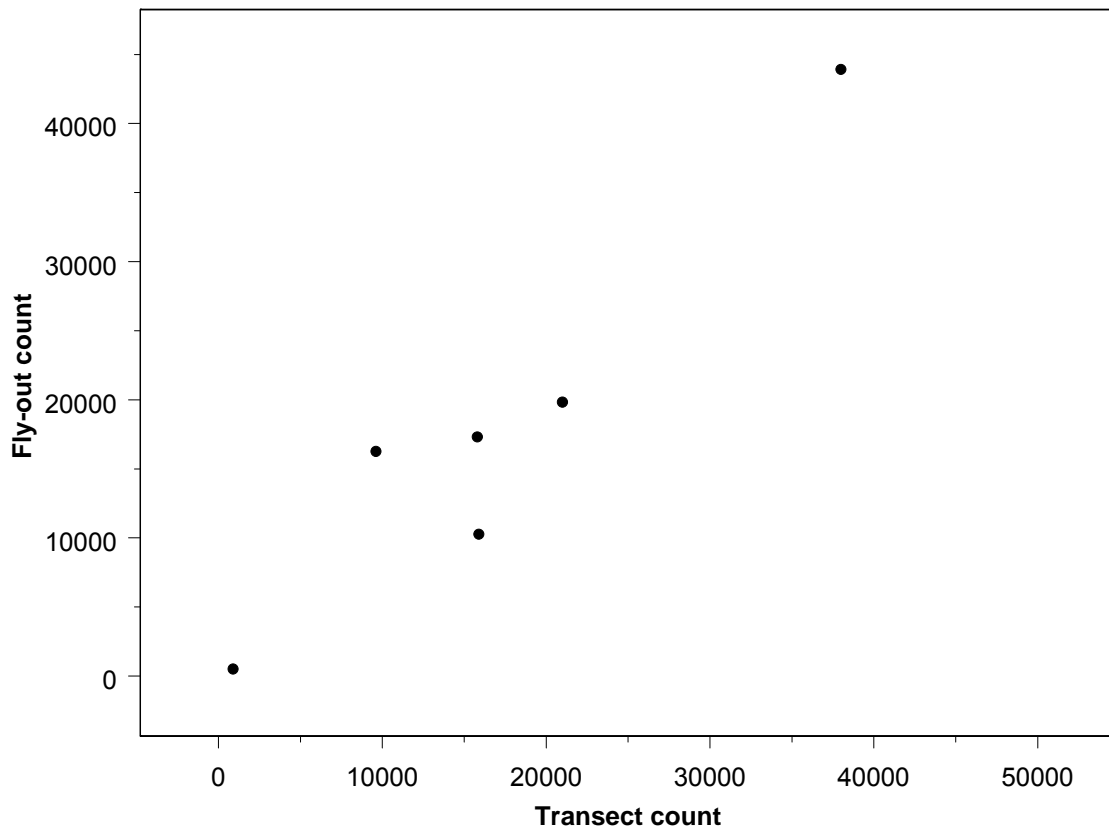
Figure 4: Comparison of two currently used techniques of count estimates, fly-out and transect counts at flying-fox camps in Townsville, northeastern Queensland (October 2006- May 2009).
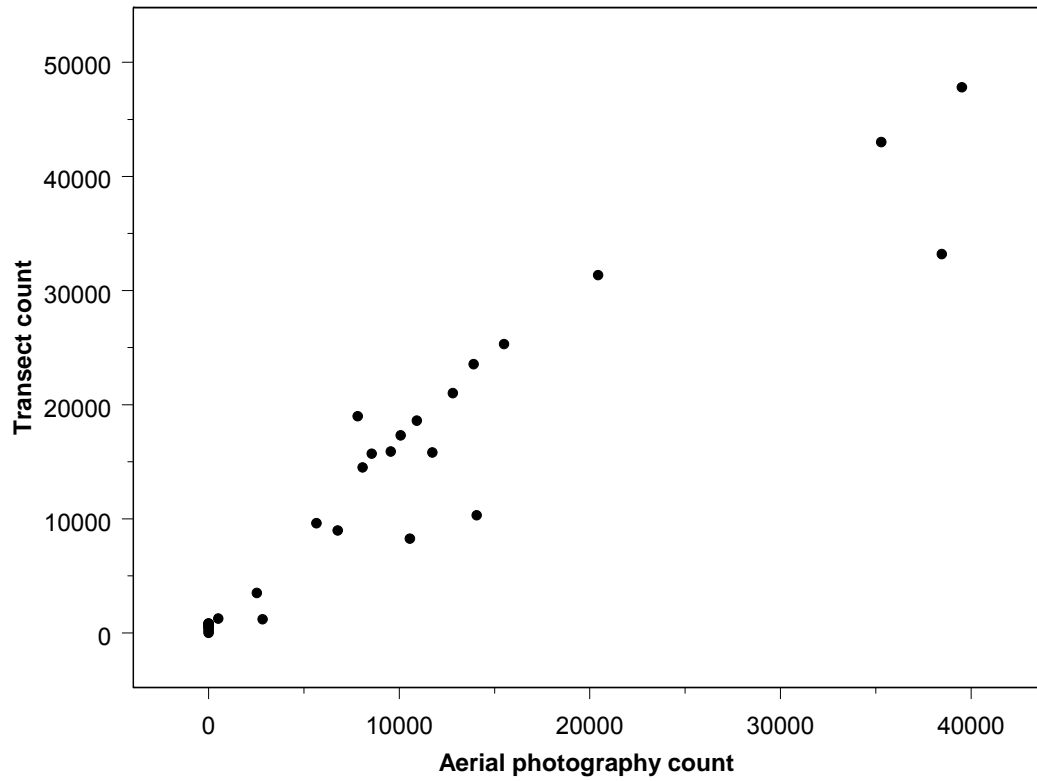
Figure 5: Comparison of aerial photography technique and transect estimates at eight flying-fox camps in Townsville, northeastern Queensland (October 2006- May 2009).

Estimated numbers at two camps had a bimodal distribution (Figure 6) indicating strong seasonal trends in occupancy. The largest estimated number of bats in a camp were counted at the Bushland Beach site in November 2008 (46 521 individuals counted). Estimated roost occupancy at the Ross River and the Bushland Beach site was highest from the late dry to early wet season (from September – December) and lowest during the winter months (from June – August). The Mystic Sands site also had its highest estimated occupancy during the late dry to early wet season but had lower occupancy occurring sporadically throughout the rest of the year (in January, March, April and July). The Magnetic Island site had its highest occupancy in July and November with fewer bats being present during February, May and December.

Discussion

While digital photographs are only capturing an image of the flying-foxes visible from above, data gained from pixels gives us an index of the number of flying-foxes present at each camp. In addition to population counts, seasonal fluctuations in camp size and vegetation use can also be detected using this technique. The key to an accurate representation of the seasonal patterns at these camps is to ensure accurate calibration and blind testing of images.

Fly-out counts are a resource intensive exercise with large numbers of people or expensive video recording equipment needed. If a camp is easily accessible, we found that transects provided a good alternative with comparable results. We also found that this technique created little disturbance to the camp, provided only one or two individuals entered the camp and that counters were quiet and measured in their movements. Neither method is suitable for camps in remote or dangerous areas where the perimeter of the camp cannot be safely reached.
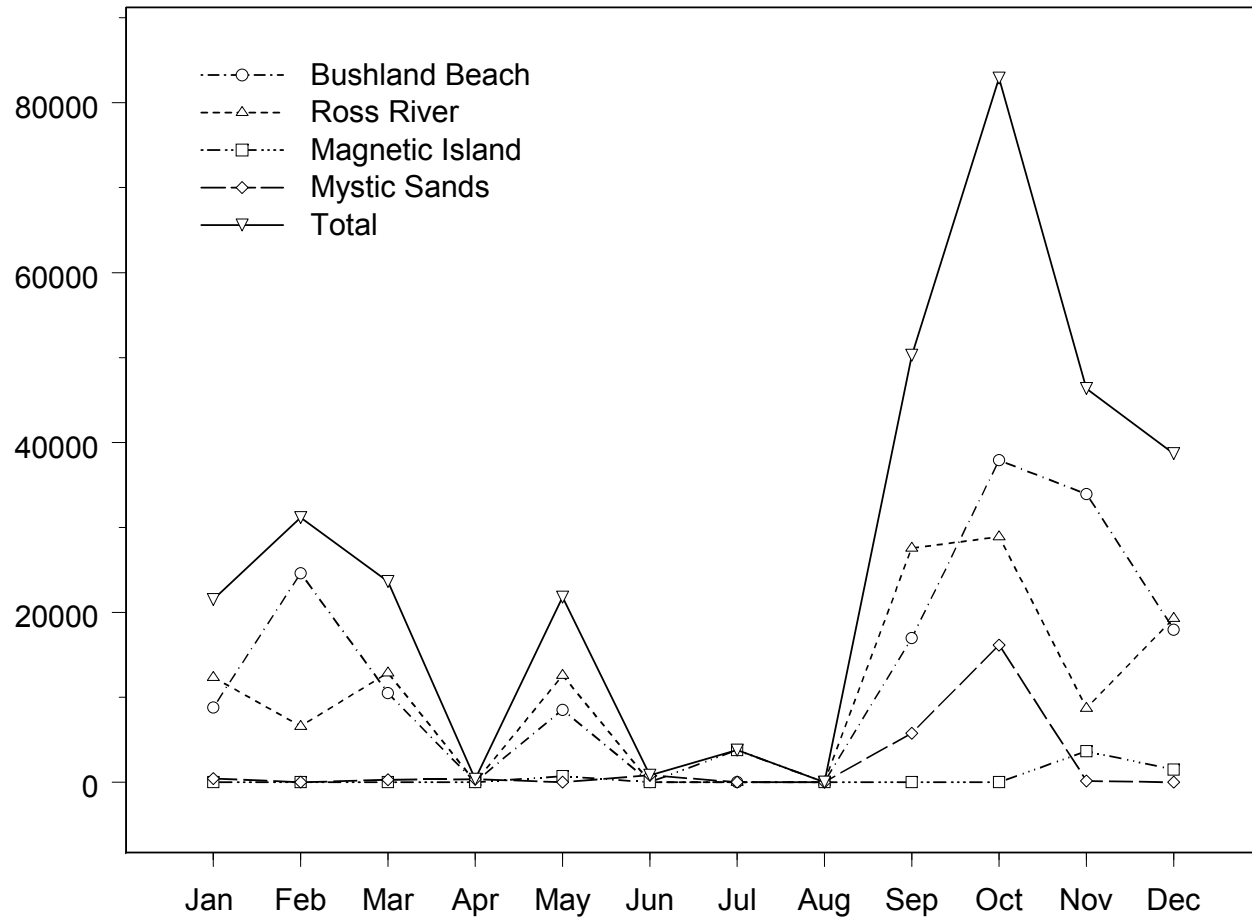
Figure 6: Estimated mean and total number of flying-foxes at four day camps in Townsville, northeastern Queensland, October 2006 - May 2009. Counts obtained from digital images of camps, each symbol represents a count averaged over 2.5 years for each month.

Similar results can be achieved using high-resolution aerial photographs and automated counting using programs like Image J. This means that camps throughout regional and remote Australia can be monitored safely and census studies need not be restricted to camps in urban settings. As the quality and resolution of satellite imaging improves with time it may also become possible to use these images to monitor flying-fox population on large scales and even to identify the location of new camps.

In our study, we were able to identify trends of roost occupancy that closely matched those of previous years (see chapter 5, this thesis) and provide a good understanding of the seasonal patterns present in Townsville's dry tropics region. It appears that the more stable camp sites (Ross River and Bushland Beach) have predictable seasonal occupancy at the roost that closely reflects the flowering phenology of the region. Flying-foxes in this dry region are more likely to rely on nectar and pollen than fruits (Parsons unpub. data) and peak flowering occurs in the late-dry to early-wet season (Boulter et al., 2006), there is also an influx of migratory little-red flying-foxes (*Pteropus scapulatus*) at this time, which is again likely to reflect the availability of floral resources for these primarily nectivorous bats.

In comparison, the sporadic use of the smaller Magnetic Island and Mystic Sands camps (<15 000 individuals), indicates a more opportunistic use of roost resources throughout the year. Differences in camp size (<1000 or >1000), sex ratios and age structure have led to the classification of main and satellite camps (Tidemann et al., 1999). While the smaller camps in our study (Magnetic Island and Mystic Sands) occasionally had numbers >1 000, they generally consisted of a high proportion of young male bats (Parsons, pers. obs.), were smaller and more sporadic in occupancy compared to the Ross River and Bushland Beach camps. For this reason, we believe that Ross River and Bushland Beach to be main camps and that Magnetic Island and Mystic Sands are satellite camps. The identification of these different seasonal patterns at individual camps has shown that patterns reflected at the population level for a

region do not necessarily reflect what is happening at all camps. There is a clear need for population census to occur at the camp level.

Our study has shown that it is possible to monitor remote flying-fox camps with decreased effort and greater safety. We have also shown similar trends in roost use and occupancy to other parts of northern Australia. As technology continues to improve, the fine scale accuracy of counts from digital imaging will also improve and it may provide an excellent tool for identifying the location of unknown camps both locally and internationally.

Chapter 3 – The distribution of flying-fox camps in Australia: new perspectives in a changing climate.

Abstract

Knowledge of the factors influencing a species distribution underpins management and conservation decisions. This is particularly so for highly mobile species whose distributions may closely match changing climatic conditions. Flying-foxes (Megachiroptera: Pteropodidae) in Australia are highly mobile animals that depend on a variety of seasonally changing food resources, yet despite some evidence for recent changes in the location of camps, little is known about their overall distribution and the environmental determinants of this distribution. We aim to fill this gap in knowledge. We use camp localities to develop a predictive climatic model to examine recent changes in distribution and use future global climate models (GCM) for 2030, 2050 and 2070 to elucidate potential changes to this distribution in the future. The climatic variables that contribute most to the location of flying-fox camps in our model are aspects of precipitation for all species. This could be due to the importance of precipitation for the fruiting and flowering phenology of flying-fox food trees. We found that mean future GCM results showed an increase in climatic space for three species (*Pteropus alecto, P. conspicillatus and P. scapulatus*) and a decrease for one (*P. poliocephalus*). We have provided important information on the distribution of flying-fox camps in Australia and the climatic factors contributing to this distribution. Our future projections should be cautiously interpreted and future models should incorporate finer detail climate data and important life history traits.

Introduction

Human induced climate change continues to result in increased temperatures and precipitation variability (Walther et al., 2002), while the frequency and severity of extreme weather events is also increasing (Easterling et al., 2000, Walsh and Ryan, 2000). These changes have had a profound influence on the distribution of a wide variety of taxa worldwide (Walther et al., 2002, Parmesan, 2006, Parmesan et al., 1999). These range shifts can be attributed to factors such as: the availability of food resources and roosts, species' temperature tolerance, changed species interactions, and phenologies (Walther et al., 2002, Dyrcz and Halupka, 2009, Hegland et al., 2009, Scheel et al., 1996). Climate-driven distributional changes can occur on an altitudinal gradient (Pounds et al., 1999) or by poleward shifts (La Sorte and Thompson, 2007) and these distributional shifts have been demonstrated in many studies located in the northern hemisphere (Perry et al., 2005, Parmesan, 1996, Gonzalez-Megias et al., 2008, Parmesan et al., 1999, Reif et al., 2008, La Sorte and Thompson, 2007, Barry et al., 1995, Dyrcz and Halupka, 2009, Thomas and Lennon, 1999). However, there is paucity in information dealing with changes in species distribution in the southern hemisphere (Isaac, 2008, Hughes, 2003). There are bodies of work concentrating on the impacts of climate change on the distribution of Australian tropical rainforest vertebrates (Meyneeke, 2004, Williams et al., 2003, Williams and Middleton, 2008) and some examples of changes in distribution do exist in other locations in the southern hemisphere (Taylor and Wilson, 1990, Pounds et al., 1999). However, due to an absence of long-term data sets and resource allocation, examples like these are certainly not as widely available or on the same scale as those from the northern hemisphere.

The dispersal or migratory capacity of a species is a critical determinant in climate driven range shifts (Walther et al., 2002). Birds in Britain, for example, extended their range northwards an average of 18.9 km in a period of 20 years (Thomas and Lennon, 1999), while the changing distribution of forest plants in

Northern Belgium is more limited as habitat fragmentation prevents dispersal into climatically suitable areas (Honnay et al., 2002). It is predicted that migratory animals or species with greater dispersal capabilities (such as birds, flying insects, and/or plants with wind-dispersed seeds) will respond more quickly to climate change as they have greater capacity to move poleward and will not be as hindered by landscape structure or fragmentation (Araujo and Pearson, 2005, Thomas et al., 2001, Parmesan et al., 1999). In contrast, species with low dispersal abilities or that are slow to adapt in the face of climate change may be at an increased risk of localised extinctions (Walther et al., 2002). By understanding the distribution and dispersal characteristics of the species at the forefront of climate driven adaptation and how climatic factors influence these distributions, we can piece together understanding of how other mobile species may respond in the future and how this dispersal will impact on more sedentary species.

Australia's mainland flying-foxes (Chiroptera: Pteropodidae, *Pteropus* spp.) are an ideal case study for understanding the response of mobile species to climate change. These species are large, highly mobile, volant mammals capable of travelling more than 20 km in one night (Parsons et al., 2006, Markus and Hall, 2004) and hundreds of kilometres whilst migrating (Tidemann and Nelson, 2004, Webb and Tidemann, 1996). Australia is a large isolated land mass with relatively good records of flying-fox distribution and while it has been shown that flying-foxes are susceptible to extreme temperatures (Welbergen et al., 2008), the implications of this and the influence of other environmental factors on flying-fox distribution have yet to be resolved. Evidence is emerging of distributional changes for all species. *Pteropus alecto* has extended its range hundreds of kilometres southwards over a number of years in the east of the country (Tidemann et al., 1999, Nelson, 1965) now extending to the Sydney Botanic Gardens (Parry-Jones, 2006), with a single individual recently being recorded as far south as Melbourne, Victoria (FFICN, 2010). *Pteropus conspicillatus* has been located 500 km south of its known range in North Queensland (Parsons et al., 2010), *Pteropus scapulatus* has been documented

in south-western Australia, (records of the South-Australian Museum) and camps have been present in Melbourne (M. Davidson pers. comm.), both being >1000 km south of its usual range. *Pteropus poliocephalus* now overwinters in Melbourne (Parris and Hazell, 2005), a single specimen has been located on the island state of Tasmania and camps have more recently been established in South Australia (FFICN, 2010), accounting for distributional changes over hundreds of kilometres.

Presence-only climate models are valuable in areas where absence data are deficient or lacking in rigor (Phillips et al., 2006a). These models are now being used widely as a method for predicting species distributions (Phillips et al., 2006a) and they have been useful for a wide range of biogeographical applications including the prediction of an organism's response to climate change (Shoo et al., 2005, Gibson et al.). Here we use the location of known flying-fox camps and environmental modeling techniques to describe the climatic range of all four Australian *Pteropus* species. We will identify which climatic variables influence the location of flying-fox camps, create a climate model and project this model into the future (2030, 2050 and 2070), using available global climate data.

Methods

The locations of camps (day roosts) were compiled from a variety of sources: *P. conspicillatus, P. alecto, and P. scapulatus* camp locations (48, 99, and 101 respectively) were derived from an online database (FFICN, 2010), published literature, local knowledge (O. Whybird *pers. comm.*), and personal observations (J. Parsons unpub. data); 57 *P. poliocephalus* camp locations were identified using published data (Parris and Hazell, 2005). Locations were excluded if precise localities were unknown. The distribution and known range for each species is shown in Figure 1.

We utilized a maximum entropy algorithm (Maxent) (Phillips et al., 2006b) to model the distribution of flying-fox camps in Australia. This algorithm represents a novel approach to species distribution modeling that has been shown to outperform other algorithms or techniques traditionally used in this type of study (Elith et al., 2006, Hernandez et al., 2006). Maxent has been optimized to use presence-only information (Phillips et al., 2006a, Phillips and Dudik, 2008) and has been shown to be insensitive to number of occurrences (e.g., can handle small samples) (Hernandez et al., 2006, Pearson et al., 2007). Maxent produces spatial predictions of environmental suitability as a value between 0 (not suitable) and 1 (most suitable). Cells in the prediction that were outside the environmental conditions of the training data were also identified (termed as clamped predictions). Because there is no simple way to project the response of an organism outside the environmental conditions of the training data set, Maxent assumes the response of the maximum or minimum value of the training data for projecting values beyond the conditions it was trained on. Thus Maxent identifies such predictions onto novel environments as clamped (levels of uncertainty in the model). Areas with a high degree of uncertainty were removed from the final model.

The climate baselines for training models were based on an 18-year summary of climate from1991-2008. This baseline represents the time that >90% of the occurrence localities were recorded. Six environmental variables were used and they were created using the Australian Water Availability Project (Raupach et al., 2008, Raupach et al., 2009). Models were projected onto climates representing 30-year averages surrounding 2030, 2050 and 2070 representing multiple global climate models (GCMs) and emission scenarios provided by the IPPC 4th assessment (Pachauri and Reisinger, 2007)**.** GCMs included BCCR, CSIRO mark 3.0 & 3.5, GISS AOM, INMCM, MIROC 3.2 high res and medium res, and NCAR CCSM 3.0. Emissions scenarios included SRES B1, SRES A2 & SRES A1B. Together this represented 25 scenarios for each of the species' predicted distributions in 2030, 2050 and 2070. The predicted distributions for
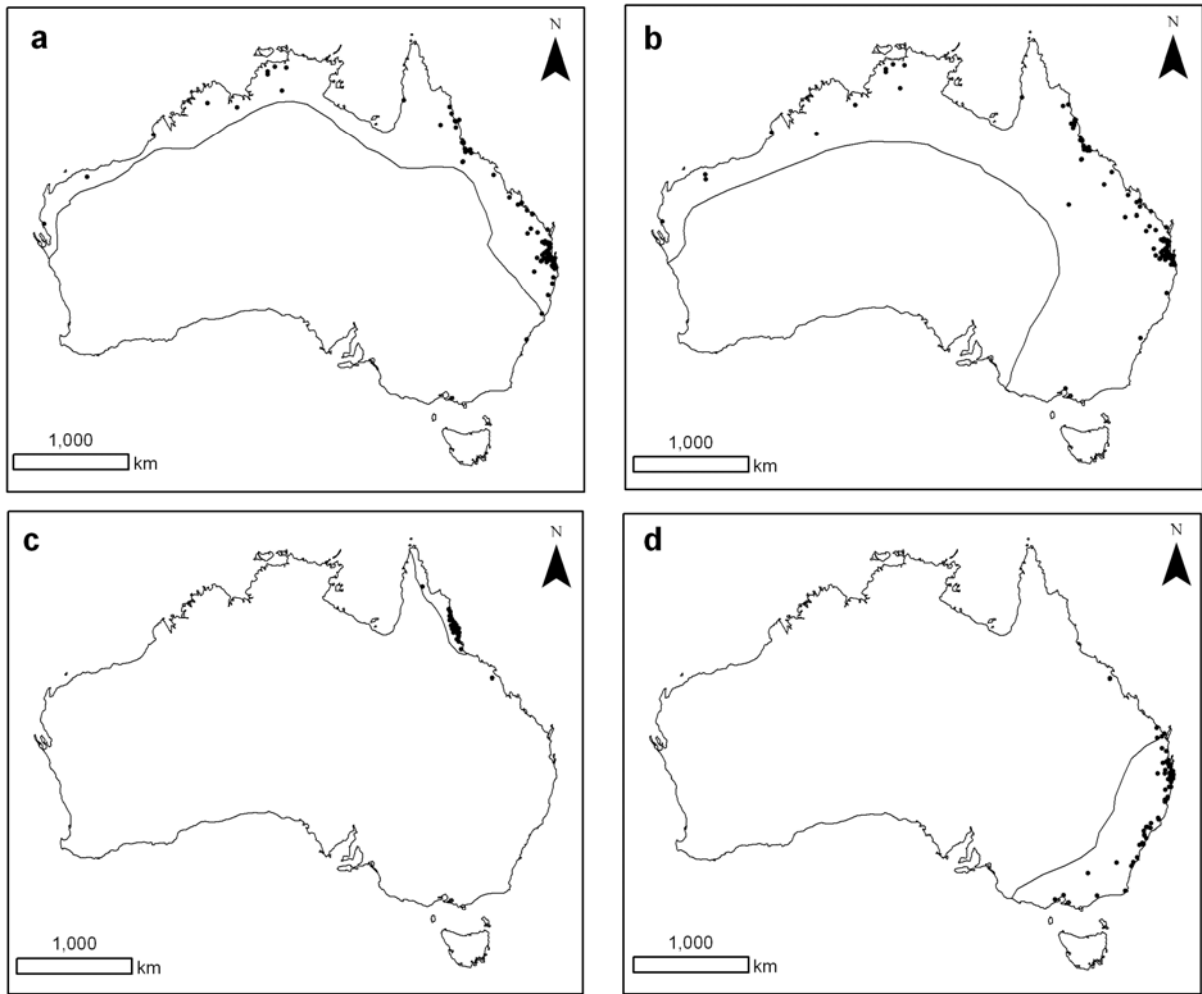
Figure 1: Actual distribution (closed circles) of camps of four Australian flying-fox species, *Pteropus alecto* (a), *P. scapulatus* (b), *P. conspicillatus* (c) and *P. poliocephalus* (d) based on records of camp occurrence. The accepted range limits of each species are shown as a line (Hall and Richards 2000).

each of the future climate periods were aggregated across all scenarios to provide a mean & standard deviation representing the 'most-likely' outcome.

An index of abundance for each species was created from MaxEnt outputs (methods described in VanDerWal *et al.* 2009). It has been demonstrated that predicted suitability can be used to provide an estimate of environmental carrying capacity (VanDerWal et al., 2009). Therefore, we were able to estimate abundance for each model prediction (recent and future) by summing the predicted environmental suitability from MaxEnt. The relative change in abundance was estimated as the ratio of the projected abundance (summed environmental suitability) with that of the climate baseline used to train the model.

Results

The current climatic space for Australian flying-fox camps is primarily restricted to coastal Australia with *Pteropus scapulatus* extending farther inland (Figure 2). The area identified for *P. conspicillatus* camps is restricted to the northern half of Queensland with two distinct areas of high suitability in the area surrounding the Atherton Tablelands and also in Cape York (Figure 2). Suitable areas for *P. conspicillatus* are also identified near Mackay, where the species has now been found (Parsons et al., 2010). The available climatic space for *P. alecto* and *P. scapulatus* camps cross eastern and northern Australia with some areas of suitability identified in Western Australia (Figure 2). *Pteropus poliocephalus* climatic space is identified along coastal southern Australia with northern areas identified around Finch Hatton and Cairns. These models are contrasted with their currently known range (Figure 2). The predictive performance of the distribution model generated under known climate was high for all species (*P. alecto* - AUC = 0.96; *P. conspicillatus* - AUC = 0.997; *P. poliocephalus* – AUC =0.983; *P. scapulatus* - AUC = 0.951).The ranked climatic variable contributions for each model are presented in Table 1, with the highest contributions for *P. alecto*, *P. poliocephalus* and *P. scapulatus* being
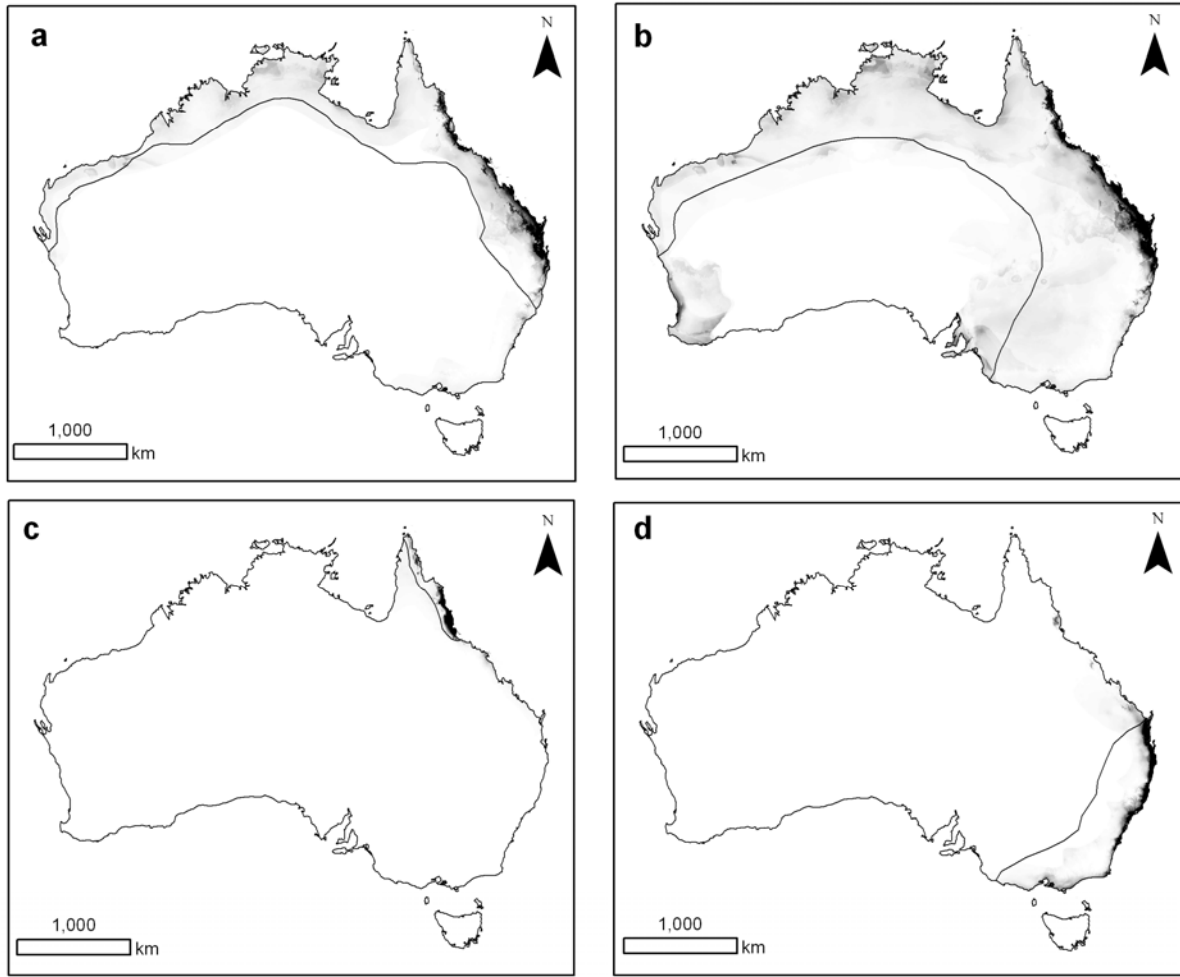
Figure 2: Modeled distribution (shaded) of four Australian flying-foxes, *Pteropus alecto* (a), *P. scapulatus* (b), *P. conspicillatus* (c) and *P. poliocephalus* (d) based on records of camp occurrence. Darker shading indicates areas of higher climatic suitability.

Table 1: List of variable contributions for flying-fox camp locations

Species	Climatic Variable	% Contribution
P. alecto	Precipitation of the driest quarter	33.2
	Minimum temperature of the coldest period	23.1
	Precipitation of the wettest quarter	21.8
	Annual precipitation	16.2
	Maximum temperature of the warmest period	5.6
	Mean annual temperature	0.1
P. conspicillatus	Precipitation of the wettest quarter	65.4
	Precipitation of the driest quarter	30.2
	Minimum temperature of the coldest period	2.2
	Mean annual temperature	2
	Annual precipitation	0.2
P. poliocephalus	Precipitation of the driest quarter	55.2
	Annual precipitation	19.4
	Minimum temperature of the coldest period	16.6
	Maximum temperature of the warmest period	6.6
	Precipitation of the wettest quarter	2
	Mean annual temperature	0.2
P. scapulatus	Precipitation of the driest quarter	36.7
	Minimum temperature of the coldest period	26.2
	Precipitation of the wettest quarter	19
	Annual precipitation	15.3
	Maximum temperature of the warmest period	2.2
	Mean annual temperature	0.6

precipitation of the driest quarter (33.2%, 55.2%, and 36.7% respectively), and for *P. conspicillatus*, precipitation of the wettest quarter (65.4%). Future predictions for each species (Table 2) indicate high levels of variation between global climate scenarios. When using means across all global climate scenarios, an increase (from current) in both area and abundance is identified for *P. alecto* and *P. scapulatus* at each projection with the amount of variability being greatest for the year 2070 (Table 2). Results for *P. conspicillatus* show a dramatic increase in area and an almost five-fold increase in abundance from present, peaking in 2050 (Table 2). *P. poliocephalus* is the only species identified with a possible decline in climatic space and abundance, again with great variability between global climate scenarios (Table 2).

Discussion

The distribution of Australian flying-foxes has changed in recent times, with evidence of all four species showing poleward expansion. Our results suggest increases in climatic space and abundance for three Australian flying-foxes and a projected decline in suitable area for one species (*P. poliocephalus*), that has already survived a significant reduction in available climatic space at the Last Glacial Maximum (Luly et al., 2010). Future climate predictions show decreases in average rainfall for southern Australia (CSIRO, 2007) and *P. poliocephalus* has the most southerly distribution of the four species presented here, which may be why the available climatic space for this species is contracting. The considerable expansion of suitable areas for *P. conspicillatus* and the marked increase in abundance in our model can be attributed to increased annual rainfall predictions for Queensland, particularly in the north and north-west (CSIRO, 2007). The high levels of variability present in our future projections are likely to be influenced by the uncertainty of future precipitation patterns and the highly seasonal rainfall patterns present across regions of Australia (CSIRO, 2007).

The success of flying-foxes in Australia's patchy landscape has been attributed to their capacity to travel great distances to exploit resources and

Table 2: Predicted distributional changes due to climate change based on our climate model.

Species	Projection Year	Change from Present Distribution Area Mean (± SD)	Change from Present Abundance Mean (± SD)
Pteropus alecto	2030	14.13% (± 12% SD)	16.59% (± 13.31% SD)
	2050	16.58% (± 15.91% SD)	7.15% (± 19.03% SD)
	2070	9.77% (± 20.48% SD)	9.16% (± 24.86 SD)
Pteropus conspicillatus	2030	65.75% (± 39.65% SD)	496.38% (± 622.81%SD)
	2050	69.98% (± 37.12% SD)	542.48% (± 625.62% SD)
	2070	73.85% (± 23.69% SD)	409.77% (± 259.94% SD)
Pteropus poliocephalus	2030	-7.4% (± 15.19 SD)	-2.65% (± 25% SD)
	2050	-15.6%(27.66% SD)	-13.33% (± 34.64% SD)
	2070	-15.6% (± 25.92% SD)	-12.51% (± 34.77% SD)
Pteropus scapulatus	2030	7.53% (± 7.3% SD)	12.34% (± 10.52% SD)
	2050	12.51% (± 15% SD)	29.44% (± 20% SD)
	2070	17.99% (± 17.39% SD)	4.79% (± 23.76% SD)

their adaptable diet (Birt et al., 1997), perhaps this ability will be what ensures the success of flying-foxes in the future. With predicted increases in temperature, CO_2 in the atmosphere and particular precipitation seasonality (Pachauri and Reisinger, 2007), the availability, nutritional quality, and distribution of resources is also predicted to change (Lawler et al., 1997, Hughes, 2003). The variables which have the greatest contribution to our model are aspects of precipitation for all species, as precipitation seasonality changes so too will the composition and distribution of the resources that organisms such as flying-foxes rely on. We will see more sporadic, larger rainfall events with increasing incidences of drought and flooding (Knapp et al., 2008) and as vegetation is largely water dependent, the diversity of vegetation in Eastern Australia is predicted to decline ≥20% with a 10% increase in precipitation and a 3° C increase in temperature and this diversity loss is doubled with decreased precipitation (Woodward and Rochefort, 1991). This will affect the timing of fruiting and flowering and in turn (Pachauri and Reisinger, 2007), these phenomena may ultimately alter reproductive timing and migratory processes of flying-foxes as dietary resource availability fluctuates and is less dependable. Competition for these valuable food resources by other mobile animals may also increase and the limited dispersal capabilities of some species compared to others will lead to unbalanced homogenous trophic systems (McKinney and Lockwood, 1999).

Incorporating life history traits of individual species and how they interact with changing climate is the next step in understanding how climate change impacts community composition (Isaac, 2008).We now know what climatic variables are the most important contributors to the distribution of flying-foxes in Australia, but our knowledge of their life history is still fairly limited. While flying-foxes do exhibit many of the traits of species that are adaptable to change [e.g. widespread, generalist diet, rapid dispersal (McKinney and Lockwood, 1999)], they do have low fecundity and considerable temperature sensitivity (Ratcliffe, 1932, Welbergen et al., 2008). Two species (*P. conspicillatus and P. poliocephalus*) are federally listed as 'vulnerable' (EPBC Act 1999), therefore the susceptibility of these species to mass fatality during extreme temperature events is of great concern. Perhaps the ability to track

valuable resources will increase interactions between species and bring susceptible species into areas with inhospitable climatic conditions. The energetic costs of increased travel between resource patches may also have deleterious effects on mobile species, particularly as the nutritional compositions of dietary items are also predicted to change.

Recent evidence suggests that using finer scale temporal climate data may be necessary for accurate model predictions of mobile species in Australia (Reside et al., 2010). This study showed that the use of long term climate data could mask the vulnerability of a species to climate change (Reside et al., 2010), so for this reason, our results should be interpreted with great caution. Compared to future models created for other vulnerable Australian species (Williams et al., 2003), flying-foxes appear to have more favourable outcomes predicted. We have provided an important baseline for future work but fine scale information on climate; vegetation and flying-fox life history traits are needed to derive more accurate predictions of their available habitat and vulnerability in the face of climate change.

Chapter 4 - The implications of sympatry in flying-foxes.

Abstract

Sympatry in flying-foxes is common throughout coastal Australia, however *Pteropus conspicillatus* and *P. poliocephalus* are thought to be allopatric. We examine the distribution of these two flying-fox species and report on the first flying-fox camp (day roost) with all four species of Australian mainland *Pteropus* co-occurring. Models were developed from previous records to determine if the location of this new camp is climatically suitable for these species. We found that this location is climatically suitable to some degree for both *P. conspicillatus* and *P. poliocephalus* but that the latter was more suited to this site. Historical records exist for *P. poliocephalus* close to this location but not for *P. conspicillatus*. The location of this mixed-species flying-fox camp is the most southerly distribution for *P. conspicillatus,* being 500 km further south than previous records. This area of overlap creates potential opportunities for interbreeding between *P. conspicillatus* and *P. poliocephalus*. Therefore, monitoring of this region for the location of further mixed-species camps and the degree of hybridisation at those locations is highly desirable.

Introduction

The distributional range of many organisms expands and contracts over considerable time periods (Lyons, 2003). This is due to natural climatic variation and temporal events like glaciations over millions of years through to regular seasonal variation and dispersal (Doak et al., 2008, Olea, 2008). However, some factors may accelerate distributional shifts; particularly for highly mobile species in spatially heterogeneous environments. With recent climate events and increased urbanization, many species are now finding refuge in new areas (van der Ree and McCarthy, 2005, Williams et al., 2006, Kurta and Winhold, 2007, Gonzalez-Megias et al., 2008) and their geographic distribution is expanding and/or contracting at a rapid rate as a result.

Climatic modeling based on known occurrences for species is an important new tool for predicting geographic distributions (Phillips et al., 2006a). These techniques also allow us to investigate records of species in contact zones and with overlapping ranges. For example, ecological niche based models have been used to predict the range of overlap in European vipers in a contact zone in northern Spain (Martinez-Freiria et al., 2008) and spiny pocket mice in South America (Anderson et al., 2002).

Large flying-foxes (*Pteropus* spp.) are capable of making long-distance flights over a sustained period of time, such as during southerly summer migrations (Ratcliffe, 1932, Nelson, 1965, Tidemann and Nelson, 2004). Studies of radio-tagged *P. poliocephalus* indicate movements of 610 km in 32 days, 210 km in ten days (Eby, 1991), and up to 750 km over 6-18 months (Spencer et al., 1991). Two satellite-tagged *P. poliocephalus* made roundtrips exceeding 2000 km and > 4° latitude over 7-10 months (Tidemann and Nelson, 2004). Similar seasonal patterns and range of movements have been recorded for three other *Pteropus* spp. in Australia, the black flying-fox, *P. alecto* (Tidemann et al., 1999), the spectacled flying-fox, *P. conspicillatus* (Shilton, Westcott and Latch unpublished data) and the little red flying-fox, *P. scapulatus* (Sinclair et al., 1996). However, we do not know if *Pteropus* spp. would intentionally travel

extensively beyond their usual roosting and breeding range. Additionally, we do not know if such events are caused by individual animals being, quite literally, blown off course by strong winds (*e.g.* King 1990), from changing habitats due to climate change or land-clearing activities or by human translocation (e.g. rehabilitated or 'pet' flying-foxes).

Range expansions and contractions have been noted in both *P. alecto* and *P. poliocephalus* in recent times (Tidemann et al., 1999, Birt, 2000a, Parry-Jones, 2006, van der Ree et al., 2006, Williams et al., 2006). The range of *P. alecto* has expanded southwards approximately 750 km in the past 75 years (Tidemann et al., 1999, Birt, 2000b, Eby, 2000) and this has been proposed as a factor contributing to the northern contraction of *P. poliocephalus (Birt, 2000b)*. Populations of *P. poliocephalus* have contracted 336 km south from 1882 (Collett, 1887) to the 1930's (Ratcliffe, 1932) and then contracted a further 384 kms south by 2000 (Birt, 2000b, Eby, 2000). In its southernmost distribution, *P. poliocephalus* has increased its range to include over-wintering in the urban environment of Melbourne (Menkhorst and Dixon, 1985, van der Ree et al., 2006), while this area was not thought to be part of the climatic niche of the species during winter, the increased temperature due to the 'urban heat island effect' has created an environment that is now suitable (Parris and Hazell, 2005).

Flying-foxes in Australia and elsewhere in their range sometimes roost in mixed-species camps (Hall and Richards, 1979, Richards, 1990a, Garnett et al., 1999, Tidemann et al., 1999, Stier and Mildenstein, 2005, Parsons et al., 2006). However, the recorded distributions of two vulnerable species (EPBC, 1999), *Pteropus conspicillatus* and *P. poliocephalus* are not known to overlap. Here we report for the first time the co-occurrence of these two species at Finch Hatton, mid-eastern Queensland, located approximately 500 km outside of each species' currently known distribution. All four Australian mainland *Pteropus* species (*P. alecto, P. conspicillatus, P. poliocephalus and P. scapulatus*) were found to inhabit this site at the same time. In this paper we will investigate the climatic space of *P. conspicillatus* and *P. poliocephalus* from

previously developed predictive models, discuss the range of overlap and its implications.

Materials and Methods

Location

This flying-fox camp or day roost is located on private property at Finch Hatton (-21.073975, 148.63495) in mid-eastern Queensland. The area is a lowland, semi-deciduous notophyll/mesophyll vine forest, fringing watercourses on alluvial plains; an endangered regional ecosystem (EPA, 2007). This site is also adjacent to Finch Hatton Gorge National Park.

Species identification

Identification of species was confirmed by the authors either by direct observation or from photographs (records and photographs collected by D. Lowe from 2005 - 2008 and by J. G. Parsons in June and July 2008). Both *P. conspicillatus* and *P. poliocephalus* are very distinctive species that are easily identified with the naked eye or as viewed through binoculars. *Pteropus conspicillatus*, while similar in features to *P. alecto* has distinctive rings or 'spectacled' markings around the eyes in addition to a pale straw-coloured mantle over the shoulders and neck. *P. poliocephalus* is the only species of the four present in Australia to have visible grey-tinged hair that extends to the feet on the dorsal surface ('trousers') and a thick band of orange fur around the neck.

Analysis

Climatic models for all Australian *Pteropus* species were created using MaxEnt (Phillips et al., 2006b), the details of these models are in Chapter 3, this thesis. Eight environmental variables were used as predictors in the final model; annual mean temperature, temperature seasonality, maximum temperature of warmest period, minimum temperature of coldest period, temperature annual range, annual precipitation, precipitation seasonality, precipitation of wettest quarter, and precipitation of driest quarter. Climate layers for the current climate

were estimated using Anuclim 5.1 software (McMahon et al., 1995) and a 9 Second Digital Elevation Model (Version 2; Geoscience Australia, http://www.ga.gov.au/). For both *Pteropus conspicillatus* and *P. poliocephalus*, MaxEnt outputs were extracted as points from both the currently known range of the species and from locality data (not including the Finch Hatton site) using Hawth's Analysis Tools version 3.2.7 (Beyer, 2004). The bioclimatic outputs for these locations were then plotted using 'R'(R, 2008).

Results

Species presence
Records kept by landowner, D. Lowe, show all four species of *Pteropus* (including, *P. conspicillatus* and *P. poliocephalus)* being present at this location from 2005 – 2008 (Table 1). As these records were not taken systematically, seasonal patterns and absences are not known. All four species were only recorded at this camp on two occasions, on the 25th December 2005 and on the 2 January 2006. *Pteropus poliocephalus* estimates have indicated the presence of hundreds to thousands of individuals at various times of the year (Parsons pers. obs) Contrasting this, *P. conspicillatus* is a regular visitor at a much smaller density though with groups of 10-20 individuals appearing usually during the warmer months of the year (Table 1). Flying-foxes at this camp will also temporarily relocate to Finch Hatton Gorge or Eungella National Park.

Pteropus scapulatus at this camp rarely roosted with any other species, while mixed species roost trees have been identified of *P. alecto*, *P. conspicillatus* and *P. poliocephalus*. On the 14th March 2006, mating was noted between a male *P. alecto* and a female *P. poliocephalus*. Frequent interspecies mating events were observed by D. Lowe but were not recorded.

Known distribution
Since *P. conspicillatus* and *P. poliocephalus* camps had not been recorded in this area before, we documented all published records. These did not show *P. conspicillatus* consistently occurring south of the dry belt of Townsville

Table 1: Records collected by landowner D. Lowe of flying-fox species presence at Finch Hatton camp. A cross indicates that the species was sighted by D. Lowe on that day, records were not collected on a regular basis and species absence does not necessarily indicate that they were not in the area.

Date	*P. alecto*	*P. conspicillatus*	*P. poliocephalus*	*P. scapulatus*
18/09/05	x	x	-	-
25/12/05	x	x	x	x
02/01/06	x	x	x	x
26/02/06	-	-	x	-
01/03/06	x	x	x	-
04/03/06	x	-	-	x
14/03/06	x	-	x	-
27/07/07	x	-	x	-
29/07/07	x	-	x	-
16/08/07	x	-	-	-
17/08/07	x	-	x	-
31/08/07	x	x	x	-
16/09/07	x	x	x	-
29/09/07	x	-	x	-
30/10/07	x	-	x	-
21/11/07	-	-	-	x
04/03/07	x	-	x	-
17/05/08	-	-	x	-
06/06/08	x	-	x	-

(Richards, 1990a, Churchill, 2008, Garnett et al., 1999, Hall and Richards, 2000, Shilton et al., 2008) (Table 2). Exceptions to this were two individual *P. conspicillatus* roosting in Brisbane, South-east Queensland, that were thought to be escaped animals from a rehabilitation centre (Richards, 1990a). Additionally, following severe category 4 Cyclone Larry in March 2006, two individual *P. conspicillatus* were seen roosting in the south of Townsville amongst a camp of *P. alecto* for several days (C. Pacey pers. comm.). This species is not known to occur south of Townsville and more recent searches have not located the species there since.

For *P. poliocephalus*, specimens have historically been reported as far north as Cape Upstart (Andersen, 1912) and Mackay (Collett, 1887), a single specimen was reported from Cape York in 1888 (Andersen, 1912) (Table 2) and two separate individual *P. poliocephalus* (L.A. Shilton, personal observation) found roosting in the Cairns region were thought to have been escapees due to their known distribution (P. Tully, personal communication). However, a range contraction from Rockhampton in the early 1930's (Ratcliffe, 1932) to Maryborough in the 1960's (Nelson, 1965, Tidemann et al., 1999, Birt, 2000a) occurred and as previously mentioned, there have been no records of *P. poliocephalus* occurring as far north as Mackay in over 120 years (Table 2). The most northerly point recorded for *P. poliocephalus* in an extensive survey in the late 90's was a state forest 40 km west of Maryborough (Birt, 2000a). Flying-fox camps between Townsville and Mackay have been regularly monitored since 2006 and Finch Hatton is now the most northerly location for *P. poliocephalus* (Parsons unpublished data), unfortunately camps between Mackay and Brisbane have not been regularly monitored by the authors, so the abundance and frequency of *P. poliocephalus* at locations south of Mackay are currently unknown.

Climatic models
When *Pteropus* camp distributions are modeled from known localities, Finch Hatton is included in the bioclimatic distribution of all four Australian mainland *Pteropus* species, including *P. conspicillatus* and *P. poliocephalus* (Fig. 1). This

Table 2: Previous records of the southern-most range of *Pteropus conspicillatus* and the northern most range of *P. poliocephalus*; distance and direction relative to the newly described mixed species camp located at Finch Hatton, Queensland.

Locality	Position	Distance and direction from Finch Hatton	Reference
Spectacled flying-fox, *Pteropus conspicillatus.*			
Hinchinbrook Island	-18.358222, 146.24823.	548 km north	Churchill 1998, Richards 1990.
Cardwell	-18.265114, 146.028558.	548 km north	Garnett et al. 1999.
Ingham	-18.650825, 146.154686.	495 km north	EPBC Act 1999. Shilton et al. 2008.
Tully	-17.934653, 145.923547.	592 km north	Hall & Richards 2000.
Grey headed flying-fox, *Pteropus poliocephalus.*			
Bundaberg	-24.866239, 152.345814.	677 km south	EPBC Act 1999.
Cape York	-10.908481, 142.469003.	1756 km north	Andersen 1912.
Cape Upstart	-19.725022, 147.778944.	233 km north	Andersen 1912.
Maryborough	-25.5402, 152.702442.	773 km south	Birt 2000b, Tidemann & Nelson 2004.
Miriam Vale	-24.328606, 151.560589	559 km south	Hall & Richards 2000.
Rockhampton	-23.379047, 150.5124.	389 km south	Churchill 1998, Nelson, 1965. Ratcliffe1932, Welbergen et al. 2008
Mackay	-21.143189, 149.186778.	63.4 km west	Collett 1887.
Southern Queensland	Unknown	Unknown	van der Ree et al. 2006
South of Townsville	Unknown	Unknown	Menkhorst & Dixon 1985.
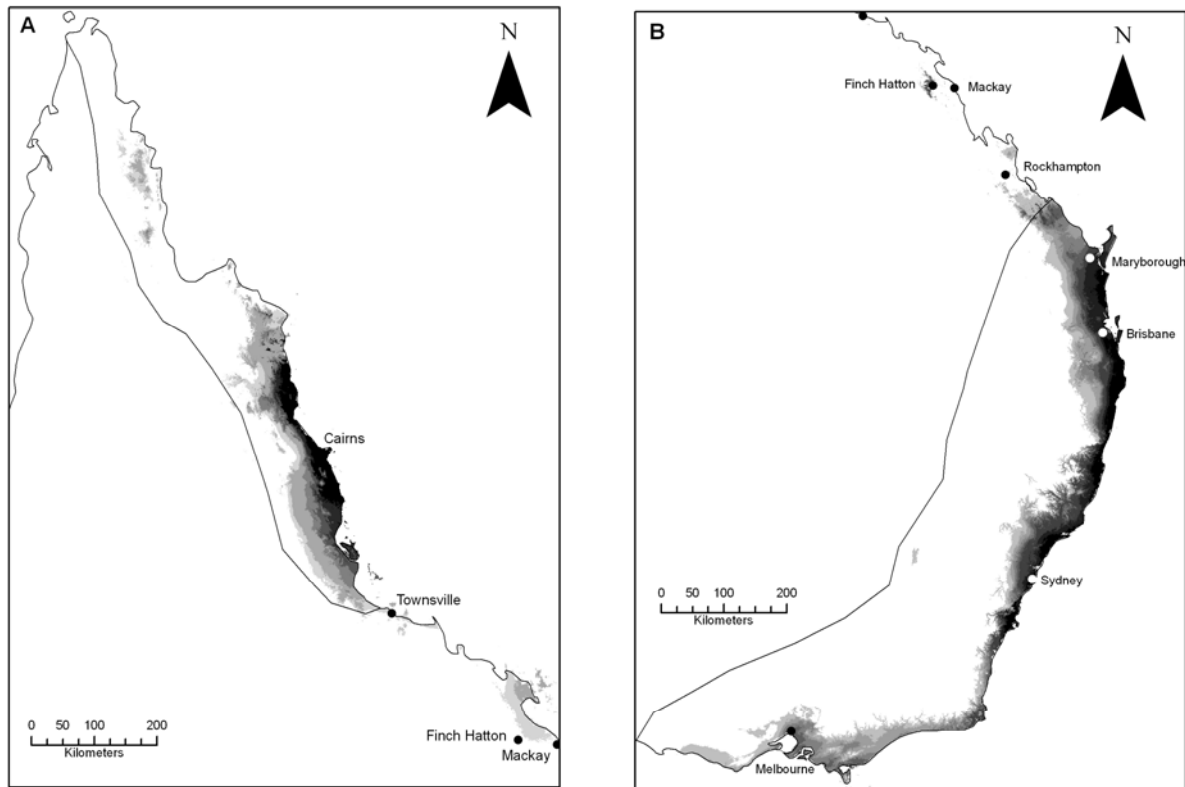
Figure 1: Modeled distribution (shaded; darker areas indicate more suitable climate) of two Australian flying-foxes, *P. conspicillatus* (A) and *P. poliocephalus* (B) based on known records of occurrence. The location of a new site (Finch Hatton) with both species present, and previously published range of both species shown as a line (Hall and Richards, 2000)

site was predicted as suitable regardless of the exclusion of the Finch Hatton site in training. Climatic suitability at this site ranged from 0.402 for *P. alecto* and *P. scapulatus*, 0.107 for *P. poliocephalus* and was lowest at 0.014 for *P. conspicillatus*. The low suitability at Finch Hatton for *P. conspicillatus* makes visualization under the locality mark on Fig. 1 difficult.

Overlapping climatic variables suitable for both species are present at the Finch Hatton site when compared with other established camps (Fig. 2). For example, Finch Hatton falls in the mid-range for mean annual precipitation and mid-high range for mean annual temperature. In contrast, temperature and precipitation seasonality is vastly different to established camps for both species, with Finch Hatton having comparatively high temperature and precipitation seasonality (Fig. 2).

Discussion

Our model shows that both *Pteropus poliocephalus* and *P. conspicillatus* have overlapping climatic space that includes the region of the newly discovered camp at Finch Hatton. The differentiation between bioclimatic parameters for *P. conspicillatus* and *P. poliocephalus* camps is most distinct for temperature and precipitation seasonality. Seasonality relates to periodic fluctuations in climate and is a conspicuous feature of the variable Australian climate (Hughes, 2003). With the Finch Hatton site being located in a climatic region that has a high degree of both temperature and precipitation seasonality (Fig. 2) it may represent a fluctuating suitable climatic environment for both species at different times. Additionally, with this site having temperature and rainfall variables overlapping the suitable temperature and rainfall variables for both species (Fig. 2), the overall climatic suitability of this site is evident.

No consistent records of *P. conspicillatus* exist this far south, extending the range of the species by approximately 500 km. Although this species is only present in small numbers, the fact that the population has persisted since at least 2005 and possibly longer suggests that this is not simply the existence of
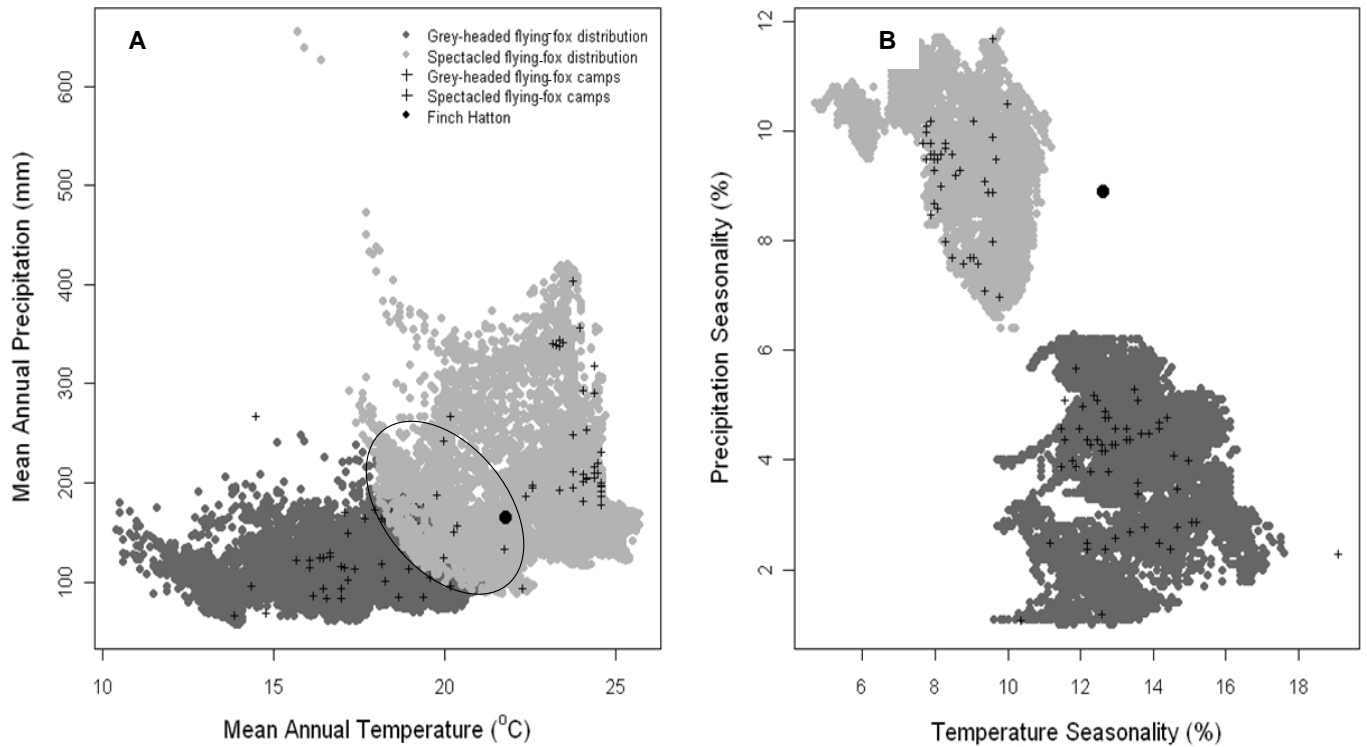
Figure 2: Climatic variables extracted from the range of both the spectacled flying-fox (*Pteropus conspicillatus*) and grey headed flying-fox (*P. poliocephalus*) overlaid with camp locations including the newly described mixed-species camp at Finch Hatton, Queensland. (A) shows mean annual temperature and mean annual precipitation (B) shows temperature seasonality and precipitation seasonality for the geographic range of both species and more specifically where camps are formed. Ellipse in (A) shows area of overlap for *P. conspicillatus* and *P. poliocephalus.*

'vagrant' individuals. While it is conceivable that individuals were blown south by severe winds, or that rehabilitated individuals were released (although unlikely given the numbers observed), it is also possible that the range of the species is expanding southwards as a response to climate change.

Flying-foxes have been shown to be particularly susceptible to sudden fluctuations in ambient temperature (Welbergen et al., 2008) and changes in climate are known to have an influence on natural systems with shifts in latitudinal distribution being attributed to recent climate events in many species (Root et al., 2003, Thomas et al., 2004). While the ecological niche of this species does not normally include drier regions (Richards, 1990a), those that are able to transverse the 'dry belt' between Townsville and Finch Hatton may find success in wet tropical environments further south. Recent evidence also suggests that *P. conspicillatus*, which was thought to be a rainforest specialist, utilizes food resources from dry regions to a much greater extent than had been previously thought (Parsons et al., 2006) and may be able to exploit drier regions while locating more suitable roosting habitat and climate further south.

Contrasting this, it appears that numbers of *P. poliocephalus* have been present in this region historically. Collett (1887) collected a series of *P. poliocephalus* from Mackay, strongly suggesting a substantial camp there at that time (Collett, 1887). Winter migrations *en-masse* north were once suggested (Ratcliffe, 1932) but later disputed and it was thought that smaller, more dispersed camps persisted during the winter months (Nelson, 1965, Parry-Jones and Augee, 1992). The presence of *P. poliocephalus* at this location is not restricted to winter, so these records do not support a winter migration of the species. Our results support the persistence of this species at this northern location with Finch Hatton being modeled as a suitable environment for *P. poliocephalus* camps. It is not known why *P. poliocephalus* was not recorded in this region for such a long time period but it is likely due to a concentrated research effort in south-eastern Australia for this species and the remote location of camps in these regional areas. Range shifts for migratory species tend to be more intermittent than continuous and can be

difficult to verify, particularly in areas like Australia that are effected by Southern Oscillation, El Nino and La Nina events (Walther et al., 2002). So perhaps this species, which is known to undertake long-distance flights, simply exhibits much more distributional elasticity than has been previously recorded, following the continuously fluctuating climate in the area.

Morphological (Andersen, 1912) and genetic analyses (Sinclair et al., 1996, Webb and Tidemann, 1995), indicate that long-distance flying-fox movements create opportunities for hybridisation. While hybridization is known for *P. alecto* and *P. poliocephalus* (Webb and Tidemann, 1995) H. Luckhoff, pers. comm.), and recent molecular studies suggest possible genetic introgression between *P. alecto* and *P. conspicillatus* (Fox, 2006), the frequency and viability of hybrids is unknown.

Hybridisation was examined in black and grey headed flying-foxes using genetic material collected from wild individuals (Webb and Tidemann, 1995). A female *P. alecto*/*P. poliocephalus* hybrid failed to produce offspring after mating with a *P. alecto* male, although a single offspring was produced after mating with a *P. poliocephalus* male (Webb and Tidemann, 1995). The genetic similarity of three large *Pteropus* spp. (*P. alecto*, *P. conspicillatus* and *P. poliocephalus*) has made it difficult to assess the extent to which these animals hybridize when they come into contact (Webb and Tidemann, 1995). However, it is conceivable that *P. poliocephalus* and *P. conspicillatus* could interbreed, should they come into contact under natural conditions. Both species have synchronous breeding and are often observed roosting in close proximity. Indeed, individuals displaying characteristics of both species have come into care, and interspecies mating has been observed regularly at this site between *P. alecto, P. conspicillatus* and *P. poliocephalus* (D. Lowe pers comm.). If interspecies breeding is occurring, the genetic consequences are entirely dependent on the success of hybrid offspring. Hybridization can be problematic when rare species encounter widespread species (Allendorf et al., 2001). These encounters have the potential to cause genetic mixing and possible extinctions caused by species replacement (Allendorf et al., 2001).

Therefore, genetic analysis of flying-foxes at this site and any others found in this area should be undertaken for evidence of this occurring.

In conclusion, we have shown evidence of sympatry in two flying-fox species previously thought to be allopatric. We have also provided the first evidence of all four species of mainland Australian *Pteropus* roosting in a single location, the consequences of which will need to be closely examined. It appears that *P. poliocephalus* has been consistently present at this location and possibly other locations close by, and that the presence of *P. conspicillatus* is due to a more recent range expansion.

Chapter 5 - Temporal roost emergence patterns in tropical flying-foxes

Abstract

The proximate cues influencing patterns of emergence from their roosts by bats have intrigued behavioural ecologists for generations and while illumination, predation risk and foraging needs are the most oft-cited explanation for variation in emergence times, few examples exist that take advantage of long temporal data sets in the tropics. Here we examine a 7-year-long data set to identify factors which influence flying-fox emergence times at a mangrove roost in the Australian dry tropics, a roost seasonally occupied by the black flying-fox (*Pteropus alecto*) and the migratory little red flying-fox (*P. scapulatus*). We found that a linear relationship with the time of civil twilight explains most of the variation in emergence time, but that significant effects of weather, month and year also exist. The effect of weather is likely to be due to its influence on light levels: bats emerge earlier than predicted by civil twilight on days with extensive cloud cover, especially in combination with heavy rainfall. The monthly variation is strongly correlated with seasonal variation in roost occupancy: high occupancy scores are associated with earlier emergence. Yearly variation in emergence time is correlated with increased activity from a nearby port, possibly reflecting increased light pollution. We suggest that variation in foraging competition drives the monthly variation and that light pollution may explain yearly patterns. Together these results suggest that emergence times are most strongly influenced by variation in light levels and that foraging competition may also influence emergence behaviour.

Introduction

Circadian rhythms govern daily patterns in animal behaviour and have been a topic of scientific interest for generations (Pittendrigh 1960). External factors such as light, temperature and season can advance or delay this rhythm in some species and examples of this have been well documented (Bronson 2004, Kerr *et al.* 2008). With extreme variability in seasonal light availability, arctic animals are an excellent example of how the impact of external effects may vary. While some species continue to maintain their circadian rhythm during the constant light present in summer and darkness in winter, others, such as arctic reindeer, will temporarily lose circadian patterns during these times (van Oort *et al.* 2005). The effect of external factors may be more difficult to discern in the tropics where twilight is comparatively brief and seasonal variability in available light is less pronounced (Mills 2008).

The emergence of bats from their daytime roost each night has led to several investigations of emergence timing (Campbell *et al.* 2005, Duverge *et al.* 2000, Jones *et al.* 1994, Petrzelkova *et al.* 2003, Russo *et al.* 2007, Wei *et al.* 2008, Welbergen 2006, 2008). Examples of bat emergence times corresponding with particular levels of illumination at night (from sunset, twilight and moon illumination) are plentiful (Erkert 1978, Law 1997, Wei *et al.* 2008) and occur in a range of species from small insectivorous bats (Campbell *et al.* 2005, Downs *et al.* 2003, Jones *et al.* 1994, Shirley *et al.* 2001) to large phytophagous flying-foxes (Banack *et al.* 2002, Welbergen 2006, 2008).

Avoiding predation has been suggested as an explanation of light-mediated emergence: diurnal predators can be avoided when darkness interferes with their vision, increasing the likelihood of a safe foraging journey (Keitt *et al.* 2004). The emergence time of bats is also influenced by energetic requirements and foraging activities. For example, insectivorous bats feeding on dipterans that swarm at dusk emerge earlier to maximize dietary intake, while bats preying on other food items such as moths may delay emergence as the risk of predation is higher than the gain from emerging earlier (Jones *et al.*

1994). Similarly, grey headed flying-foxes in south-eastern Australia may emerge earlier, relative to twilight, during summer in order to maximize foraging time (Welbergen 2006).

Flying-foxes (*Pteropus* spp.) are large gregarious bats that roost in a variety of vegetation communities throughout coastal Australia, ranging from mangroves to rain forest and riparian vegetation (Eby 1991, Markus *et al.* 2004, Parsons *et al.* 2006, Tidemann *et al.* 1999). Their roosts can contain tens to hundreds of thousands of individuals from a single species or a combination of the four species present in the region (*P. alecto, P. conspicillatus, P. poliocephalus* and *P. scapulatus*, Birt *et al.* 1998, Parsons *et al.* 2006, Tidemann *et al.* 1999). Flying-foxes are challenging to monitor because their patterns of resource use are seasonally variable; they exploit spatially heterogenous environments, following the flowering and fruiting of food trees (Markus *et al.* 2004, Parsons *et al.* 2006, Vardon *et al.* 2001). The flowering of food trees is highly seasonal in the tropics (Boulter et al., 2006), so consumers in the region must migrate, exhibit a degree of nomadism or show a much greater dietary flexibility during times of shortage (van Schaik *et al.* 1993).

In this paper, we use a long-term data set to examine temporal patterns in the emergence timing of flying-foxes in the dry tropics of northern Australia and consider the relationship of emergence times to both natural and anthropogenic processes. Examples of light-mediated bat emergence in tropical regions are few and we aim to determine if similar patterns exist in tropical flying-foxes. We hypothesise that tropical flying-foxes will emerge earlier than their temperate counterparts due to the shorter duration of twilight and that their emergence timing will be more profoundly influenced by extrinsic factors.

Methods

Study site

The Ross River flying-fox camp is located in a mangrove forest on the intertidal zone of Ross River, Townsville, Queensland, Australia (-19.2738, 146.8343), where the vegetation community is dominated by *Avicennia marina* and *Rhizophora* spp. This is a day roost (camp) which local people say has been occupied seasonally for at least 80 years. Two flying-fox species use this location, the black flying-fox (*Pteropus alecto*) and the migratory little red flying-fox (*P. scapulatus*). The site is in close proximity to the port of Townsville (approximately 1.5 km away) and the city centre. Ross River is a commonly used recreational area for fishing and boating.

Observations

Data were collected by a subsection of The Ross Island Volunteers for Estuarine Research (RIVER), a group primarily interested in surveying birds. Data on flying-foxes were recorded opportunistically as they shared this roost with Australian white ibis (*Threskiornis molucca)* who evacuate the roost during daylight and return around sunset. Bird counts were undertaken over a 2-h period, 90 min before and 30 min after sunset. Identification and counts of all birds were recorded during this time and the identity and emergence time of the flying-foxes present was also recorded. These data were collected approximately every fortnight for a 7-y period (with some exceptions) from 5 March 1998 to 5 May 2005 (n = 188). Predator presence was identified from counts of white-bellied sea eagle (*Haliaeetus leucogaster)* and wedge-tailed eagle (*Aquila audax)* as these are known to prey upon flying-foxes at the roost (Welbergen 2006) (Parsons, pers. obs). The main group of observers remained consistent throughout the study, reducing the impact of observer error and keeping methods consistent.

Environmental data

Fifteen abiotic and biotic variables were considered as possible factors in predicting emergence time (Table 1). The Australian Bureau of Meteorology (BOM) provided information on weather variables from 1998 to 2005 from the Townsville aero site (-19.25, 146.77) which is located approximately 7 km from

the Ross River day roost. Data on sunset, civil twilight times, lunar phase, moonset and rise for this period were obtained from GeoScience Australia (http://www.ga.gov.au/geodesy/astro/). The time of civil twilight was used to characterize seasonal variation in the time of dusk. Other possible variables (sunset and astronomical twilight) are highly correlated with it, and civil twilight was closest to the time of emergence. Solar cycle data were obtained from the Space weather prediction centre at the National Oceanic and Atmospheric Administration [NOAA, (http://www.swpc.noaa.gov/ftpdir/warehouse/)]. Yearly port activity thoroughfare was available from the Townsville Port Authority (http://www.townsville-port.com.au/trade_stats). Flowering phenology data were compiled from published material (Boulter *et al.* 2006, Hansman 2001), information from experienced botanists (B. Jackes and C. Lockers pers. com.) and field records (Parsons, unpubl. data).

Analysis

All time variables were converted to decimal hours for calculation and we used S-Plus 8 for Windows to conduct the analysis. Flower availability from food trees was summarized by month and categorized as clumped or random (relating to flowering syndrome, Boulter *et al.* 2006). Meteorological variables were first reduced with a principal components analysis, using the correlation matrix (as the variables are in different units and are unequally weighted), the first two components explained 67% of the variance. We examined models which used either the PCA components or the individual meteorological variables. When using individual meteorological variables, precipitation values were categorized as high (10 mm or more) or low (<10 mm) in a 24 hour period.

Weather and astronomical data are available for each day of the study, but flowering phenology and bat breeding periods are, as indicated above, monthly average values obtained from the literature. Similarly, the data for levels of urban and port development are available only as yearly means. For this reason, we do not use these variables directly in the analysis, but instead

include month and year among the variables examined. A roost occupancy score was calculated for each month of the year by adding the proportion of times flying-foxes were present at the camp in that month over the 7-year period. This is used as a surrogate for population number as the pattern of variation is almost identical to that of more recent population censuses at this camp (Chapter 2).

To examine the relationship between emergence time and environmental variables, we used linear regression and analysis of variance using Type III sums of squares, together with the Akaike information criterion (AIC) to compare models. Time of emergence was the dependent variable and we initially included all of the variables listed in Table 1 as predictor variables. The model was then progressively reduced to identify the factors most strongly associated with time of emergence. Models using alternative techniques for characterizing the weather data (individual weather variables vs PCA components) were formally compared, as were other models, to select the set of variables which best explained variation in emergence times.

Results

Patterns of roost use and emergence

The general pattern of occupancy by *Pteropus alecto* at this camp is bimodal, with peaks early and late in the dry season (March-May and September-November). Figure 1 shows the pattern of occupancy and the timing of ecologically significant events. *Pteropus scapulatus* were consistently present from September to November and occasionally visited during other months. The same 3-mo period corresponds with peak flowering and the birthing period of *P. alecto. Pteropus alecto* can be present year round at this camp but may vacate it for part of the winter (June-August), and part of the summer wet season (December-February).

Time of emergence has distinct yearly variation, corresponding with sunset and civil twilight (Figure 2). Emergence time was most strongly correlated with civil twilight throughout the duration of the study (Figure 3).

Deriving the model

The initial model included all variables for which daily data were available, and their estimable interactions. Terms were then progressively dropped, starting with higher-level interactions, and using the Akaike information criterion (AIC) to identify an appropriate termination point. The final model in this sequence included main effects of civil twilight, cloud cover, precipitation, year and month, and an interaction between cloud cover and precipitation (Table 2). We then repeated this analysis replacing the meteorological variables with their principal components scores, a technique used in a similar study (Welbergen 2006) but this substitution significantly reduced the explanatory power of the model and was therefore rejected. Predator presence, moon illumination, temperature, wind speed and interactions involving these variables did not improve the model in either sequence.

Table 1: Variables tested in the analysis of flying-fox emergence times and their description, also provided is the frequency that data was recorded and available for analysis.

	Factor	Description	Data available
Abiotic	Civil twilight	The instant in the evening, when the centre of the sun is at a depression angle of six degrees (6°) below an ideal horizon.	Daily
	Precipitation	Precipitation in the 24 h before 9h00 (local time) in mm, categorised into <10 mm or > 10 mm	Daily
	Temperature	Air temperature observation at 15h00 local time in °C	Daily
	Wind speed	Wind speed at 15h00 local time measured in km h^{-1}	Daily
	Cloud cover	Total cloud amount at 15h00 in eighths.	Daily
	Sunspot number	Areas of the sun's surface marked by increased magnetic activity leading to decreases in solar surface temperature. Sunspots are counted and used as a measure of the variable solar cycle.	Daily
	Moon illumination	If the moon was visible before civil twilight on that day; the proportion of the moon face illuminated according to moon phase (0, 0.5, 1).	Daily
	Port activity	Total yearly trade throughput from the Townsville Port (imports and exports) measured as mass (Mg).	Mean activity per year
	Year	Year categories from 1998–2005.	Yearly
	Month	Month categories from January-December.	Monthly
Biotic	Random flowering	Species of food trees that flower randomly over time.	Average monthly
	Clumped flowering	Food trees with flowers that are temporally clumped, categorised monthly as <6 or >6 species.	Average monthly
	Predator presence	The presence or absence of either white-bellied or wedge-tailed eagles.	Daily
	Presence of little red flying-foxes	The presence or absence of migratory little red flying-foxes.	Daily
	Black flying-fox birthing season	The season that black flying-foxes give birth to pups. Categorised as "birthing" or "not birthing".	Average monthly
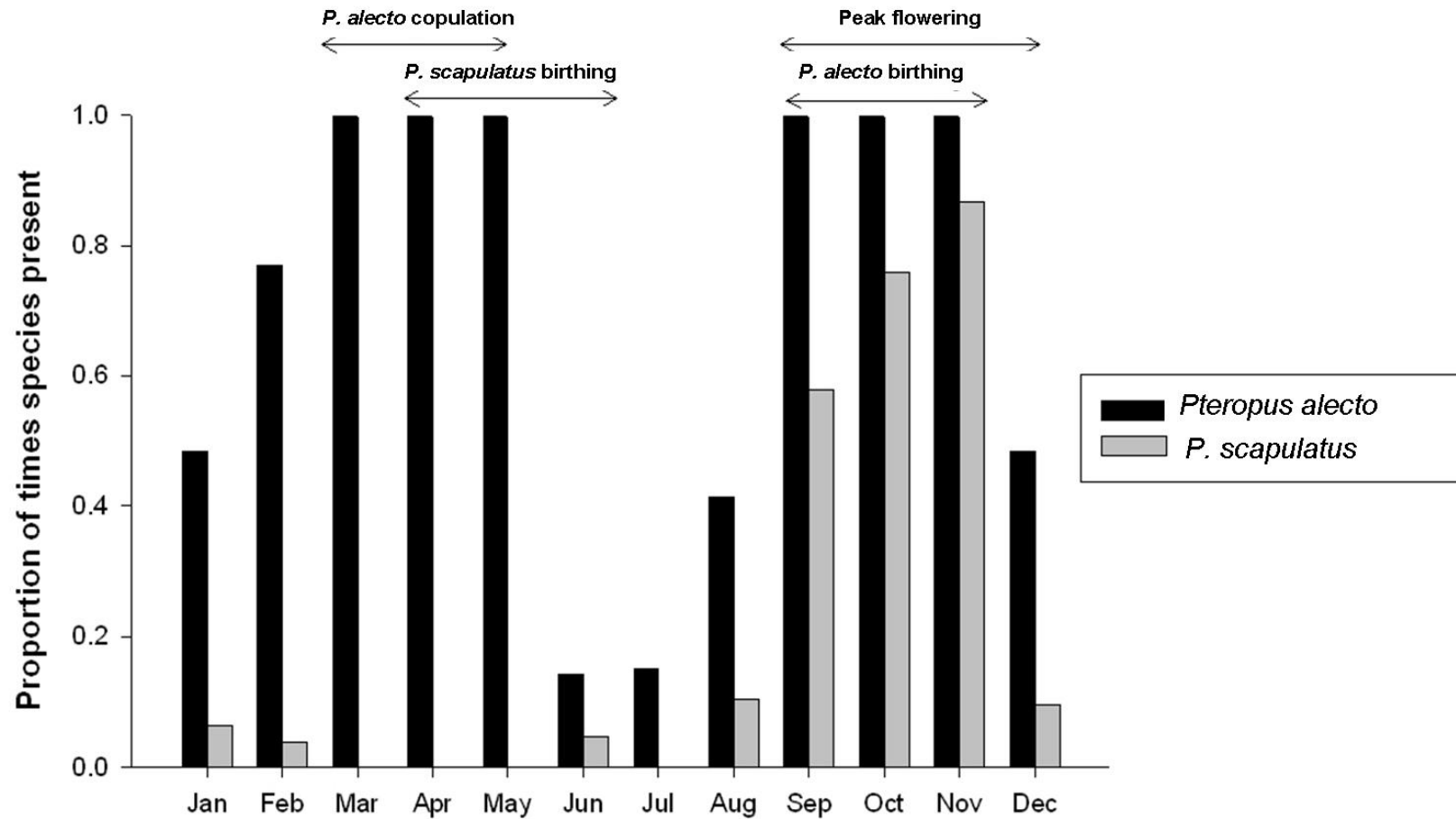
Figure 1: Roost use by two flying-fox species, the black (*Pteropus alecto*) and little red flying-fox (*P. scapulatus*) at the Ross River camp from 1998-2005. Lines indicate the birthing season for both species and the copulation season for *P. alecto* (Nelson, 1965, Ratcliffe, 1932) and the peak flowering time for the region (Boulter et al., 2006).
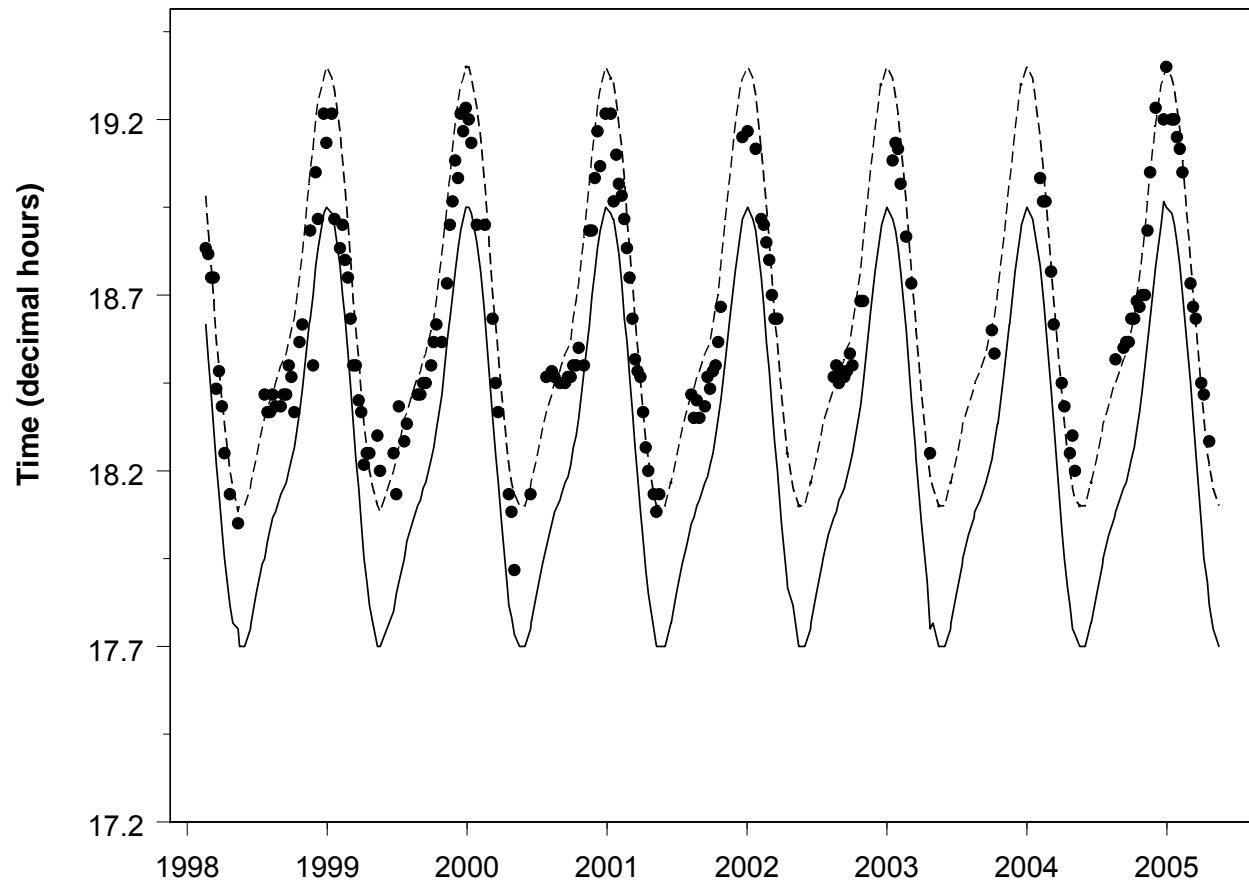
Figure 2: Yearly variation in flying-fox emergence time (black circles), sunset (solid line) and civil twilight (dashed line) at Ross River, north-eastern Australia (1998 – 2005).
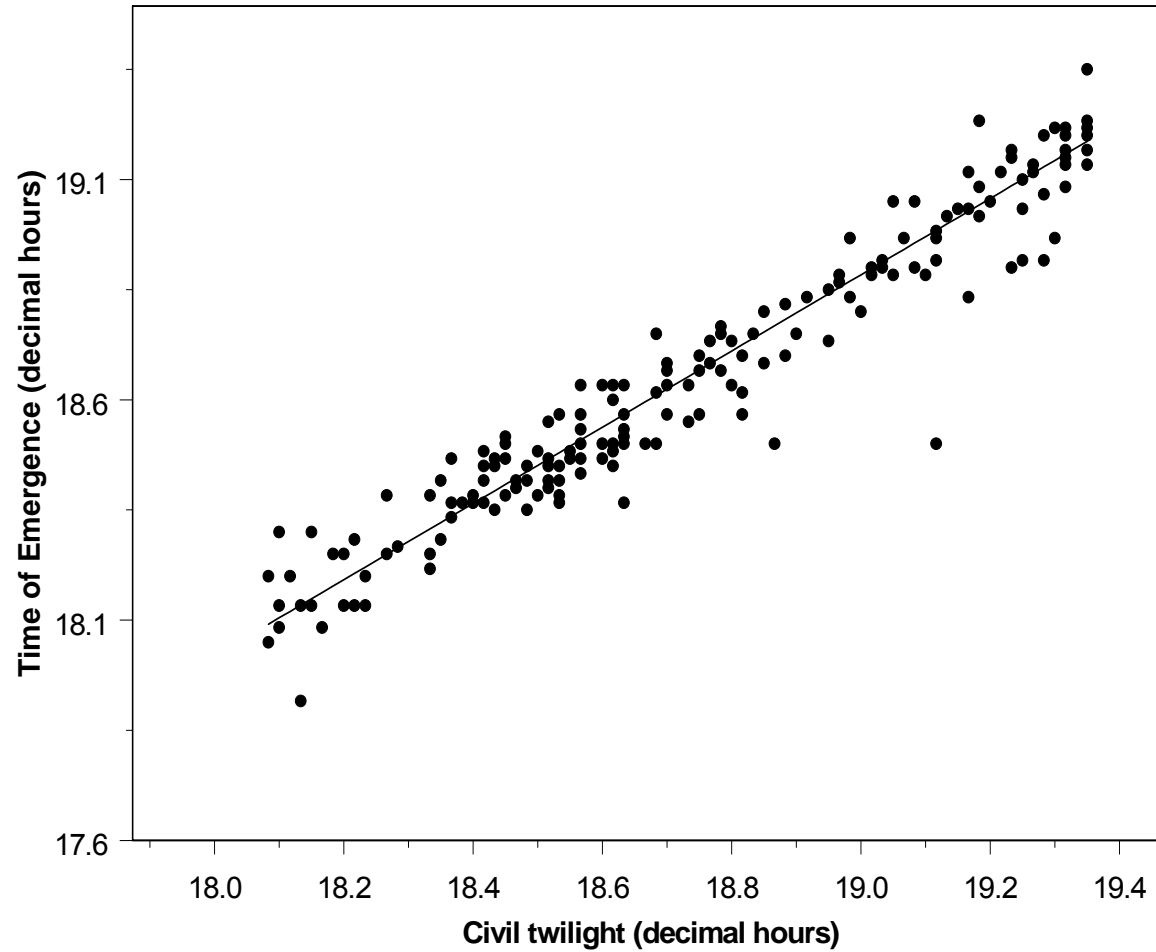
Figure 3: The relationship between emergence time for flying-foxes at the Ross River camp and civil twilight, from 1998–2005.

Interpreting the model

Our final model accounts for 96.4% of the variance in emergence times observed in the study. They key factors influencing emergence times are as described below.

Civil twilight

The relationship with civil twilight alone accounts for almost 93% of the total variation in emergence time. As shown in Figure 3, the relationship is linear, described by the equation:

Emergence time = 2.45 + 0.865 Civil twilight

where both emergence time and civil twilight are measured in decimal hours. This means that in mid-winter when civil twilight is earliest (about 18h00) the bats emerge less than 2 min before civil twilight on average. In midsummer, when civil twilight is at its latest (about 19h30), they emerge about 11 min before civil twilight.

The other factors described below result in variations of up to 24 min from the predicted time obtained using the equation above.

Cloud cover and precipitation

These meteorological variables together account for approximately 16% of the residual variation in emergence time after the effect of civil twilight is taken into account. (The total variation explained increases to about 94.1%.) In general, increasing cloud cover results in earlier emergence. This effect is much more pronounced on days with substantial rain than on days with little or no rain (Figure 4). For example, when cloud cover is at its highest and rainfall is 10 mm or more, bats leave up to 24 min earlier (Figure 4).

Table 2: The contribution of each factor to the model for the onset of flying-fox emergence at Ross River camp, North Queensland, Australia. Calculations use type III sums of squares.

Factor	df	Sum of squares	F value	P
Civil twilight	1	0.761	180	<0.0001
Cloud cover	1	0.0560	13.2	0.0003
Precipitation category	1	0.0068	1.62	0.2051
Cloud-cover precipitation interaction	1	0.0298	7.05	0.0086
Month	11	0.184	3.96	<0.0001
Year	7	0.250	8.46	<0.0001
Model Residuals	165	0.693		

Month

Adding month effects allowed the model to explain almost 95% of the variation in emergence time. Bats emerged earlier than expected in spring (between September and November) and later on average at other times (Figure 5), than civil twilight and the meteorological variables alone would predict. The difference was up to 8 min earlier in November and up to 10 min later in December.

Year

Adding year to the model increased the proportion of variation explained to 96.4%. There is a pattern of progressively later emergence times over the 7 y of this study. The latest average emergence time was in 2004 (7.2 min later than predicted using other variables) and the earliest in 2000 (almost 8 min earlier than predicted).

In order to resolve the monthly and yearly patterns further, we investigated the mean residuals associated with different months and different years when civil twilight and weather variables were accounted for. Monthly variation was strongly correlated with the month's occupancy score (Figure 5): flying-foxes emerged earlier in months with a higher occupancy score at the camp (Spearman's rank correlation, r_s = -0.88, z = -2.93, P < 0.01. Figure 6). The annual variation in mean residual (Figure 7), was correlated with increasing trade at the nearby port (whose growth is likely to have resulted in increased light levels) (Spearman's rank correlation, r_s = -0.93, $z_{(2)}$ = -2.43, P < 0.05, Figure 8). As trade has increased over this 7-y period, bats have been emerging later relative to civil twilight.
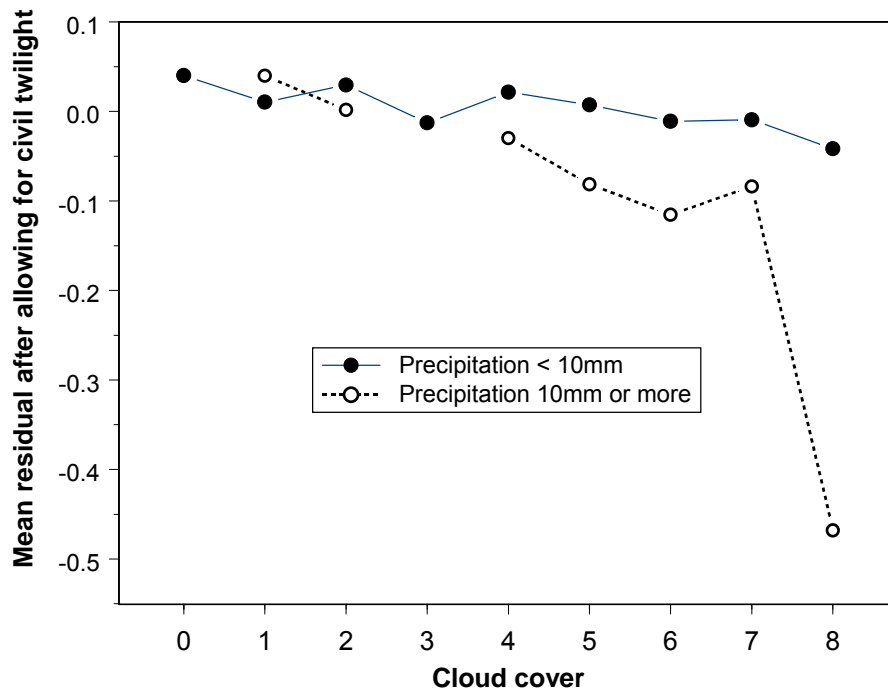
Figure 4: The interaction between precipitation and cloud cover on model residuals. The residuals represent differences from values predicted from civil twilight alone. There is a weak trend towards earlier emergence with little or no rain and a stronger trend when precipitation is high.
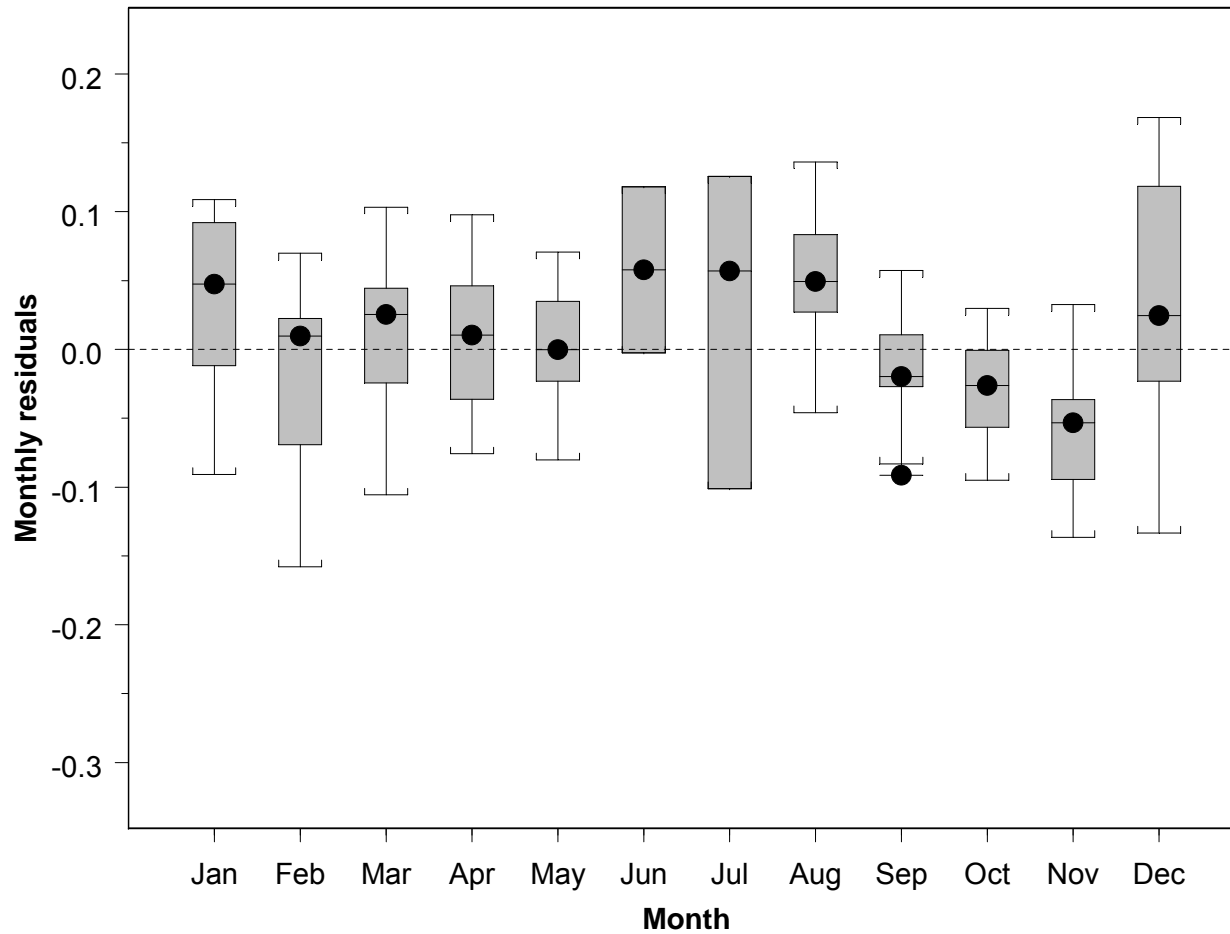
Figure 5: Monthly variation in emergence time of model residuals for tropical flying-foxes from 1998-2005. Emergence time is significantly earlier from September to November and latest between June and August. The residuals represent differences from values predicted by a combination of civil twilight and meteorological variables.
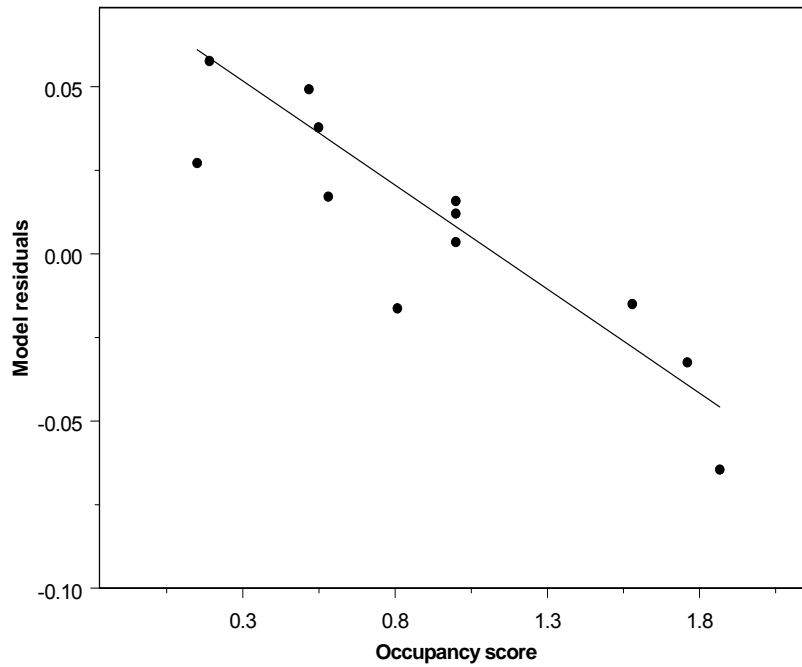
Figure 6: Mean monthly residuals decrease with higher occupancy at the camp, bats leave earlier when more bats are present. Residuals represent differences from values predicted by civil twilight and weather variables.
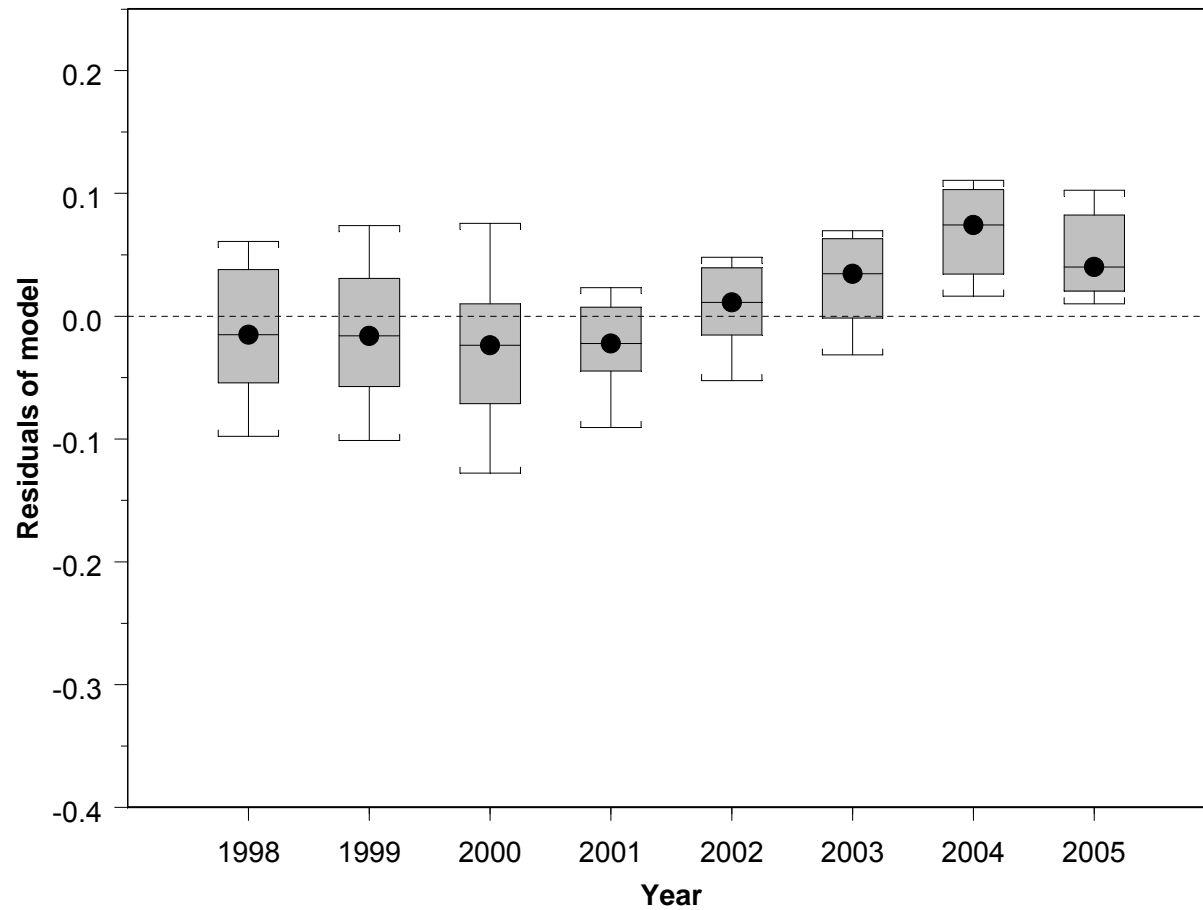
Figure 7: Yearly variation in model residuals of emergence time for tropical flying-foxes (1998 – 2005). Flying-fox emergence time is later in the years 2002-2005.
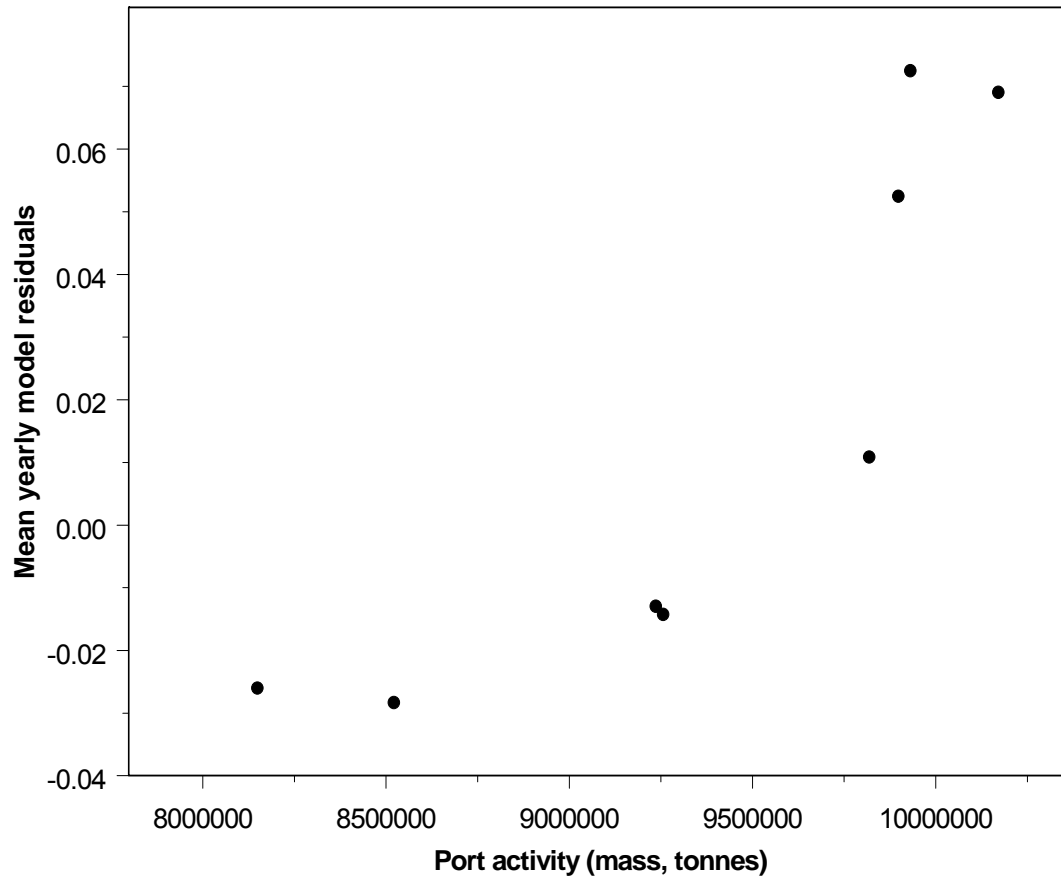
Figure 8: Mean yearly residuals of flying-fox emergence time increase with activity at the Townsville port (1998–2005).

Discussion

Flying-foxes at this camp display similar emergence patterns to those exhibited by bats worldwide; that emergence time is strongly related to the time of sunset (Erkert 1978 , Isaac et al. 1993) or civil twilight (Welbergen 2008). This coupled with the effect of cloud cover suggests that a critical illumination level triggers emergence at this camp. The interaction between cloud cover and rainfall may also be explained by illumination. Higher levels of cloud cover lead to earlier emergence times, especially when precipitation exceeded 9 mm in a day. An association between heavy rain and heavy cloud cover is probably responsible for this interaction. *Pteropus tonganus* also emerge early from the roost on cloudy days (Banack and Grant, 2002). Heavy cloud dramatically reduces light levels so that the light level which triggers emergence would be achieved earlier in the evening.

Predator avoidance is another reasonable explanation for twilight-driven emergence. Some investigators have found a delayed emergence time when predators are present – e.g. in the grey headed flying-fox (Welbergen 2006) and many echo-locating bats (Duverge *et al.* 2000 , Jones *et al.* 1994 , Petrzelkova *et al.* 2003 , Russo *et al.* 2007), but we did not find such an influence. The absence of a significant effect of predators in our study could be explained by the consistent presence of birds of prey at this site: on every sampling occasion, at least one predatory bird species was recorded. For our analysis we selected white-bellied sea eagle and wedge-tailed eagle as key predators, but other birds of prey might also present a threat to flying-foxes at this camp when they emerge, or conceivably, the sheer number of birds of prey present year round at the camp conceals any potential effect.

Which variables influence emergence times on a monthly basis?

Flying-foxes are most consistently abundant in the roost between March and May and between September and November (Figure 2). Figure 5 indicates two general patterns in deviations from expected emergence times: (1) Flying-foxes

emerged earlier than expected in the late dry season, between September and November. (2) They also tended to emerge later than expected outside the periods of peak abundance. This pattern can be explained by considering occupancy score at the roost as a surrogate for population number. As the number of bats at the roost increases, emergence times are much earlier than expected (particularly from September to November).

When there are multiple food trees flowering that are temporally clumped (most commonly *Melaleuca* in this region), the little red flying-fox regularly arrives at this camp in large numbers. The ecomorphology of the tongue of *P. scapulatus* suggests a nectarivorous diet (Birt *et al.* 1997) and their migrations have been attributed to flowering phenology in the past (Ratcliffe 1932). Their arrival at existing camps (already occupied by other *Pteropus* spp.) can be dramatic, sometimes leading to a three-fold increase in camp size (Parsons, pers obs) and it has been argued that these seasonal patterns lead to the displacement of other flying-fox species at a roost (Birt *et al.* 1998). It is possible that the arrival of these migratory heterospecifics increases pressure on food resources in the region.

There are clear benefits of leaving the roost earlier at times of high resource competition; flying-foxes with high energy demands (like black flying-foxes with young pups) could access nearby feeding trees earlier, allowing them to gain a competitive advantage. Female forest bats in Italy have earlier emergence times in the period from pregnancy to late lactation (Russo *et al.* 2007) and female grey headed flying-foxes in southern Australia have an advanced emergence time that corresponds with decreased body condition at the time of birthing and young rearing (Welbergen 2006). Black flying-foxes may face the same constraints at this time of year. Lactation is energetically expensive (Gittleman *et al.* 1988) particularly in times of high foraging pressure (Schubert *et al.* 2009). Foraging flying-fox mothers have the additional burden of carrying their pups for the first 3 wk of life (Nelson 1965, Ratcliffe 1932). An earlier start to nightly foraging may well be advantageous given these energy demands. Black flying-foxes undertake fewer nocturnal movements in times of increased

resource availability (Markus *et al.* 2004) and guarding food trees from competitors is more noticeable at this time of year (Parsons et al., unpubl. data). Increased foraging time is unlikely to explain earlier emergence as the variation we are describing is in minutes, hardly enough time to make a significant contribution to an entire night's forage. However, this amount of time could be significant for flying-foxes with higher energetic demands, by arriving earlier at food trees, these flying-foxes can stay and guard this resource, reducing the amount of energy expenditure required to move between trees.

Which variables are influencing emergence times on a yearly basis?

Light pollution has been a cause for concern for astronomers for some time (Riegel 1973). However the impact of light pollution on ecological systems is an issue that has only recently received much attention in the literature (Longcore et al. 2004). Behavioural changes resulting from light pollution have been demonstrated in a variety of taxa (Baker *et al.* 2006, Barber-Meyer 2007, Bird *et al.* 2004, Miller 2006, Rodriguez *et al.* 2009). For example, American robins affected by artificial light sing earlier than those in natural settings (Miller 2006), migrating birds experience disorientation and high mortality rates from artificial light sources (Rodriguez *et al.* 2009), and the feeding and reproductive behaviour of a range of vertebrates is affected by artificial lights (Baker *et al.* 2006, Barber-Meyer 2007, Bird *et al.* 2004) . While our study did not measure light levels during this period, we used activity at the port as a surrogate for increased light pollution. At this port, activity is not restricted to daylight hours and as trade has increased in this area (a distance of approximately 1.5 km from the Ross River flying-fox camp) the emergence times of flying-foxes are later, perhaps as a result of artificial illumination increasing. This is not the only light source in close proximity to the camp, there is a marina and army barracks that are also well lit at night, which have also expanded over the period of the study; all of these light sources could influence illumination in the area. The extent and intensity of artificial lighting is increasing rapidly with human population growth on a global scale and increased outdoor lighting (Crawford *et*

al. 2002, Riegel 1973) and it is likely that the ecological consequences of light pollution will continue to be evident in the future.

Conclusions

While tropical regions have less pronounced variation in length and timing of twilight, flying foxes in this region display similar relationships between activity patterns and illumination to those in temperate regions. We have shown that there are distinct monthly and yearly cycles that are influencing this timing. Flying-foxes in Australia's dry tropics, like other bat species, use illumination as a trigger for emergence with a seasonal influence of occupancy at the roost. There is also a potential effect of light pollution (from increased activity at the nearby port) leading to variation in these activity patterns. Emergence time appears to be influenced by both natural and anthropogenic factors, future studies should incorporate measures of illumination at the roost and long term ecological patterns at the roost to test this relationship further and monitor change.

Chapter 6 - Roost fidelity in spectacled flying-foxes

Abstract

Roost trees at three *Pteropus conspicillatus* camps in the Australian Wet tropics were monitored for the presence and absence of individuals over a four month period. The number of individual *P. conspicillatus* in roost trees varied on a variety of time scales, with seasonal changes in abundance overlain on highly variable day-to-day patterns of roost use. Although the presence of individual high site fidelity behaviour could not be precluded, the high turnover of flying-fox numbers on a within-tree basis precludes the presence of highly stable social groups, over the duration of this study at least. Further clarification of the extent of roost fidelity within camps is likely to be a significant component for the conservation and management of flying-foxes.

Introduction

Flying-foxes are gregarious and they typically roost during the day in large numbers (<10 to hundreds of thousand individuals) in patches of trees within a wide range of vegetation types including, rainforest, mangroves, riparian vegetation and urban green-spaces (Tidemann et al., 1999, Vardon et al., 2001, Parsons et al., 2006, Williams et al., 2006). Knowledge of the roost fidelity of individual flying-foxes within a day-time camp has important implications for our understanding of their general biology, conservation and management. High roost fidelity opens the possibility of more stable social bonds between individuals with possible impacts on the development of social foraging and information transfer at roosts e.g. the spear nosed bat *Phyllostomus hastatus* (Wilkinson and Boughman, 1998) and the evening bat *Nycticeius humeralis* (Wilkinson, 1992). Similarly, high roost fidelity (inferring limited mixing of individuals on a within-camp basis) could impact the methods used to census camp numbers, due to the non-random movement of individuals within a camp.

Unfortunately, monitoring the roosting position of flying-foxes within a camp is difficult. Marking individuals is a time consuming and mostly invasive procedure and we do not yet have a solid understanding of the degree of individual site fidelity within camps. As part of a larger study into the diet of the spectacled flying-fox, *Pteropus conspicillatus* (Parsons et al., 2006) we monitored the number of individual bats in specific trees at three camps in the Wet Tropics bioregion of North Queensland. In this paper we analyse the level of flying-fox numbers in these trees over a four month period to infer patterns of individual tree-roost fidelity. Although this approach includes some limitations because bats have not been individually marked, the degree of changes in the numbers of individuals in particular trees provides some insight into individual roost fidelity.

Methods

The numbers of flying-foxes roosting in ten trees at each of three camps were recorded: two camps on the Atherton Tablelands (Whiteing Road and Tolga Scrub) and one in the adjacent lowlands (at Gordonvale, Figure 1). The Atherton Tablelands is located in tropical North Queensland and consists of a complex mosaic of habitat types with large areas cleared for agriculture. This has created small rainforest fragments of varying plant composition that occur throughout the landscape.

Roosting trees were marked along a 50m line transect (about 5m apart), with the central roosting tree being located at the centre of the camp. This data was collected during the wet season between November 2004 and March 2005, this time period included the peak of *P. conspicillatus* birthing (November and December). Records were taken every morning of the number and species of flying-foxes at selected roost trees using Pentax XCF 16x50 binoculars. The observer was situated at the base of the tree when recording bat numbers. The high canopy at one site (Whiteing Road) meant that observer presence did not disturb roosting bats and at the other two sites, numbers were only recorded once flying-foxes were habituated with observer presence, usually after two consecutive days. There was difficulty in observing the sex of flying-foxes at Whiteing Road due to high canopy height, so this information was not recorded. Camp size estimates provided are from L.A. Shilton, P. Latch, A. McKeown and D. A. Westcott (unpublished data).

The Whiteing Road camp (145°36.3′E, 17°33.36′S, at 760 m a.s.l.) is in a fragmented highland rainforest west of Milla Milla, surrounded by pasture. This is a seasonally occupied maternity camp used by both *P. conspicillatus* and *P. scapulatus* (little red flying-foxes). During this study, the numbers of *P. conspicillatus* fluctuated between 12000 and 20000 individuals. This camp was monitored for four months.
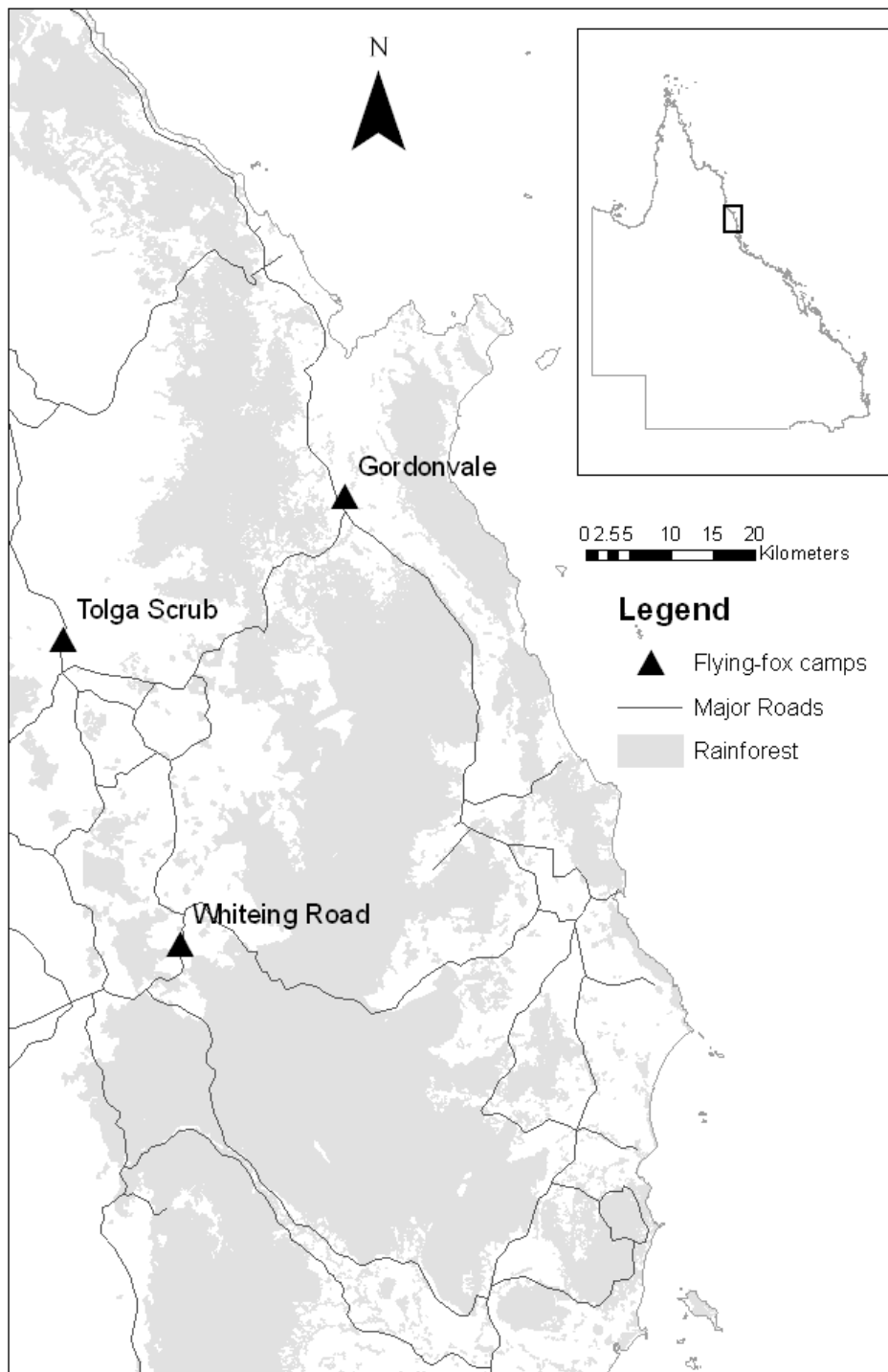
Figure 1: Location of Spectacled flying-fox camps surveyed in this study

The Tolga Scrub camp (145°28.8′E, 17°13.86′S, at 770 m a.s.l.) is located in a small and isolated fragment of Complex Notophyll Vine Forest Type 5b (Tracey 1982), outside the township of Atherton. Tolga Scrub is occupied by *P. conspicillatus* throughout the year (a permanent maternity roost), and numbers of *P. conspicillatus* fluctuated from 10000 to 25000 during the period of the study. Large numbers (>100000) of *P. scapulatus* were also present at this site during the study period. This camp was also monitored for four months.

The Gordonvale camp (145°46.74′E, 17°4.86′S, at 40 m a.s.l.) is in low to medium mixed shrubland and woodland with *Melaleuca quinquinerva* as the dominant tree species. It is surrounded by agricultural land (mainly sugarcane plantations) and suburban housing. This was the largest camp sampled, with over 40000 *P. conspicillatus* present during this study. This is a permanent maternity camp. No other flying-fox species were sighted at the Gordonvale camp during this study. This camp was only monitored for two months (December and January).

Results

The number of flying-foxes in 10 trees in the Whiteing Road camp over a five day period in November are presented as a representative example of the overall pattern of tree use detected in this study (Figure 2). The pattern of flying-fox numbers roosting within individual trees over time varied between trees, and different trees could display opposite trends. Over the five day period the total number of flying-foxes were relatively constant in Trees #1, 2, 4 and 8, increased in Trees #5 and 6, and decreased in Trees #3, 9 and 10.

The pattern of tree use within a camp varies across trees, months and days (Figure 3), the number of flying-foxes roosting in each tree, organized by camp, day and month is shown. Again, marked differences between trees exist. The number of flying-foxes roosting in Tree #5 in the Whiteing Road camp appears to be significantly higher in November than in the other months
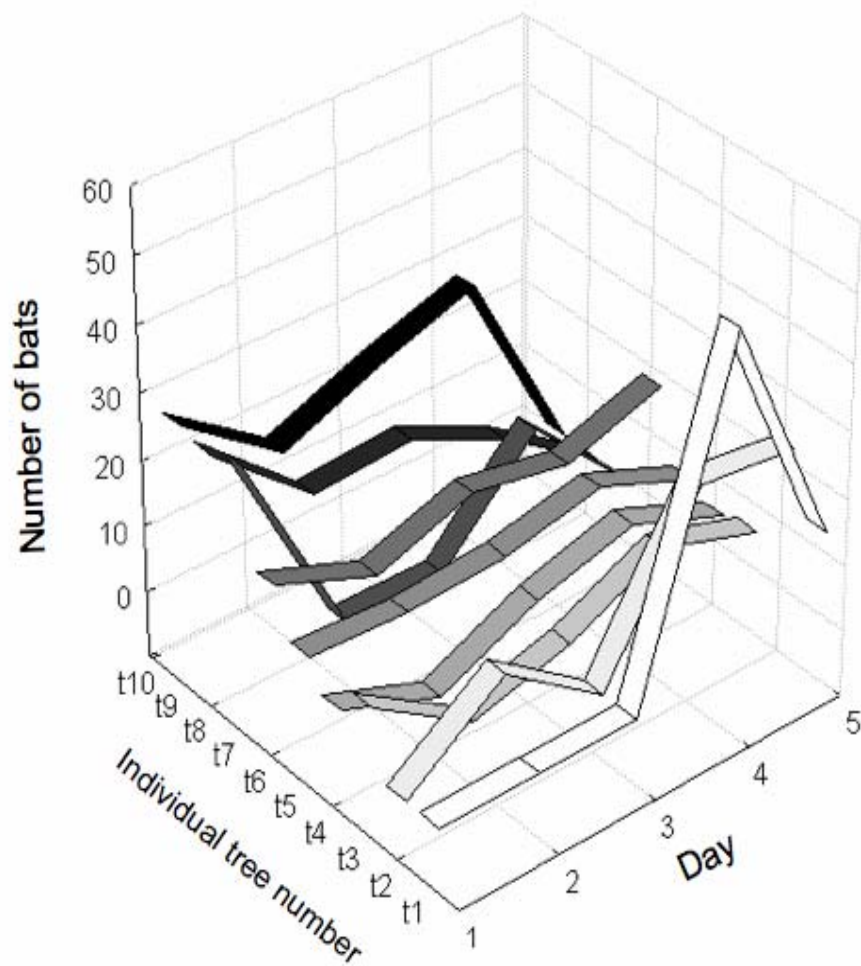
Figure 2: Evidence of extreme day to day variability in the number of flying-foxes roosting in ten individual trees at Whiteing Road flying-fox camp, November 2005. Each ribbon represents the daily number of bats at individual trees.
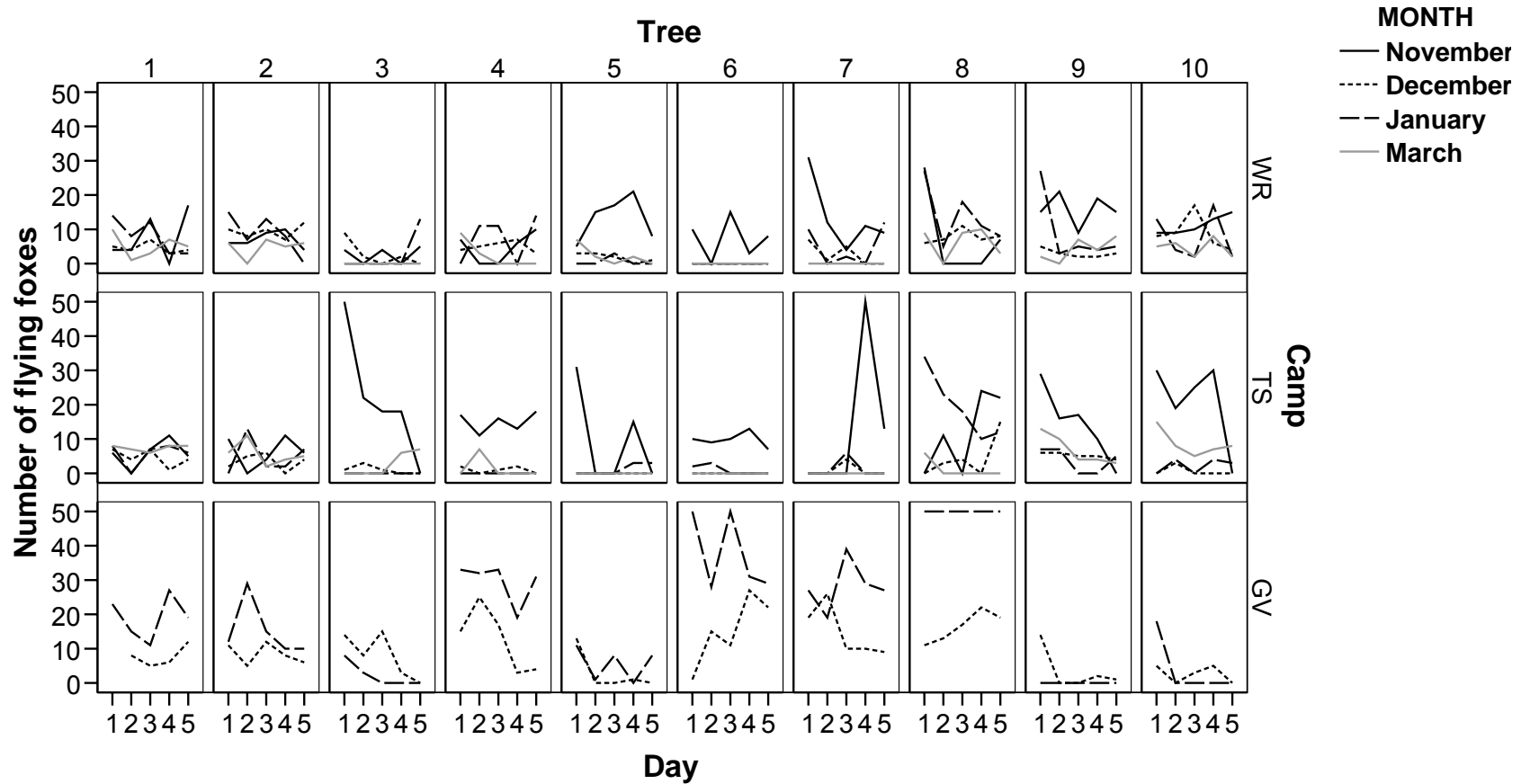
Figure 3: Variability of *Pteropus conspicillatus* numbers at ten roost trees in three camps recorded for five consecutive days in each month over a four month period.

sampled, while the number of flying-foxes roosting in Trees # 1, 2 and 3 appears similar across months.

The variation in roost number is represented by the coefficient of variation (CV) in the number of flying-foxes roosting in an individual tree over the five day census period (Figure 4). The CV is used to standardize the measure of variability by the number of flying-foxes occupying each tree. This frequency distribution indicates a high level of variability in the number of flying-foxes roosting in individual trees over the 5 day census periods, with the CV ranging from 0 to 223% (median = 72.5%).

Discussion

Pteropodids have been shown to display seasonal movements relating to food availability (Nelson, 1965, Parry-Jones and Augee, 1991, Spencer et al., 1991, Vardon and Tidemann, 1999, Tidemann and Nelson, 2004). While these movements traditionally relate to the availability of native fruit and blossom (Ratcliffe, 1932, Eby, 1991), it can also be influenced by the availability of exotic food sources such as planted non-native trees in urban environments (Parry-Jones and Augee, 2001, Markus and Hall, 2004). This consistent movement pattern between camps is also supported by molecular studies for *Pteropus conspicillatus* (Fox, 2006) and for *P. scapulatus* (Sinclair et al., 1996) where a significant level of gene flow between camps has been demonstrated. Although Australian flying-foxes may use alternate camp sites at different times of the year, they do show high camp fidelity to traditional camps over longer time periods (Tidemann et al., 1999).

The results of our study suggest that the high camp fidelity shown by Australian pteropodids is not matched by level of within-camp fidelity. The number of individual *P. conspicillatus* roosting within particular trees can vary significantly on a day-to-day basis. However it is worth noting that describing the behaviour of bats that are not individually marked does limit our ability to resolve patterns of roost site fidelity within a camp. A number of factors such as temperature
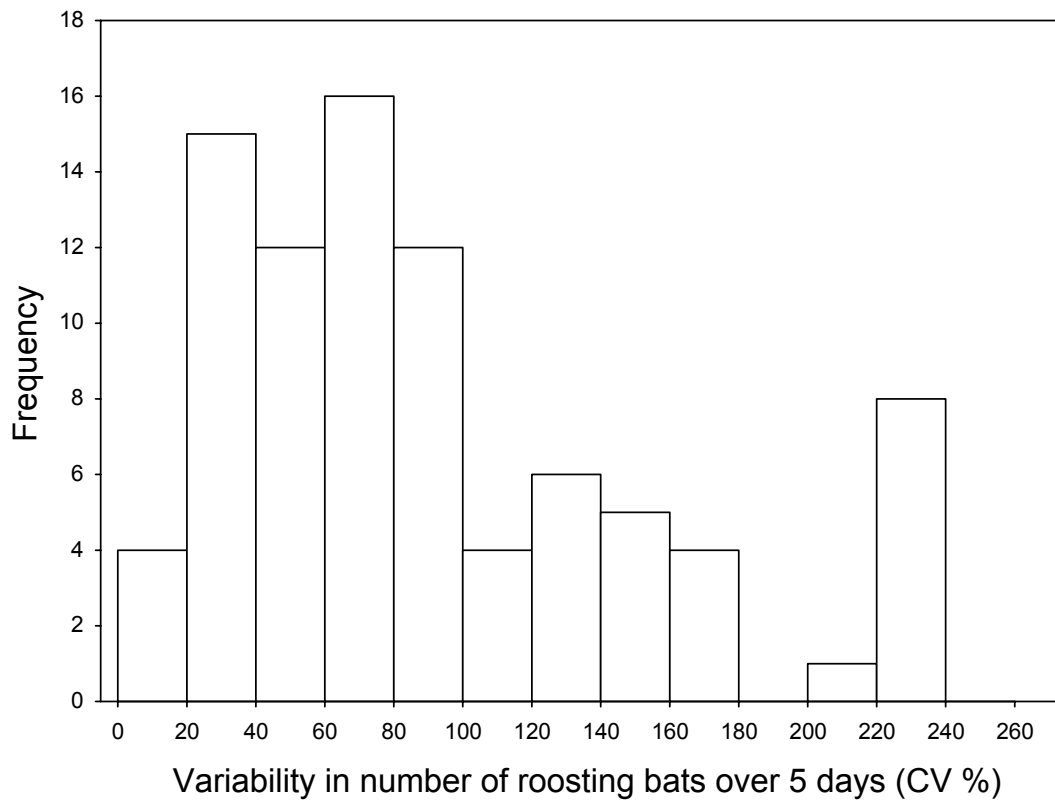
Figure 4: Within-tree variability in the number of roosting flying-foxes in an individual tree over a 5 day census period, as indicated by the coefficient of variation.

preferences, avoiding predation and parasite loads and attempts to gain access for mating are likely to determine individual patterns of roost tree fidelity (Lewis, 1995), but are difficult to assess in *P. conspicillatus* in the absence of knowledge of individual identities. Although the number of *P. conspicallatus* roosting in individual trees can vary on a day-to-day basis some trees do contain a relatively constant number of bats over the five day period and it is possible that a small number of stable groups did exist. Resolving these relationships further represents a rich area of future research.

The number of flying-foxes at a camp at any given time is highly variable and it may be possible that our results simply reflect this temporal variation in camp size. It is possible that large influxes of bats to a camp would cause a redistribution of bats within particular trees seasonally. However, the high-degree of day to day variability at these camps suggests that this is not the only contributing factor to roost tree fidelity.

With bat species declining worldwide (Mickleburgh et al., 1992, Hutson et al., 2001) and two species of Australian flying-fox, *P. conspicillatus* and *P. poliocephalus* listed as nationally threatened in 2001 and 2002 (EPBC, 1999), conservation strategies should address seasonal variations and internal variability in roosting habitats. Bats are important pollinators (Williams and Adam, 1994, Tschapka, 2004), dispersers of seed (Shilton, 1999, Hodgkison et al., 2003) and other regenerative plant material (Parsons et al., 2007) which makes this decline a serious concern to the wider ecosystem. Many threats to roost trees and available camp sites, such as increased urbanisation, climate change and severe weather events are influencing the distribution and seasonal use of camps (Garnett et al., 1999, Parris and Hazell, 2005, Shilton et al., 2008). Preservation of existing roosts and knowledge of how these roosts are used is an important feature of flying-fox conservation. The information provided from this study indicates a significant variability in the roost fidelity of flying-foxes within individual trees within camps. Although the basis for these patterns remains uncertain, the ecological and behavioural factors that underlie them are likely to significantly influence our management decisions. Developing

methods to elucidate the dynamics of roost patterns within individual camps remains an important challenge.

Chapter 7 - Temporal movement patterns of nocturnal fauna

Abstract

Wildlife strike is an increasing risk to aviation safety worldwide, however wildlife monitoring at airports is restricted to diurnal species due to logistical difficulties. In our study, we trialed new infra-red camera technology to monitor nocturnal wildlife movements at a tropical Australian airport to mitigate this little understood risk. We found that flying-foxes dominate the nocturnal wildlife activity at this airport and that there are seasonal peaks of activity in the periods preceding and following the wet season. There was also a nightly activity peak at 19:00 hours, a peak time for aircraft movements. These results mirror wildlife strike data in Australia. Distinct directional patterns were also found for flying-foxes and diurnal birds which move in different directions in the evening and morning. Both groups move towards the urban centre at the start of their feeding times (at night for flying-foxes and in the early morning for birds).The presence of increased food resources in this area could be contributing to this directional pattern. The similarity of local studies to national patterns provides evidence that nocturnal monitoring of wildlife can provide an excellent mitigation strategy. The parameters from this study can be used for future simulation exercises to model the strike risk at individual airports. Infra-red cameras can provide an efficient and inexpensive monitoring tool for aviation managers. An insight into the location and phenology of food resources surrounding an airport is the key to understanding bird and flying-fox movements.

Introduction

Wildlife strike poses a real risk to the aviation industry (ATSB, 2010, Dolbeer et al., 2009, Anon., 2001, Hesse et al., 2010). This risk includes the potential loss of lives and injury but more commonly the disruption of flight services and monetary loss from the damage to aircraft and associated on-costs (Allan and Orosz, 2001, Dolbeer et al., 2009). Worldwide, these incidents cost the industry an estimated US$ 1.28 billion annually (Allan and Orosz, 2001) and since 1988, wildlife strike has been responsible for the death of over 229 people and the destruction of over 210 aircraft (Dolbeer et al., 2009). As aircraft movements increase along with the incidence of strikes (ATSB, 2008, Dolbeer et al., 2009, Hesse et al., 2010), aviation agencies have responded by investing in research and the training of staff in wildlife management in order to mitigate this risk (Hesse et al., 2010, Brown et al., 2001).

While the majority of wildlife strikes involve aircraft colliding with diurnal birds, strikes are not restricted to either this taxa or this period of time alone (Parsons et al., 2008, Dolbeer et al., 2009). In North America, deer and alligators (Dolbeer et al., 2009) impact aircraft and as a whole terrestrial mammals are more likely to strike aircraft at night than birds (Dolbeer et al., 2009). In Australia, strikes from large nocturnal bats (flying-fox strikes) are also increasing and present a high risk at tropical airports in particular (Parsons et al., 2008).

A lack of observers available at night and low light conditions make nocturnal monitoring difficult. Recent developments in low-light and infra-red video equipment have the capacity to fill this knowledge gap but these techniques are yet to be widely implemented for management at airports. In this study we develop infra-red motion detecting video equipment to record nightly wildlife movements at a tropical Australian airport over an eighteen month period. We then explore the possibility of using environmental factors to predict the wildlife movement patterns observed, in order to inform management options.

Materials and methods

A motion-sensitive infra-red camera unit was installed at the eastern end of the main runway on a permanent road sign, at Townsville Airport, Queensland, Australia (-19.237035, 146.772529). Townsville Airport is a joint user airport with commercial aircraft sharing facilities with aircraft from the adjacent Royal Australian Air Force base. The unit consisted of a Sony IP57 Long Range Professional Colour infra-red Day/Night Camera (wavelength: 850 nm) with a SVAT CVP800 mini portable security recorder that used 2GB SD cards for video storage. Cards were collected after each night of recording. It was powered with a 12V battery recharged by a 12V, 4.5 watt solar panel with a solar switch (set to turn on at dusk and off at first light). Video footage captured any movement in a 2.5 km range from the camera location, using LED infra-red lights in combination with ambient lighting. Motion detecting sensitivity was calibrated monthly through the mini recorder. Video footage was collected for four nights per month (from dawn until dusk) for an eighteen month period (May 2007-November2008). Repairs to the camera in January 2008, meant that no footage was recorded in that month. Video footage was viewed and identity of individuals, time and direction of movement were recorded based on their image and wing-beat pattern. Individuals were categorised as flying-fox, bird, small bat, insect or unknown.

Information on weather variables were provided by The Australian Bureau of Meteorology (BOM, 2009) and data on sunrise, sunset, civil twilight times, lunar phase, moonset and rise for this period was obtained from GeoScience Australia (http://www.ga.gov.au/geodesy/astro/). Flowering phenology data were compiled from published material (Boulter et al. 2006, Hansman 2001), information from botanists familiar with the region (B. Jackes and C. Lockers pers. com.) and observations at the site (Parsons, unpubl. data). Flower availability from food trees was summarised by month and categorised as clumped or random (relating to flowering syndrome, Boulter et al. 2006). We used Pearson's correlation and stepwise regression to examine relationships between nocturnal wildlife movements and environmental variables. The number of nocturnal movements (per species group) was the dependent

variable and we initially included all of the variables listed in Table 1 as predictor variables. Variables including moon phase, civil twilight and sunspot number were included as light levels are known to influence the emergence times of flying-foxes (Chapter 5, this thesis). The model was then progressively reduced to identify the factors most strongly associated with nocturnal movements. Analyses were performed using Minitab 16 and @Risk software (www.palisade.com).

Results

A total of 4461 wildlife movements were recorded through the duration of the study, consisting of: 2525 flying-foxes, 602 small bats, 565 birds, 566 insects and 203 movements that could not be identified (unknown taxa). Overall, the probability of encountering flying-foxes is high at almost 57% with, bird, small bat and insect probabilities being much lower at 12.3, 13.6 and 12.75% respectively.

Seasonal patterns

The total number of nocturnal movements was highest in November corresponding with each taxa separately (Figure 1). The probability of encountering flying-foxes was greatest in August September and October (65, 62 and 60%), for birds was in February, May, Jun and July (20, 19, 18 and 21%), for small bats was in February (22%) and for insects was in March (24%).

Nightly patterns

Over the duration of the study, total flying-fox, insect and bird movements peaked at 19:00 hours, while small bat movements peaked at 21:00 (Figure 2). Flying-foxes were the most abundant taxon recorded with movements decreasing over the duration of the night (Figure 2). Flying-fox probability increases over the night as the probability of encountering birds decreases (Figure 3). Conversely, in the early morning, the probability of encountering flying-foxes decreases and birds increase again (Figure 3). There is a high probability of encountering flying-foxes throughout the evening, peaking at

Table 1: Variables tested in the analysis of nocturnal movement times and their description, also provided is the frequency that data was recorded and available for analysis.

Factor	Description	Data available
Civil twilight	The instant in the evening, when the centre of the sun is at a depression angle of six degrees (6°) below an ideal horizon.	Daily
Sunrise	The instant in the morning under ideal meteorological conditions, with standard refraction of the sun's rays, when the upper edge of the sun's disk is coincident with an ideal horizon.	Daily
Precipitation	Precipitation in the 24 hours before 09:00 (local time) in mm.	Daily
Temperature	Air temperature observation at 15:00 local time in °C	Daily
Wind speed	Wind speed at 15:00 local time measured in km h^{-1}	Daily
Cloud cover	Total cloud amount at 15:00 in eighths.	Daily
Sunspot number	Areas of the sun's surface marked by increased magnetic activity leading to decreases in solar surface temperature. Sunspots are counted and used as a measure of the variable solar cycle.	Daily
Moon illumination	If the moon was visible before civil twilight on that day; the proportion of the moon face illuminated according to moon phase (0, 0.5, 1).	Daily
Random flowering	Species of food trees that flower randomly over time.	Average monthly
Clumped flowering	Food trees with flowers that are temporally clumped, categorised monthly as <6 or >6 species.	Average monthly
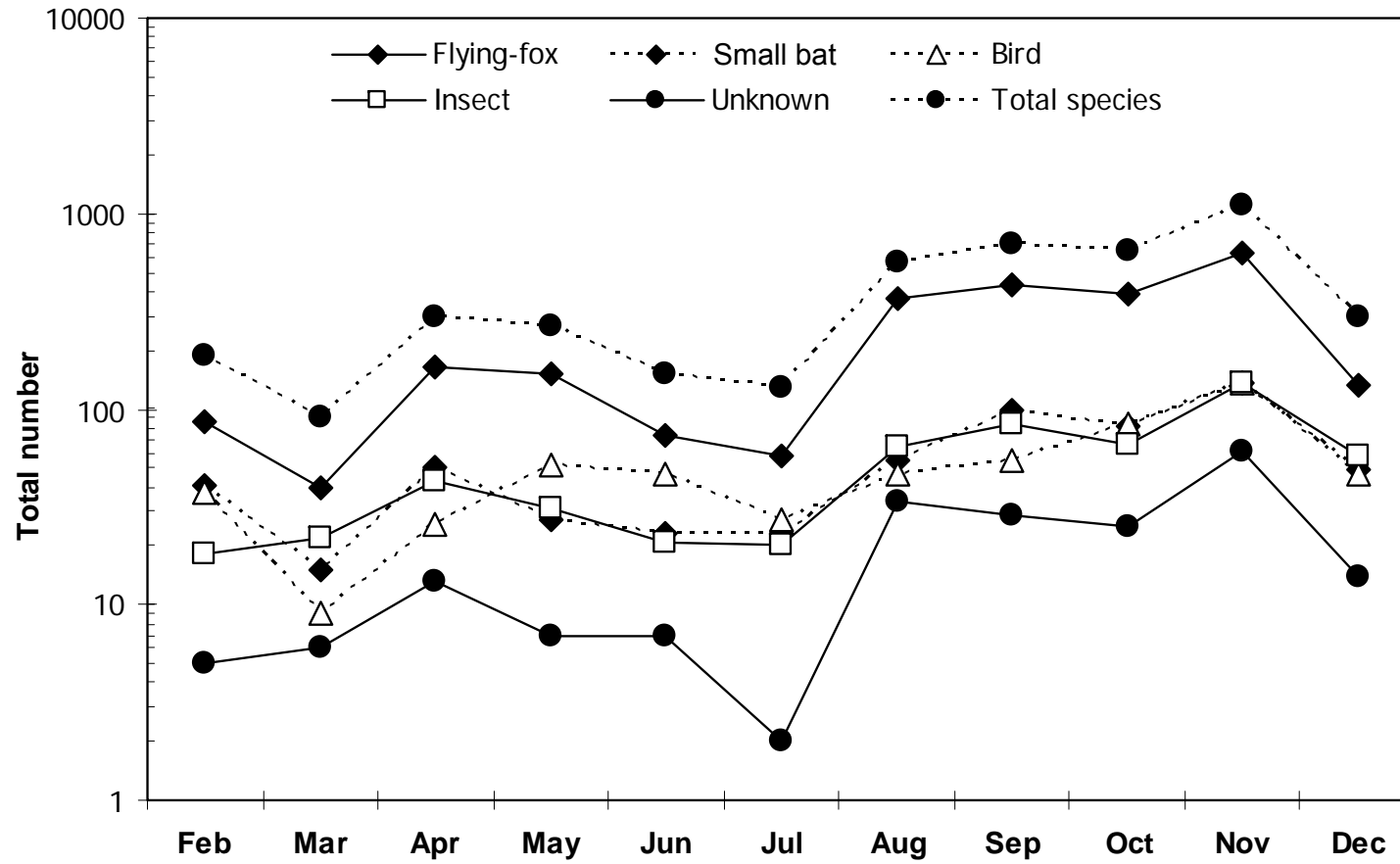
Figure 1: The seasonal pattern of nocturnal wildlife movements at Townsville Airport from May 2007 – November 2008.
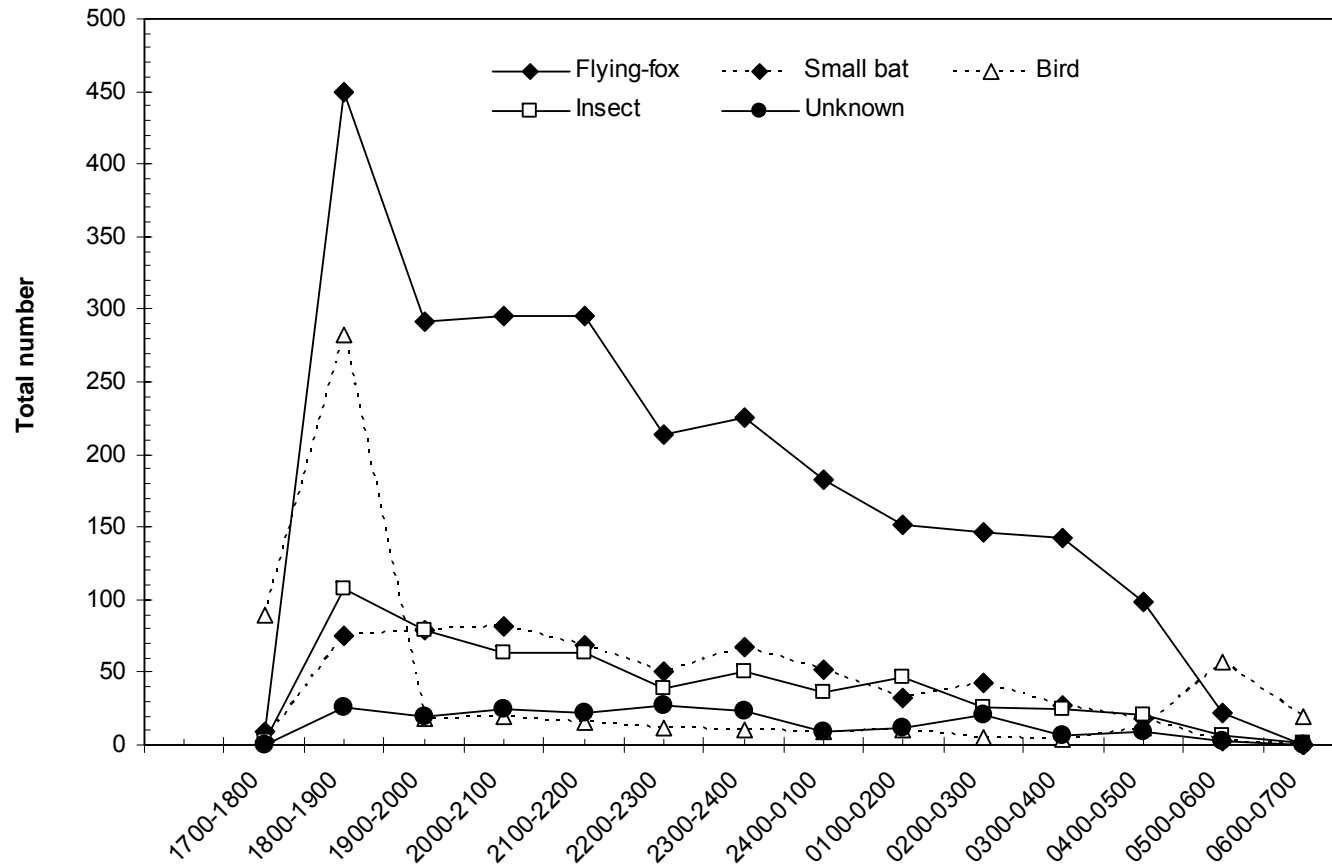
Figure 2: The nocturnal pattern of wildlife movements at the Townsville Airport from May 2007 – November 2008. Shaded area indicates sunset and sunrise times.
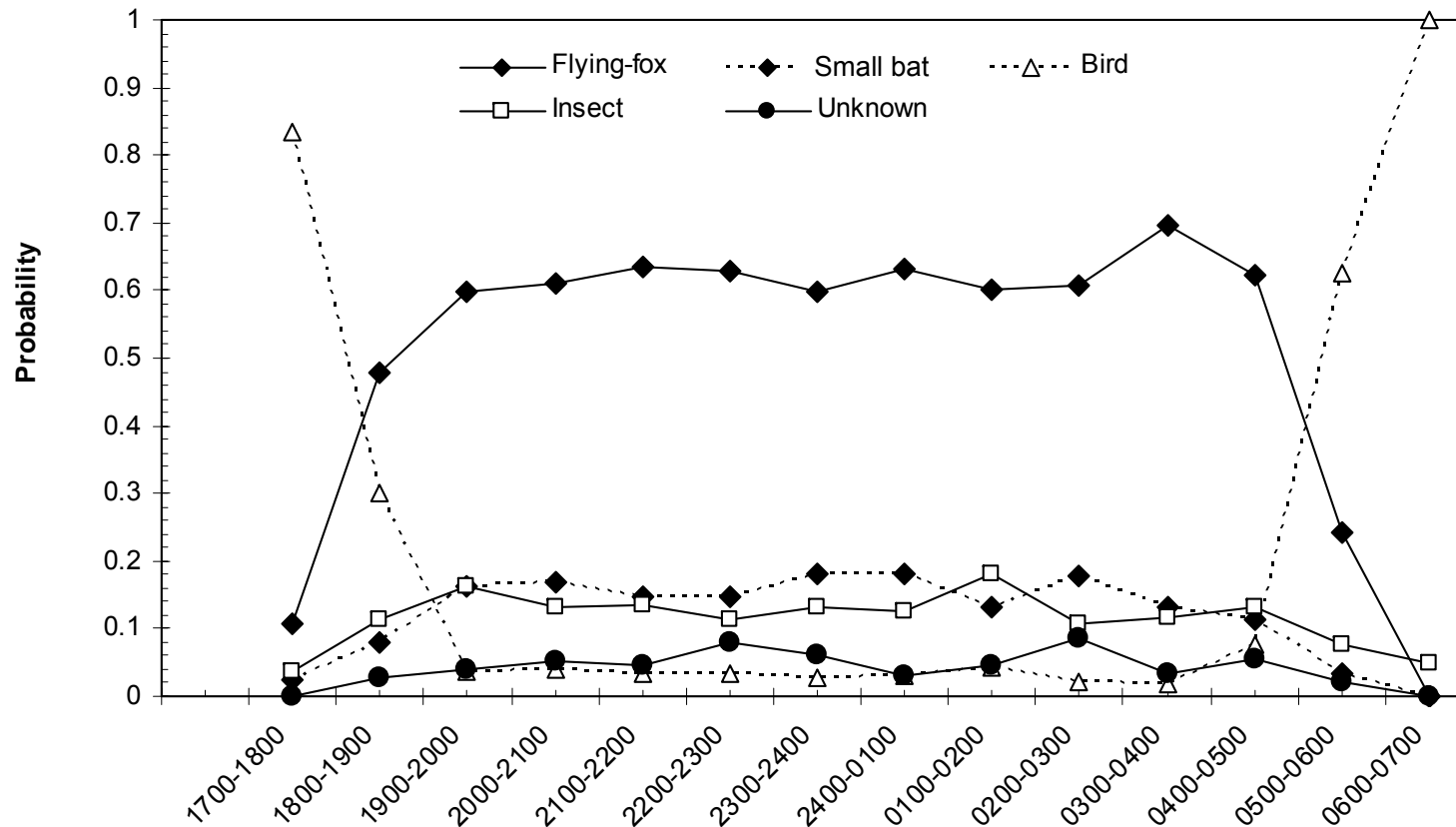
Figure 3: The probability of encountering species groups at each time period for nocturnal wildlife at Townsville Airport from May 2007 – November 2008. Shaded area indicates sunset and sunrise times.

69%, between 3-4 am (Figure 3). The highest probability of encountering birds is between 06:00 at 07:00(100%) and all other species have fairly equal probability throughout the night (Figure 3). It is likely that the unknown taxa consisted of a mix of the other species groups that were not in the frame long enough to categorise or were obscured in the footage.

Directional patterns

There is a distinct directional change for flying-foxes before and after midnight (Figure 4), before midnight 72% of flying-fox movements are in a southward direction and after midnight this changes to 62% travelling east (Figure 4). The direction of movement is different before and after midnight for flying-foxes (χ^2=386.664, df=1, p<0.001), birds (χ^2=52.47, df=1, p<0.001) and small bats (χ^2=5.6, df=1, p=0.018). Birds have no clear directional trend before midnight but after midnight, 74% of movements are towards the south (Figure 4). Small bats show similar patterns to flying-foxes with more southward movements before midnight and more eastward movements after midnight (Figure 4). Insect and unknown movements have similar numbers heading in each direction both before and after midnight (Figure 4).

Model

Our final model for flying-foxes accounts for 52 % of the variance in flying-fox movements observed in the study. The significant factors influencing flying-fox movements at this site are: the timing of sunrise (*SR*) (t = -6.40, P<0.001) and the presence of trees exhibiting a random flowering syndrome (*RF*) (t = 4.95, P=<0.001). The model is:

$$Y = 224.3 - 840SR + 6.8RF \qquad (R^2adj = 52.5) \qquad (1)$$

Sunrise was measured as decimal time and random flowering was measured as the number of species exhibiting that syndrome flowering per month. Daily variability in small bats, insects and birds could not be explained by the regression model. The timing of the sunrise (*SR*) was the single most explanatory variable explaining 38.7 %, 27.5% and 21.6% of the variability in small bats, insects and birds respectively, movements increased for all
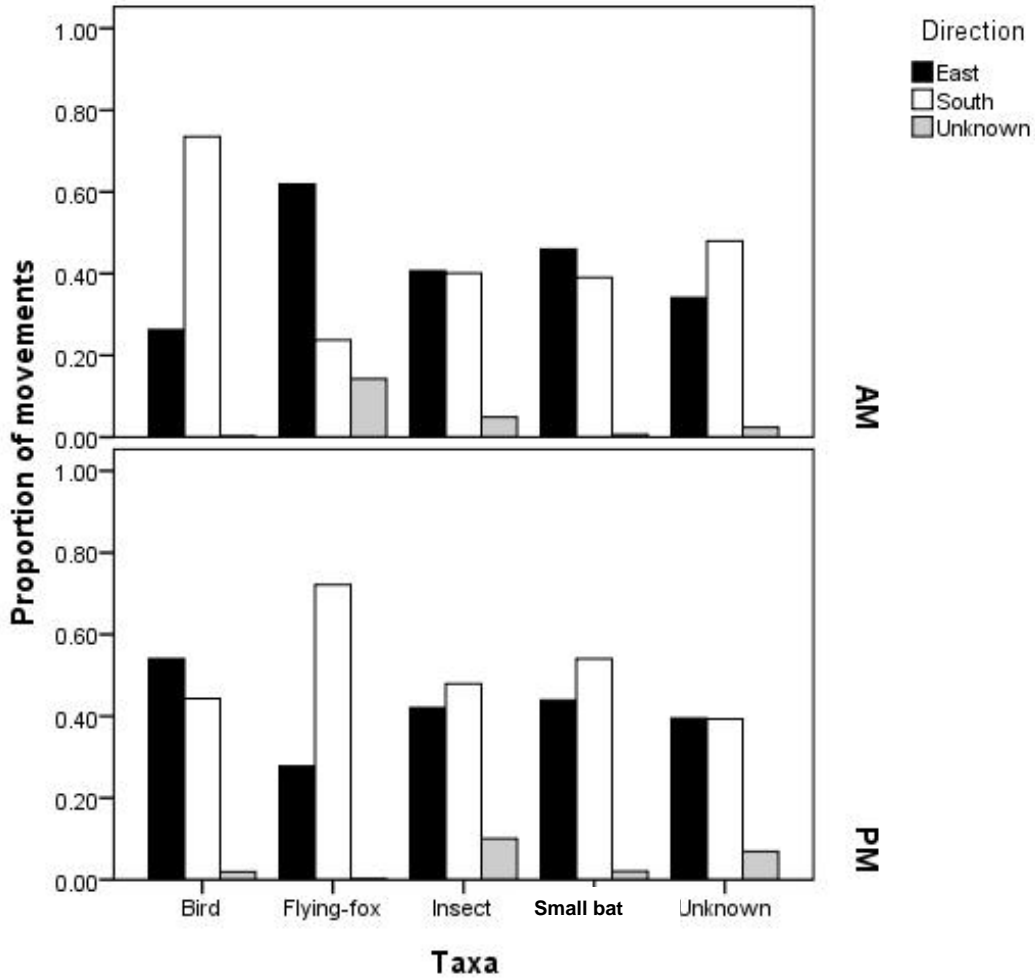
Figure 4: Directional movements of nocturnal wildlife before and after midnight at Townsville Airport from May 2007 – November 2008.

species when sunrise was earlier. The Monte-Carlo method was used for stochastically simulating daily variables for each group. All groups exhibited negative binomial probability density function (PDF, goodness of fit tested by Chi-square using equal probability bins), with different success and probability. We simulated temporal patterns at an experimental airport, where all group variability, including flying-foxes, was explained by a discrete probability distribution (Table 2).

Discussion

Of the five groups observed, flying-foxes and birds are likely to pose the greatest threat to aircraft at this airport due to their size and the large numbers detected. This is because species that are large in size and have a tendency to flock are more likely to cause serious damage to aircraft (Paton, 2009). Small bats and insects are less likely to cause a major impact when colliding with aircraft; therefore we will concentrate on the aforementioned groups. Here we have demonstrated that flying-foxes clearly dominate nocturnal wildlife movements at this airport. These bats emerge from a common roost that can contain thousands of individuals around sunset (Welbergen, 2008, Welbergen, 2006), returning throughout the evening and early morning in a less organised fashion (Ratcliffe, 1932). There is a surprising paucity of nocturnal birds detected, however, nocturnal birds only account for a small portion of bird species at this location. Also, these species (for example, owls and nightjars) tend to be solitary predators with a guarded home range (G. Baker pers. comm.).

Seasonal patterns
All species groups were most active in the early wet season (from October to December); this period of high rainfall results in peak productivity of plant resources for the region (Boulter et al., 2006, Williams and Middleton, 2008). Increased food resources attract migratory species and provide opportunities for reproduction. For flying-foxes, the early wet season includes the birthing period for black flying-foxes (*Pteropus alecto*) and the annual visitation of

Table 2: Probability distribution for each species group in the study.

Species group	Distribution
Flying-foxes	Negative binomial distribution (2^a,0.044^b)
Small bats	Negative binomial distribution (3,0.224)
Insects	Negative binomial distribution (3,0.235)
Birds	Negative binomial distribution (3,0.235)

Note: a = number of success and b = probability of a single success

migratory little red flying-foxes *P. scapulatus* (Ratcliffe, 1932, Nelson, 1965) (Chapter 5, this thesis). An increase in camp size at this time of year is known and is most likely due to the aforementioned variables (Chapter 6, this thesis). These increased numbers result in a higher number of flying-foxes commuting through the airport and therefore a higher risk to aviation at this time of year. A smaller peak in movement also occurs between March and May, at the end of the wet season which is also a time of high plant productivity (Parsons et al., 2008).

Nightly patterns

At this airport, most nocturnal movements occurred at 19:00 hours, indicating that this is the time of greatest danger to aircraft. It appears that birds which dominate the airfield during the day are replaced by flying-foxes in the early evening. There are two peaks of activity from birds at dusk and dawn, perhaps relating to movement between roosting and feeding grounds by diurnal species. This site is occupied by large numbers of magpie geese (G. Baker pers. comm.), which will account for some of these dusk and dawn movements.

The high number of flying-foxes present at 19:00 can be explained by the evening emergence of flying-foxes from roosts surrounding the airport. This time period also includes some of the busiest times for aircraft movements in Australia (ATSB, 2008) Therefore, this should be considered as a time with a high likelihood of flying-fox strikes, due to the number of flying-foxes present and the possibility of multiple strikes, These factors and the results of previous studies on the altitude (Parsons et al., 2009) and frequency (Parsons et al., 2008) of flying-fox strikes should be seriously considered in future risk assessment models. .

Directional patterns

The distinct directional movement of flying-foxes before and after midnight also reflects the evening emergence and return to the roost. It appears that flying-foxes from northern roosts (at Bushland Beach and Bohle River) are crossing the airport following their emergence and travelling south for access to food

resources and are returning in the opposite direction after midnight to return to the roost. Contrasting this, birds are moving south in the early morning, heading towards the Townsville suburbs. This difference can be simply explained by the different activity times of bats and the majority of birds detected in this study. While they are moving in different directions in the evening and morning, the nocturnal habits of bats mean that they are moving to feeding grounds in the evening and conversely birds are moving towards feeding grounds in the early morning. Suburbs with low to moderate human development provide an overabundance of feeding opportunities for some species, particularly birds and bats (Munyenyembe et al., 1989, McKinney, 2002). This is because of increased spatial complexity and food resources from planted trees that are irrigated year-round (McKinney, 2002, Williams et al., 2006). Flying-foxes and birds could be moving towards these additional food resources or perhaps using the prominent Mt Stuart (also in this direction) as a landmark for further travel.

Model and scale

For flying-foxes, our model identified the presence of trees with a random flowering syndrome as the variable influencing movements in this area. This type of flowering strategy means that these floral resources are separated both spatially and temporally, providing a commuting challenge for species relying on them. Flying-foxes move more frequently and greater distances to access this resource which means they would spend a larger percentage of their evening commuting between food trees. Australian flying-foxes are known to feed from a variety of plants and habitats (Tidemann et al., 1999, Parsons et al., 2006, Parry-Jones and Augee, 1991, Schmelitschek et al., 2009) and while individuals in camps across a region may display similar feeding patterns, flying-foxes from individual camps will feed on a distinct subset of the available resources (Parsons et al., 2006). Perhaps in our example, examining the diet of flying-foxes from the Northern camps would be beneficial to further resolve these movement patterns.

The timing of sunrise was also identified as a contributing variable for both flying-foxes and birds, with more movements being detected when sunrise was earlier. This pattern can be explained by a number of variables that are highly correlated with sunrise (that were therefore removed from the model). Earlier sunrise correlates with the summer months and also the wet season, both of which have been identified as the times of highest movement.

Wildlife strikes throughout Australia show similar patterns to the wildlife movements detected in this study. For example, there is a general bimodal pattern of wildlife strikes on a monthly basis with peaks identified in March-May (Parsons et al., 2008, ATSB, 2008) and October to January (ATSB, 2008), with troughs between June and July (ATSB, 2010). Also, a corresponding time period between 15:00 and 21:00 nationally has a high number of strikes recorded (ATSB, 2008).

Conclusions

We have shown that the use of infra-red camera technology provides an excellent tool for monitoring nocturnal wildlife activity and as night flights increase, it will continue to provide an important mitigation strategy. The Monte-Carlo approach described here allows for future simulations of the temporal variability of nocturnal species at an airport. We show that flying-foxes dominate nocturnal activity at this airport and that they have different activity patterns to birds. Our results are similar to wildlife strike patterns at a national scale and support the use of infra-red technology as a method of monitoring nocturnal wildlife movements at airports.

Chapter 8 - Bat strikes in the Australian Aviation industry

Abstract

Bat collisions are a threat to commercial and military aircraft in Australia. We examined bat strike records from Australia during 1996-2006 and found that risk of impact from bats is increasing, is greatest in tropical versus temperate regions, and is more likely during early evening and while an aircraft is landing rather than departing. While the most frequent collision height recorded was 152.4 meters (500 ft, 63.16% of all records), collisions between planes and bats were recorded at up to 1524 meters (5000 ft). This suggests that although flying-foxes can reach relatively high altitudes of around 1500 meters, the majority commute much closer to the ground at elevations of approximately 150 meters. Temporal patterns of bat strikes differ from those of birds, highlighting the need to employ taxon-specific management strategies to minimize animal impacts on the aviation industry. The use of genetic typing for identification of strike remains and the implementation of nocturnal survey techniques by wildlife managers at airports will contribute to the mitigation of bat strikes.

Introduction

Wildlife strikes to aircraft have been responsible for loss of human lives and damage to aircraft worldwide resulting in a loss of billions of dollars annually. As a result, the aviation industry dedicates substantial time and energy to minimize this risk (Anon., 2001). The majority of risk minimization strategies involve modifying the airport environment to reduce its attractiveness to hazardous species, or the use of disturbance regimes to frighten wildlife from airport environs (Brown et al., 2001, ATSB, 2002). Most strikes on a global scale result from impact with birds (Thorpe, 2003); however, airports throughout the South Pacific and Paleotropics region are faced with the additional threat of bat strikes from large flying-foxes (*Pteropus* spp.). Flying-foxes are large bats with a dense body mass up to 1,000 g (Churchill, 2008) and, unlike birds, do not have light pneumatised bones. This results in a greater and more concentrated impact force from bat strike and a greater capacity to perforate an aircraft's exterior than bird strikes do (Anon., 2001).

Ecological factors influencing bat strikes are also distinct from those of most birds. Australian flying-foxes roost gregariously and emerge from roosts in flocks, which may include thousands of flying-foxes, thus increasing risk of multiple, simultaneous strikes (Ratcliffe, 1932). Whereas birds are often attracted specifically to airports because of grass, lights, water, feeding trees, or roosts (ATSB, 2002, Barras and Seamans, 2002), it is most likely that flying-foxes come in contact with aircraft while transiting between food and roosting sites. The nocturnal behaviour of bats makes it difficult to determine their foraging habits at night, especially in regards to the height or altitude at which they fly. This is particularly true for the larger flying-foxes that can travel up to 40 km in a single night (Parsons et al., 2006, Spencer et al., 1991). Despite the value of such information for many aspects of the foraging ecology and ecophysiology of bats, gathering information on the flight altitudes used by bats remains a challenge that has led to the use of inventive sampling techniques. Active radar systems monitoring aircraft movements have detected the Brazillian free-tailed bat (*Tadarida brasiliensis)* flying at altitudes of nearly 10

000 ft (3048 m) (Williams et al., 1973), while helium filled kite balloons in combination with bat echolocation detection devices have identified molossid and emballonurid bats foraging at heights of almost 2000 ft (609.6 m)(Fenton and Griffin, 1997). More recently, modern weather surveillance radar has been used to identify streams of Brazillian free-tailed bats (*Tadarida brasiliensis)* emerging from their roosts (Horn and Kunz, 2008). The diurnal Samoan flying-fox, *Pteropus samoensis,* has been observed soaring on thermal updrafts (Lindhe Norberg et al., 2000, Richmond et al., 1998, Thomson et al., 2002), but unfortunately knowledge on the actual flying altitude of this or any other Pteropodid species remains unknown.

To date, no one has quantified occurrence of bat strikes in Australia, therefore, we analysed 10 years of data compiled by The Australian Transport Safety Bureau (ATSB) to better understand this phenomenon.

Methods

Data were collected from registered airports located throughout Australia. Australia has an extremely variable weather pattern and encompasses a wide variety of vegetation associations. Most urban centers and therefore airports are located in coastal regions.

In Australia, reporting of wildlife strikes by aircraft involved in air transport operations or using licensed aerodromes is mandatory under the Transport Safety Investigation Act and Regulations 2003 (Attorney-General's Department 2003). We examined 10 years of strike data (1996-2006) collected from Australian airports, which we obtained from the Australian Transport Safety Bureau (ATSB). The ATSB database typically contains information on the location of strikes (with reference to local airports, altitude), the type of aircraft involved and any damage received, and the identity of the impacting organisms if known.

According to the Australian Aviation Wildlife Hazard Group (AAWHG) a reported bird or animal strike is deemed to have occurred when 1) a pilot reports a strike to the ATSB, 2) aircraft maintenance personnel find evidence of a bird or animal strike on an aircraft, 3) personnel on the ground report seeing an aircraft strike ≥1 birds or animals, 4) bird or animal remains are found on the airside pavement area or within the runway strip, unless another reason for the bird or animal's death can be found (AAWHG, 2007). The ATSB database contains detailed records of all wildlife strikes regardless of taxonomic grouping. We based our analysis on all records that included the words, "bat", "fruit bat", or "flying-fox". We obtained data on aircraft movements at individual airports from the Bureau of Infrastructure, Transport, Regional Development and Regional Economics (BITRE). We classified airports as either tropical or temperate, with reference to the Tropic of Capricorn (23.4°S). Strike locations can include sites outside of Australia, if they involve Australian aircraft. Reports can be submitted by a variety of airport staff but they are usually submitted by the aircrew involved in the incident or afterwards during inspections.

We analysed bat strike data using a mixed model approach with restricted maximum likelihood within SAS V9.1 (SAS Institute Inc., Research Triangle Park, NC). We treated each observed bat strike as a dependent variable. We treated geographical region in which each airport was located as a fixed factor, individual airports as a random factor (nested within region), and year as a repeated measure. We standardized number of bat strikes per airport per year by dividing number of strikes by number of aircraft movements at each airport over the relevant time period and square-root transformed these values to resolve normality issues. We therefore report strike rate as number of strikes per 10,000 aircraft movements. We selected an autoregressive covariance structure (AR(1)) in the mixed model to minimize the Akaike's Information Criterion (Littell et al. 1996) and used chi-square goodness-of-fit to test effect of moon and flight phase on bat strike occurrences. A-priori alpha levels were $p < 0.05$. We present results as means $\pm$ standard errors. All heights are listed as feet above ground level, the usual practice of the airline industry.

Results

The ATSB database included 327 records of bat strikes from 91 airports during 1996-2006, of which 75 (23.93%) records also included the altitude at which the strike occurred. Bat strikes were identified by presence of an identifiable carcass (n = 198; 60%), presence of hair and blood (n = 8; 2.5%), visual identification (n = 94; 29%), and "guessing" (n = 1; 0.5%). No reason for identification was stated for 26 records (8%). Of the 327 bat strikes 62 (19%) caused major damage to aircraft including smashed windscreens, perforated aircraft skin and engine ingestion.

The highest rate of bat strikes occurred at the Townsville Airport, located in northeastern Queensland (Figure 1). There was no interaction between region and year on strike ($F_{10,839}$ = 1.32, p = 0.22). Bat strike rates were influenced by year ($F_{10,839}$ F = 4.63, p < 0.001), which explained 38% of variance in bat strike rates. Strike rates increased from a mean of 0.003 $\pm$ 0.002 per 10,000 aircraft movements in 1996 to 0.164 $\pm$ 0.11 in 2006 (Figure 2).

Strike rates differed in airports located in tropical versus temperate regions (0.221 $\pm$ 0.054 and 0.030 $\pm$ = 0.006 respectively, $F_{1,85}$ = 5.83, p < 0.05) with the 5 highest ranking airports for strikes all located in tropical regions (Figure 1). All bat strikes occurred within the known flying-fox range in Australia with 3 exceptions: one strike each in Alice Springs, Perth, and Kingscote (Figure 1). Two of these records were based on bat remains on the runway that may have been transported from elsewhere, but the Perth record was a confirmed flying-fox strike.

The largest proportion of bat strikes occurred between March and May (39%, n = 105) and in the year 2003 (23.6%, n = 77), with most strikes occurring around sunset, between 1700 hours and 2000 hours (57.2%, n = 283). There was no effect of moon phase on occurrence of bat strikes (x^2= 0.82, df = 7, p = 1.00). Proportion of strikes differed between landing, take-off, circuiting, and cruising phases (x^2= 301.60, df = 3, p < 0.001). More strikes occurred during landing

(74%, n = 173) than take-off (24.8%, n = 58). Few bat strikes occurred during circuiting and cruising phases (1.28%, n = 3).
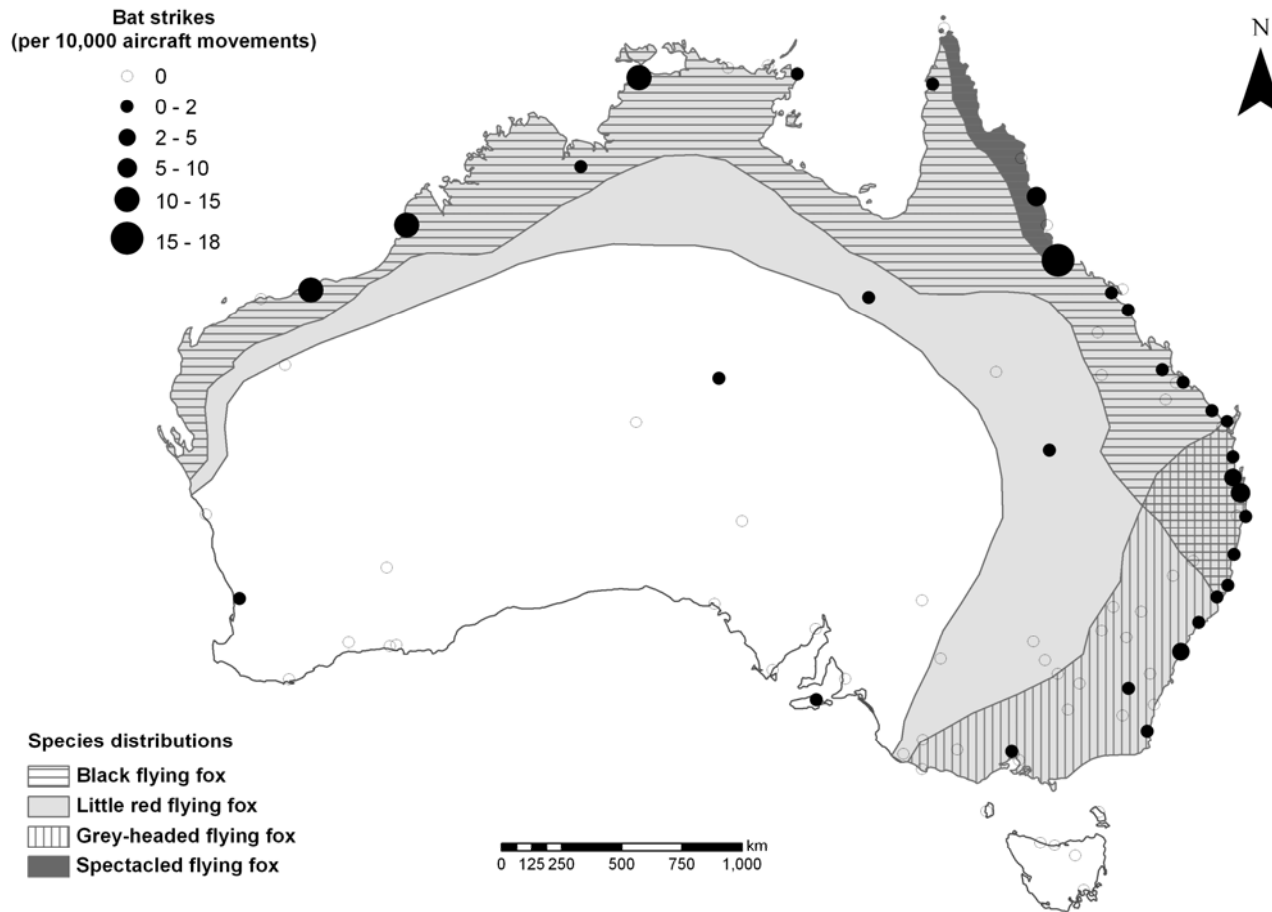
Figure 1: Location map of major airports in Australia with an index of bat strike occurrence (from 1996 – 2006) overlain with the range of flying-foxes in Australia (Hall and Richards 2000).
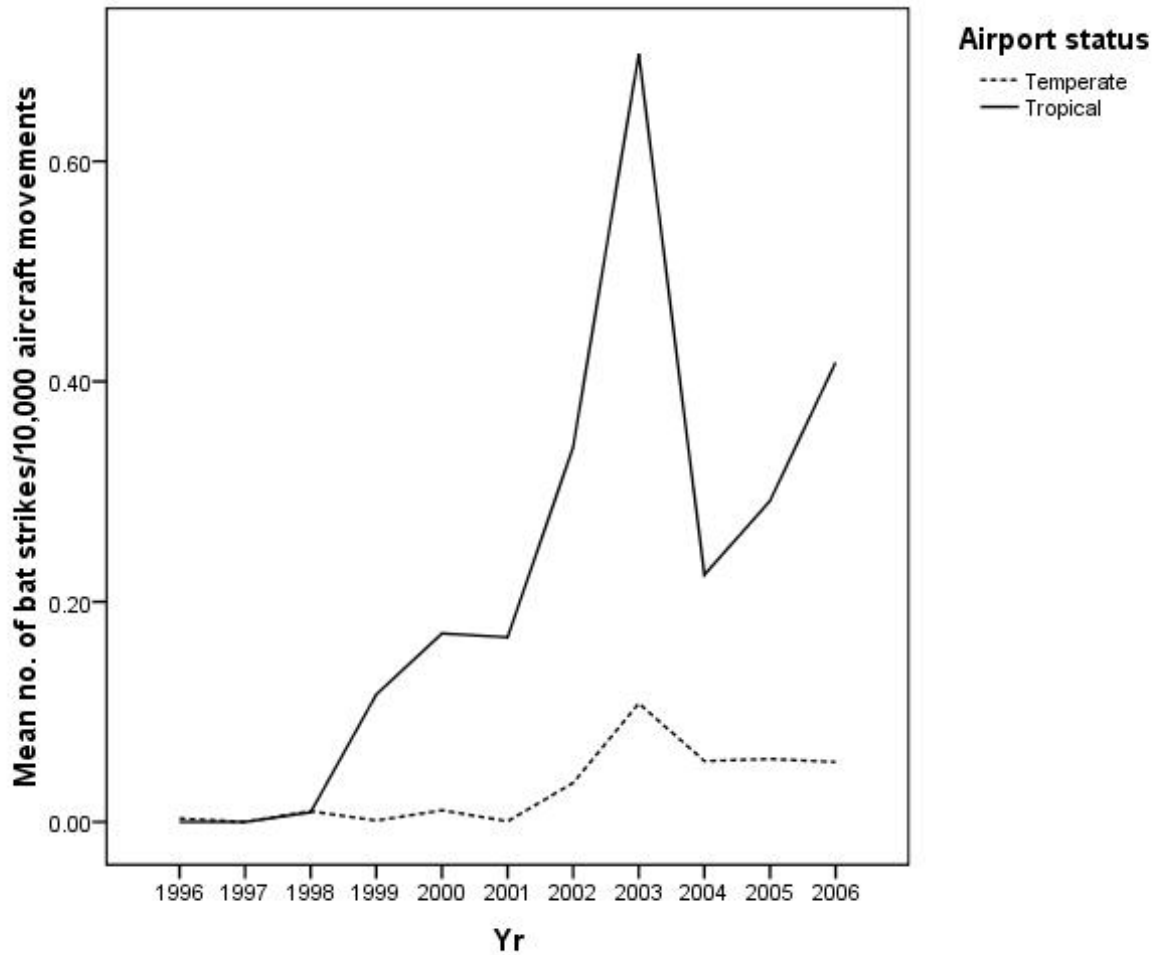
Figure 2: Mean number of bat strikes per 10,000 aircraft movements at Australian airports from 1996-2006 (n = 327) located in either tropical or temperate regions.

The altitudes at which bats and aircraft collided represent a skewed frequency distribution, with a range from zero to 5000 feet and a median and mode of 500 feet (Figure 3). The majority of strikes (96%) occurred at or below 1000 feet (mean $\pm$ SE = 566 $\pm$ 88 feet) with a large proportion of strikes occurring at 500 feet (63.16%). The two highest strikes (5000 feet) were recorded near the Darwin aerodrome in northern Australia and by an Australian aircraft descending into Changi Airport, Singapore.

Discussion

Most bat strike identifications were based on detection of identifiable bat remains after a collision. Given the damage aircraft inflict on bats, it is highly likely that these results are an underestimate of the true rate of impact. Genetic techniques can be used to identify species of birds involved in strikes based on blood and tissue smears only (Christidis et al., 2006) and should be applicable to bats.

Rate of bat strikes was greater in tropical than temperate regions, has increased over a 10-year period, and closely matches the range map of flying-foxes in Australia (Figs. 1, 2). An increase in recorded strikes may reflect changes in bat distributions as a function of changing food resources. The increase in suitable urban food plants (Markus and Hall, 2004) could increase bat densities around urban airports. The high rate of bat strikes occurring in 2003 (Fig. 2) may reflect the El Niño event of 2002-2003 (BOM, 2008), which reduced agricultural (ABS, 2008) and natural food production and may have increased movement of bats throughout Australia. The increase may also reflect improvements in accuracy with which airline industry staff record animal strikes, though reporting rates for animal strikes are considered to underestimate true strike rate (Barras and Dolbeer, 2000).

On a yearly basis, peak of bat strikes occurred during April-May, possibly reflecting high plant productivity that occurs at the end of the wet season in the
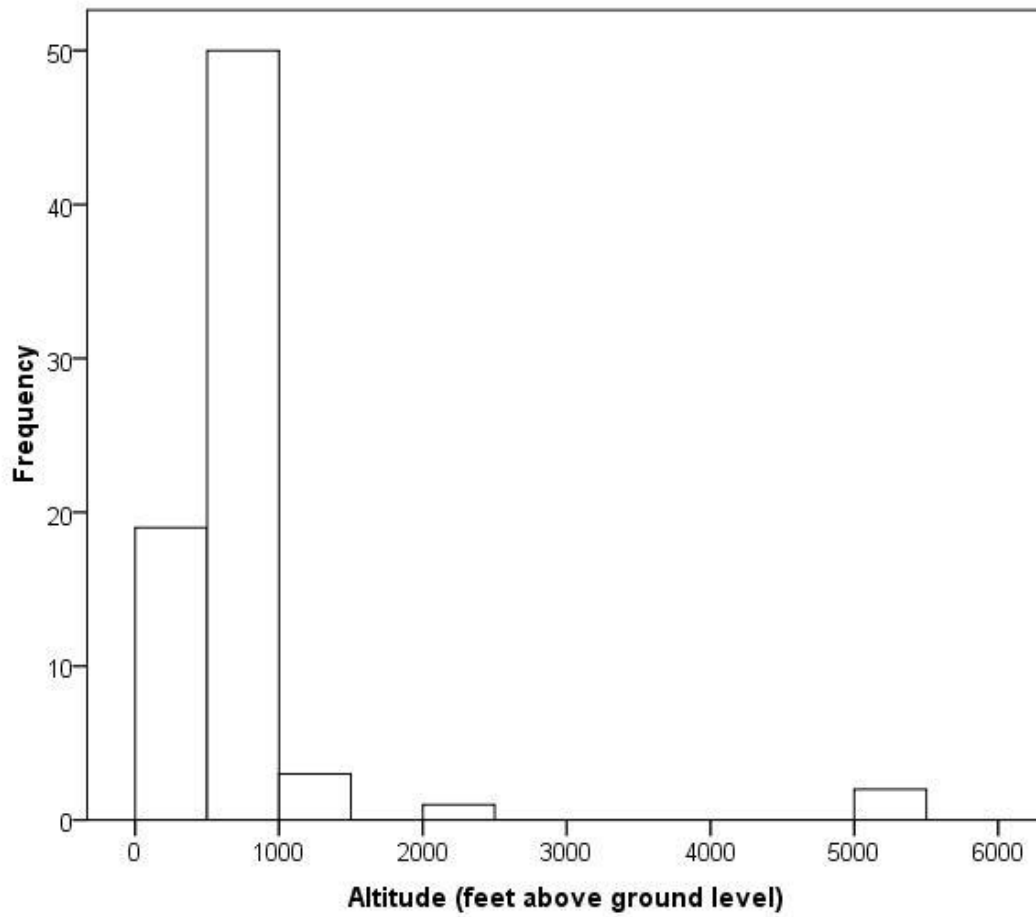
Figure 3: Altitudinal distribution of bat strikes in Australia (n = 75).

tropics. With increased food resources, there may also be an increase in flying-foxes moving from inland areas to tropical coastal regions. The little red flying-fox (*Pteropus scapulatus*) is known to migrate in response to flower availability (Sinclair et al., 1996, Tidemann et al., 1999), and favoured flowers such as those from paperbarks (*Melaleuca* spp.) would be readily available at this time in coastal areas.

Australian flying-foxes typically leave their day roost and fly to foraging sites within 30 minutes after sunset (Parry-Jones and Augee, 1992, Welbergen, 2006), this thesis, chapter 5), and it may be the presence of concentrated streams of commuting bats that makes them most dangerous for aircraft. There was no effect of moon phase on bats strikes, suggesting that activity patterns of flying-foxes are independent of the lunar cycle. This was surprising as activity patterns of the Australian blossom bat, *Syconycteris australis* (Law, 1997) and the Jamaican fruit bat, *Artibeus jamaicensis* (Morrison, 1978) are reduced during periods of higher lunar light. Much evidence suggests that flying-foxes are capable of engaging in long-distance movements, on both a diurnal and a longer seasonal basis. Spectacled Flying-foxes *Pteropus conspicillatus*, Black flying-foxes *P. alecto* and Grey headed flying-foxes *P. poliocephalus* travel >20 km in a single night (Markus and Hall, 2004, Parsons et al., 2006, Spencer et al., 1991) and the migratory patterns of Grey headed flying-foxes have been well documented with individuals migrating hundreds of kilometres in a single year (Eby, 1991, Spencer et al., 1991, Tidemann and Nelson, 2004). Two Grey headed flying-foxes travelled over 2000 km across Australia in a 12 month period (Tidemann and Nelson, 2004) and a single Little Red flying-fox *Pteropus scapulatus* was discovered in New Zealand, 1600 km from Australia where its journey presumably originated (Daniel, 1975).

The strike data contained in the ATSB data base now provides some evidence of the elevation at which flying-foxes fly. If these data represent an unbiased estimate of flight heights then it suggests that the majority of flying-foxes travel at heights of approximately 500 feet above the ground, with a few individuals flying at much higher elevations of 5000 feet. Although it might be difficult to

resolve some of the biases associated with using aircraft collisions as a sampling method for determining the height at which bats fly, it is likely that the detection of a modal flying height of approximately 500 feet is a conservative estimate of the relative number of bats flying at this height. Aircraft in Australia spend a relatively small proportion of their total flight time at this elevation. With the exception of ultra-light aircraft, even aircraft forced to circuit the airport while waiting to land are required to do so above 1000 feet (AP Bell pers comm.).

The maximum heights reached by flying-foxes of 5000 feet are less than those detected for the two species in which this data is known: the Brazillian Free-tailed bat *Tadarida brasilliensis* at 10,000 feet (Williams et al., 1973) and the Hoary bat *Lasiurus cinereus* at 8000 feet (Peurach, 2003), and these differences may reflect basic differences in the ecology of flying-foxes and other bats respectively. High altitude flights have been considered to benefit insect eating bats by allowing them access to insects drawn up into the air column (Fenton and Griffin, 1997) and by the reduced physiological costs due to the decreased air temperature and associated water loss experienced at higher elevations (Williams et al., 1973). The frugivorous diet of larger megachiropterans precludes dietary benefits *per se*, but the physiological benefits associated with migrating at higher elevations may be realised and it is possible that the collisions at 5000 feet may have involve migrating flying-foxes. Migrating birds can reach altitudes of up to 29 000 feet and many of the morphological and physiological adaptations possessed by birds that allow greater oxygen exchange at higher altitudes (where oxygen concentration is reduced) (Maina, 2000, Pennycuick, 1969, Scott and Milsom, 2007) are also present in bats (Maina, 2000).

The pattern of bat strikes we observed is different from that observed for birds. Most bat strikes occur around sunset, whereas most bird strikes occur in the morning (Chilvers et al., 1997, ATSB, 2002). Bat strikes are also more likely to occur during the landing phase, whereas most bird strikes occur during the take-off phase. This pattern in birds has been considered due, in part, to

increased fan forces in modern engines during takeoff (Dolbeer, 2007). Why a similar pattern is not found in bats is unknown.

Management Implications

This study has increased understanding of risks associated with bat strike in Australia. Determining the stage at which bats and birds typically collide with aircraft strongly supports the need for taxon-specific studies and management strategies. Regional differences in rate of bat strikes indicate that airports may require location-specific management plans. Development of molecular techniques to positively identify species of bats involved in strikes would be valuable, as would the implementation of nocturnal monitoring of the airport environment.

Chapter 9 – Synthesis of results and implications for management

As environmental heterogeneity and resource patchiness increase with anthropogenic climate change, the development of new techniques for monitoring the movement of species will become increasingly important. While traditional monitoring techniques may still be widely used, new techniques and technology are emerging that will allow the successful identification of key habitats for mobile species and the ecological factors contributing to these movements.

Historically, Australian *Pteropus* have employed movement strategies to track food resources in an environment that undergoes significant seasonal fluctuations. *Pteropus poliocephalus* and *P. scapulatus* undertake long-distance migrations to cope with this resource patchiness but *P. alecto* and *P. conspicillatus* have not been recorded using this strategy (although it cannot be ruled out). The evidence presented in this thesis (Chapters 4, 5 and 7) suggests that long distance movements may also be occurring in these species. The recent observation of *P. conspicillatus* at a site 500 km south of it's known range indicates a significant dispersal event and the expansion of the southern range of *P. alecto* supports a similar occurrence.

The visitation of migratory *P. scapulatus* explains some of the high degree of seasonal variability in camp numbers in north Queensland but this fluctuation is not dependent on their presence or absence. Variation also occurs on a daily scale, indicating that a degree of nomadism may also be exhibited by *P. alecto and P. conspicillatus* at these camps. The irregular availability of food resources during winter means that greater distances need to be travelled to access the resources necessary for survival, nomadic behaviour would be beneficial in these circumstances. As flying-foxes cross regional, state and international boundaries this information is vital for their management.

Summary of major findings

In this project I aimed to find new techniques for studying mobile species and to provide information on the ecological factors influencing the location of highly mobile flying-fox species in Australia. I also sought ways to apply this information to a specific management issue, flying-fox strikes in the aviation industry. I have:

- Provided important information on the ecological factors influencing flying-fox distribution, movement and behaviour on both local and national scales
- Developed a new method for monitoring local camps using aerial photography, that can be implemented on a regional scale
- Developed and tested a new method for monitoring nocturnal wildlife
- Provided new range maps for Australian flying-foxes
- Identified the climatic determinants of flying-fox camp location and modeled future distributions based on predicted climate change
- Found patterns of movement at a local airport and patterns of bat strike on a national scale that corresponded with the ecological information that I collected.

Methods and techniques for monitoring flying-foxes

I identified new techniques for monitoring flying-foxes, using aerial photography to identify seasonal trends in camp use and movement across an airport using infra-red video technology. Traditional observation techniques were used to monitor roost tree use at spectacled flying-fox camps. I used "citizen science" to identify the ecological factors influencing emergence times at a tropical Australian flying-fox camp and used historical databases to create climate models for all four flying-fox species present on mainland Australia and identify the factors influencing bat strikes in Australia. Each of these techniques successfully identified ecological factors contributing to the monitoring and

management of these highly mobile species. I have shown that it is possible to monitor these species on a variety of temporal and spatial scales from the individual roost tree through to a national level. I have used techniques that have ensured this was done in a safe and relatively inexpensive manner.

Patterns at a local scale

Highly variable levels of roost tree use by individuals at camps was shown over several months showing that fine scale monitoring is possible using traditional techniques (observation at the camp). There are shortcomings to this method though; the study camp must be accessible by foot and the flying-foxes at the camp not easily frightened by the presence of the observer (camps with high canopies). A much more successful fine-scale monitoring of camp usage over a large temporal scale is demonstrated when data collected by volunteers over a 7 year period is analysed to identify emergence patterns. Similar results were observed to those in published studies, suggesting that this is a successful way of gathering important information on camp use. Emergence times are most strongly influenced by variation in light levels and increased foraging demands and competition may also influence emergence behaviour. *Pteropus poliocephalus* was also found to have emergence times that corresponded with light levels and the earlier emergence of lactating females (Welbergen, 2006), support our findings. There is also a long-term trend of later emergence time at the Ross River camp, a possible effect of artificial lighting was identified from a nearby port which may explain this but without light measurements being collected at the time, this cannot be verified.

At a regional level, seasonal patterns of camp occupancy are not reflected at all camps. This is explained by the presence of different types of camps; main camps and satellite camps, the latter consisting of fewer than 1000 individuals and having a bias towards male occupants (Tidemann et al., 1999). While peak occupancy at most camps corresponded with food availability, the presence of these camps may relate to sex and age based behaviours. What

this outlines is that regional population monitoring should focus on the camp level, as trends extrapolated across a region may be inaccurate.

Despite this, consistent local movement patterns corresponding with food availability were identified at the airport. While camp occupancy may have many other inter-related components, the foraging journeys of flying-foxes across an airport closely matched the seasonal patterns and direction of available forage. Additionally, these local movements closely corresponded with information available on timing of flying-fox strike at a national level, with the largest number of movements and strikes at 19:00 hours and preceding and following the wet season.

Patterns at a national scale

By using data collated from a variety of sources, I was able to build climate models for all four *Pteropus* species found in Australia, allowing me to investigate their distribution. I apply this model to future climate scenarios, allowing an investigation of climate suitability over broad temporal scales. In the climate models I developed, I identified a single climatic factor as the highest contributor to all climate models, aspects of precipitation. The highly seasonal precipitation found in Australia, particularly in the tropics has a strong influence on the flowering and fruiting phenology of flying-fox food trees, indicating that flying-fox camps are situated in regions with precipitation cycles matching these resources. As future global climate scenarios are variable in their outcomes particularly when predicting precipitation changes in Australia, our results in this area are highly variable. However, when looking at the mean change in available climatic space for Australian *Pteropus*, we see an increase in both area and abundance for three species (*P. alecto*, *P. conspicillatus* and *P. scapulatus*) and a decrease for one (*P. poliocephalus*). Past-climate models suggest a long-term survival pattern in the same flying-fox species, *P. poliocephalus* (Luly et al., 2010). With significant reductions of available climatic space during the Last Glacial Maximum, the species was able to persist (Luly et al., 2010). Without further knowledge on the life history traits of

flying-foxes, these results should be interpreted with great caution. An area of potential concern has already been identified with the range of all Australian *Pteropus* shifting in recent times. A camp has now been identified that contains all four species and the implications of this new mixed species camp are still unknown. As the susceptibility of some *Pteropus* to extreme temperature events has now been demonstrated (Welbergen et al., 2008) and the low longevity of one (*P. conspicillatus)* shown (Fox et al., 2008), the identification of other life-history traits may highlight other possible vulnerabilities. Historically, *P. poliocephalus* has shown an intrinsic capacity to recover from serious habitat loss (Luly et al., 2010) and this may be what is necessary to ensure their persistence in the future.

Flying-fox strikes in the aviation industry

The range of each species identified also covers the area where most flying-fox strikes occur, with many strikes occurring in the tropics. On a national scale, peak flying-fox strikes occurred at the end of the wet season, a time of high plant productivity. As migratory *P. scapulatus* follow the flowering of their food trees, large numbers could move to coastal areas for feeding, an area that contains most of our commercial airports. Increased flying-fox strikes were also identified in a time of great drought (2003), suggesting that greater numbers of flying-foxes had to commute large distances to feed. Locally, in the Townsville region, flying-foxes are commuting across the airport, both at the end of the wet and preceding it. Like the national strike results, most movements are occurring around sunset, as flying-foxes emerge from the camp. The direction of movements towards the urban centre of Townsville at the beginning of the evening could be due to the increased food resources available from planted, irrigated gardens.

Management applications

For the aviation industry, there is no easy solution. Flying-foxes are intrinsically linked to ecological processes that ensure their survival. Even if every tree in a

50 km radius was removed from the airport surrounds, nomadic and migratory bats would still traverse the area. The most sensible solution is to include a monitoring program for both nocturnal wildlife and local flying-fox food trees in daily operations. This information can then be disseminated to airlines and times of high risk, both daily and seasonally, can be identified. The airlines can then weigh up the risk and schedule flights accordingly.

The management of flying-foxes will continue to be a controversial topic; as long as humans and flying-foxes interact there will be strong opinions across all areas of the spectrum. The completion of this thesis has contributed important information to aid both in the management and conservation of these highly mobile species. Importantly, the identification of a technique for monitoring flying-fox camps remotely creates opportunities for the synchronised monitoring of camps over large areas. It also provides a safe, cost-effective technique for managers of flying-fox camps in areas that are remote and difficult to access. In the past, a focus on absolute numbers has been the goal of managers, while this information can be important; we are still only sampling a portion of the population as a whole. We can include a much greater number of camps using remote sensing and by identifying seasonal trends of camp use we can also have a greater understanding of camp use by highly mobile Australian flying-foxes.

I have shown that important ecological information can come from a variety of sources to aid in management decisions. There is valuable data available in community groups, government departments and other organizations that can be used to identify spatial and temporal patterns of resource use. The results of this study could be translated to other populations of mobile species and to other regions. All of the techniques described here can also be applied to a variety of taxonomic groups.

For Australian flying-foxes, the importance of food resources and the ecological factors influencing them cannot be overstated. It has been demonstrated throughout this thesis that knowledge of the flowering and fruiting phenology of

flying-fox food trees will provide important answers for the management of flying-foxes and specifically for the mitigation of flying-fox strike in the aviation industry.

Future Directions

While this study has expanded our knowledge of the ecological factors influencing flying-foxes in Australia and has found new ways to study these species, there are still several key areas for future research: most importantly, the continued monitoring of flying-fox camps in Australia. There are no broad-scale, national monitoring efforts and I have provided a technique that will allow this to occur. By establishing a continuous national monitoring regime, we have the opportunity to observe the effects of climate change on a highly mobile species by creating occurrence databases as extensive as those held in the northern hemisphere for birds and butterflies. The improving resolution of satellite images may also provide a way of locating new flying-fox camps by identifying the spectral signature of damaged vegetation or the use of thermal infrared imaging to identify masses of animals.

Another very important area requiring further research is the monitoring of flying-fox food trees, their distribution, fruiting and flowering phenology. This could be achieved using remote sensing and will provide important links to flying-fox behaviour and movement patterns. Also, research on the nutrient flux present in these food items and how this is influenced by spatial, temporal and environmental factors would provide an important contribution. The confirmation of migratory movements in both *P. alecto* and *P. conspicillatus* through telemetry would expand our knowledge on the dispersal of these species and add great value to our future projections. As identified in Chapter 5, the monitoring of a newly discovered camp containing all four species of Australian *Pteropus* is vital for the identification of hybrid animals. Molecular studies at the Finch Hatton camp and surrounding camps will resolve this. Another rich area of future research is the continued investigation of the life history traits of Australian flying-foxes. This key information is needed for

understanding how climate change will influence their distribution and persistence in the future.

Literature Cited

AAWHG (2007) *Working policy on definitions of bird and animal strike*, Australian Aviation Wildlife Hazard Group.

ABRAMOFF, M. D., MAGALHAES, P. J. & RAM, S. J. (2004) Image processing with ImageJ. *Biophotonics International,* 11**,** 36-42.

ABS (2008) Year Book Australia. *Australian Bureau of Statistics, Canberra.*

ALLAN, J. R. & OROSZ, A. P. (2001) The costs of birdstrikes to commercial aviation. *Bird Strike 2001,Transport Canada.* Calgary, AB, Canada.

ALLENDORF, F. W., LEARY, R. F., SPRUELL, P. & WENBURG, J. K. (2001) The problems with hybrids: setting conservation guidelines. *Trends in Ecology & Evolution,* 16**,** 613-622.

ANDERSEN, K. (1912) *Catalogue of the Chiroptera in the Collection of the British Museum, Vol. 1, Megachiroptera,* London, Trustees British Museum (Natural History).

ANDERSON, R. P., GOMEZ-LAVERDE, M. & TOWNSEND PETERSON, A. (2002) Geographical distributions of spiny pocket mice in South America: insights from predictive models. *Global Ecology and Biogeography,* 11**,** 131-141.

ANDERSSON, M. (1980) Nomadism and Site Tenacity as Alternative Reproductive Tactics in Birds. *Journal of Animal Ecology,* 49**,** 175-184.

ANON. (2001) Sharing the skies: An aviation industry guide to the management of wildlife hazards. *Transport Canada.*

ARAUJO, M. B. & PEARSON, R. G. (2005) Equilibrium of species' distributions with climate. *Ecography,* 28**,** 693-695.

ATSB (2002) Australian Transport Safety Bureau (ATSB) Research paper November 2002: The Hazard Posed to Aircraft by Birds.

ATSB (2008) An analysis of Australian birdstrike occurences 2002 to 2006. *ATSB Transport Safety Investigation Report. Aviation Research and Analysis Report AR-2008-2007.* Canberra, A.C.T.

ATSB (2010) Australian aviation wildlife strike statistics: bird and animal strikes 2002 - 2009. . *ATSB Transport Safety Investigation Report. Aviation Research and Analysis Report AR-2008-2007.* Canberra, A.C.T.

BANACK, S. A. & GRANT, G. S. (2002) Spatial and temporal movement patterns of the flying fox, *Pteropus tonganus*, in American Samoa. *Journal of Wildlife Management,* 66**,** 1154-1163.

BARRAS, S. C. & DOLBEER, R. A. (2000) Reporting bias in bird strikes at John F Kennedy International Airport, New York, 1979 - 1998 *International Bird Strike Committee.* Amsterdam.

BARRAS, S. C. & SEAMANS, T. W. (2002) Vegetation management approaches for reducing wildlife-aircraft collisions. *Federal Aviation Administration Technology Transfer Conference.*

BARRY, J. P., BAXTER, C. H., SAGARIN, R. D. & GILMAN, S. E. (1995) Climate-Related, Long-Term Faunal Changes in a California Rocky Intertidal Community. *Science,* 267**,** 672-675.

BEAUMONT, L., J., MCALLAN, I. A. W. & HUGHES, L. (2006) A matter of timing: changes in the first date of arrival and last date of departure of Australian migratory birds. *Global Change Biology,* 12**,** 1339-1354.

BEAUMONT, L. J. & HUGHES, L. (2002) Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Global Change Biology,* 8**,** 954-971.

BEYER, H. L. (2004) Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/tools.

BIRT, P. (2000a) Salient points from papers presented at the workshop. IN RICHARDS, G. & HALL, L. (Eds.) *Workshop to Assess the Status of the Grey-headed Flying Fox.* Canberra, Australia, Australasian Bat Society.

BIRT, P. (2000b) Summary information on the status of the grey-headed (*Pteropus poliocephalus*) and black (*P. alecto*) flying-fox in New South Wales. IN RICHARDS, G. & HALL, L. (Eds.) *Workshop to Assess the Status of the Grey-headed Flying Fox.* Canberra, Australia Australasian Bat Society.

BIRT, P., HALL, L. S. & SMITH, G. C. (1997) Ecomorphology of the tongues of Australian Megachiroptera (Chiroptera: Pteropodidae). *Australian Journal of Zoology,* 45**,** 369-384.

BOM (2008) El Niño - Detailed Australian Analysis. *http://www.bom.gov.au/climate/enso/australia_detail.shtml*.

BOM (2009) Climate of Townsville.
http://www.bom.gov.au/weather/qld/townsville/climate.shtml.

BOULTER, S. L., KITCHING, R. L. & HOWLETT, B. G. (2006) Family, visitors and the weather: patterns of flowering in tropical rain forests of northern Australia. *Journal of Ecology,* 94**,** 369-382.

BOYLE, W. Â. & CONWAY, Â. J. (2007) Why Migrate? A Test of the Evolutionary Precursor Hypothesis. *The American Naturalist,* 169**,** 344-359.

BROWN, K. M., ERWIN, R. M., RICHMOND, M. E., BUCKLEY, P. A., TANACREDI, J. T. & AVRIN, D. (2001) Managing birds and controlling aircraft in the Kennedy Airport-Jaimaca Bay Wildlife Refuge Complex: the need for hard data and soft opinions. *Environmental Management,* 28**,** 207-224.

BROWN, S. C., SCHULTE, S., HARRINGTON, B., WINN, B., BART, J. & HOWE, M. (2005) Population size and winter distribution of eastern American oystercatchers. *Journal of Wildlife Management,* 69**,** 1538-1545.

CHAMBERLAIN, D. E., WILSON, A. M., BROWNE, S. J. & VICKERY, J. A. (1999) Effects of Habitat Type and Management on the Abundance of Skylarks in the Breeding Season. *Journal of Applied Ecology,* 36**,** 856-870.

CHILVERS, B. L., RYAN, C. J. & HICKLING, G. J. (1997) Factors affecting pilot-reported bird-strikes at Christchurch International Airport, New Zealand. *New Zealand Journal of Zoology,* 24**,** 1-7.

CHRISTIDIS, L., NORMAN, J. A., JOHNSON, R. N. & LINDSAY, S. (2006) Forensic Identification of Aviation Bird Strikes in Australia Australian Transport Safety Bureau.

CHURCHILL, S. (2008) *Australian Bats,* Sydney, Australia, New Holland Publishers.

COHN, J. P. (2008) Citizen Science: Can Volunteers Do Real Research? *BioScience,* 58**,** 192-197.

COLLETT, R. (1887) On a collection of mammals from central and northern Queensland. *Zoologische Jahrbucher Zeitschrift fur Systematik, Geographie und Biologie der Thiere***,** 829 - 940.

COOPER, C. B., DICKINSON, J., PHILLIPS, T. & BONNEY, R. (2007) Citizen science as a tool for conservation in residential ecosystems. *Ecology and Society* 12**,** 11.

CSIRO (2007) Climate Change in Australia - Technical Report 2007. CSIRO, Bureau of Meteorology, Melbourne, Australia.

DANIEL, M. J. (1975) First record of an Australian fruit bat (Megachiroptera: Pteropodidae) reaching New Zealand. *New Zealand Journal of Zoology,* 2**,** 227 - 231.

DEAN, W. R. J. (1997) The distribution and biology of nomadic birds in the Karoo, South Africa. *Journal of Biogeography,* 24**,** 769-779.

DINGLE, H. & DRAKE, V. A. (2007) What is migration? *Bioscience,* 57**,** 113-121.

DOAK, D. F., ESTES, J. A., HALPERN, B. S., JACOB, U., LINDBERG, D. R., LOVVORN, J., MONSON, D. H., TINKER, M. T., WILLIAMS, T. M., WOOTTON, T., CARROLL, I., EMMERSON, M., MICHELI, F. & NOVAK, M. (2008) Understanding and predicting ecological dynamics: are major surprises inevitable? . *Ecology,* 89**,** 952-961.

DOLBEER, R. A. (2007) Bird damage to turbofan engines in relation to phase of flight - Why speed kills. *Birdstrike 2007.* Kingston, Canada.

DOLBEER, R. A., WRIGHT, S. E., WELLER, J. & BEGIER, M. J. (2009) Wildlife strikes to civil aircraft in the United States 1990-2008. *Report of the Associate Administrator of Airports, Office of Airport Safety and Standards. National Wildlife Strike Database, Serial Report Number 15.* Washington D.C.

DYRCZ, A. & HALUPKA, L. (2009) The response of the Great Reed Warbler *Acrocephalus arundinaceus* to climate change. *Journal of Ornithology,* 150**,** 39-44.

EASTERLING, D. R., MEEHL, G. A., PARMESAN, C., CHANGNON, S. A., KARL, T. R. & MEARNS, L. O. (2000) Climate Extremes: Observations, Modeling, and Impacts. *Science,* 289**,** 2068-2074.

EBY, P. (1991) Seasonal movements of Grey-headed flying foxes, *Pteropus poliocephalus* (Chiroptera:Pteropodidae), from two maternity camps in Northern New South Wales *Wildlife Research,* 18**,** 547 -559.

EBY, P. (2000) The results of four synchronous assessments of relative distribution and abundance of grey-headed flying fox *Pteropus poliocephalus.* IN RICHARDS, G. & HALL, L. (Eds.) *Workshop to Assess the Status of the Grey-headed Flying Fox.* Canberra, Australia, Australasian Bat Society.

EBY, P., RICHARDS, G., COLLINS, L. & PARRY-JONES, K. (1999) The distribution, abundance and vulnerability to population reduction of a nomadic nectarivore, the grey- headed flying-fox *Pteropus poliocephalus* in New South Wales during a period of resource concentration. *Australian Zoologist,* 31**,** 240-243.

ELITH, J., GRAHAM, C. H., ANDERSON, R. P., DUDÍK, M., FERRIER, S., GUISAN, A., HIJMANS, R. J., HUETTMANN, F., LEATHWICK, J. R., LEHMANN, A., LI, J., LOHMANN, L. G., LOISELLE, B. A., MANION, G., MORITZ, C., NAKAMURA, M., NAKAZAWA, Y., OVERTON, J., TOWNSEND PETERSON, A., PHILLIPS, S. J., RICHARDSON, K., SCACHETTI-PEREIRA, R., SCHAPIRE, R. E., SOBERÓN, J., WILLIAMS, S., WISZ, M. S. & ZIMMERMANN, N. E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography,* 29**,** 129-151.

EPA (2007) Environmental Protection Agency. Regional Ecosystem Description Database (REDD), Version 5.2. Database maintained by Queensland Herbarium, Environmental Protection Agency, Brisbane.

EPBC (1999) Environmental Protection and Biodiversity Conservation Act. *Australian Government - Department of the Environment, Water, Heritage and the Arts.*

FENTON, M. B. & GRIFFIN, D. R. (1997) High altitude pursuit of insects by echolocating bats *Journal of Mammalogy,* 78**,** 247-250.

FFICN (2010) Flying Fox Information Conservation Network, http://au.groups.yahoo.com/group/FFICN/.

FLEMING, T. H. & EBY, P. (2003) Ecology of bat migration. IN KUNZ, T. H. & FENTON, M. B. (Eds.) *Bat Ecology.* Chicago, USA., The University of Chicago Press.

FORSYTH, D. M., SCROGGIE, M. P. & MCDONALD-MADDEN, E. (2006)
Accuracy and precision of grey-headed flying-fox (*Pteropus poliocephalus*) flyout counts. *Wildlife Research,* 33**,** 57-65.

FOX, S., LULY, J., MITCHELL, C. B., MACLEAN, J. & WESTCOTT, D. A.
(2008) Demographic
indications of decline in the spectacled flying-fox (*Pteropus conspicillatus*) on
the Atherton Tablelands of northern Queensland. *Wildlife Research,* 35**,**
417-424.

FOX, S. J. (2006) Population structure in the spectacled flying fox, *Pteropus conspicillatus* : a study of genetic and demographic factors. PhD thesis. *School of Marine and Tropical Biology.* Queensland, Australia, James Cook University.

FRITZ, H., SAID, S. & WEIMERSKIRCH, H. (2003) Scale dependent hierarchical adjustments of movement patterns in a long range foraging seabird. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 270**,** 1143-1148.

GARNETT, S., WHYBIRD, O. & SPENCER, H. (1999) The conservation status of the spectacled flying fox *Pteropus conspicillatus* in Australia. *Australian Zoologist,* 31**,** 38-54.

GIBSON, L., MCNEILL, A., TORES, P. D., WAYNE, A. & YATES, C. Will future climate change threaten a range restricted endemic species, the quokka (*Setonix brachyurus*), in south west Australia? *Biological Conservation,* 143**,** 2453-2461.

GONZALEZ-MEGIAS, A., MENENDEZ, R., ROY, D., BRERETON, T. & THOMAS, C. D. (2008) Changes in the composition of British butterfly assemblages over two decades. *Global Change Biology,* 14**,** 1464-1474.

HALL, L. & RICHARDS, G. (1979) Bats of Eastern Australia. *Queensland Museum Booklet No.12.* Brisbane, Queensland Museum.

HALL, L. & RICHARDS, G. (2000) *Flying foxes, fruit and blossom bats of Australia.,* Sydney, Australia., UNSW Press.

HEGLAND, S. J., NIELSEN, A., LAZARO, A., BJERKNES, A. & TOTLAND, O. (2009) How does climate warming affect plant-pollinator interactions? *Ecology Letters,* 12**,** 184-195.

HERNANDEZ, P. A., GRAHAM, C. H., MASTER, L. L. & ALBERT, D. L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography,* 29**,** 773-785.

HESSE, G., REA, R. V. & BOOTH, A. L. (2010) Wildlife management practices at western Canadian airports. *Journal of Air Transport Management,* 16**,** 185-190.

HIBY, L., THOMPSON, D. & WARD, A. (1987) Improving census by aerial photography - an inexpensive system based on non-specialist equipment. . *Wildlife Society Bulletin,* 15**,** 438-443.

HODGKISON, R., BALDING, S. T., ZUBAID, A. & KUNZ, T. H. (2003) Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rainforest. *Biotropica,* 35**,** 491-502.

HONNAY, O., VERHEYEN, K., BUTAYE, J., JACQUEMYN, H., BOSSUYT, B. & HERMY, M. (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters,* 5**,** 525-530.

HORN, J. W. & KUNZ, T. H. (2008) Analyzing NEXRAD doppler radar images to assess nightly dispersal patterns and population trends in Brazilian free-tailed bats (Tadarida brasiliensis). *Integrative and Comparative Biology,* 48**,** 24-39.

HUGHES, L. (2003) Climate change and Australia: Trends, projections and impacts. *Austral Ecology,* 28.

HUTSON, A. M., MICKLEBURGH, S. & RACEY, P. A. (2001) Microchiropteran Bats: Global Status Survey and Conservation Action Plan. Gland, Switzerland., International Union for Conservation of Nature and Natural Resources.

ISAAC, J. L. (2008) Effects of climate change on life history: implications for extinction risk in mammals. *Endangered Species Research,* doi: 10.3354/esr00093.

KAREIVA, P. (1990) Population-dynamics in spatially complex environments - theory and data. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences,* 330**,** 175-190.

KENNEY, R. D., MAYO, C. A. & WINN, H. E. (2001) Migration and foraging strategies at varying spatial scales in western north Atlantic right whales: a review of hypotheses. *Journal of Cetacean Research and Management,* 2**,** 251-260.

KINDVALL, O. (1996) Habitat heterogeneity and survival in a bush cricket metapopulation. *Ecology,* 77**,** 207-214.

KIRBY, J. S., STATTERSFIELD, A. J., BUTCHART, S. H. M., EVANS, M. I., GRIMMETT, R. F. A., JONES, V. R., O'SULLIVAN, J., TUCKER, G. M. & NEWTON, I. (2008) Key conservation issues for migratory land and waterbird species on the world's major flyways. *Bird Conservation International,* 18**,** S49-S73.

KNAPP, A. K., BEIER, C., BRISKE, D. D., CLASSEN, A. T., LUO, Y., REICHSTEIN, M., SMITH, M. D., BELL, J. E., FAY, P. A., HEISLER, J. L., LEAVITT, S. W., SHERRY, R., SMITH, B. & WENG, E. (2008) Consequences of more extreme precipitation regimes for terrestrial ecosystems. *Bioscience,* 58**,** 811-821.

KOLEČEK, J., REIF, J., ŠŤASTNÝ, K. & BEJČEK, V. Changes in bird distribution in a Central European country between 1985–1989 and 2001–2003. *Journal of Ornithology,* 151**,** 923-932.

KRUMMEL, J. R., GARDNER, R. H., SUGIHARA, G., O'NEILL, R. V. & COLEMAN, P. R. (1987) Landscape Patterns in a Disturbed Environment. *Oikos,* 48**,** 321-324.

KUNZ, T. H., GAUTHREAUX, S. A., JR., HRISTOV, N. I., HORN, J. W., JONES, G., KALKO, E. K. V., LARKIN, R. P., MCCRACKEN, G. F., SWARTZ, S. M., SRYGLEY, R. B., DUDLEY, R., WESTBROOK, J. K. & WIKELSKI, M. (2008) Aeroecology: probing and modeling the aerosphere. *Integr. Comp. Biol.,* 48**,** 1-11.

KURTA, A. & WINHOLD, L. (2007) Range expansion and changing abundance of the Eastern Pipistrelle (Chiroptera:Vespertilionidae) in the Central Great Lakes region. *American Midlands Naturalist,* 157**,** 404 - 411.

LA SORTE, F. A. & THOMPSON, F. R. (2007) Poleward shifts in winter ranges of North American birds. *Ecology,* 88**,** 1803-1812.

LALIBERTE, A. S. & RIPPLE, W. J. (2003) Automated wildlife counts from remotely sensed imagery. *Wildlife Society Bulletin,* 31**,** 362-371.

LAURANCE, W. F. (1997) Responses of mammals to rainforest fragmentation in tropical Queensland: a review and synthesis. *Wildlife Research,* 24**,** 603-612.

LAW, B. S. (1997) The lunar cycle influences time of roost departure in the common blossom bat, *Syconycteris australis. Australian Mammalogy,* 20**,** 21-24.

LAWLER, I. R., FOLEY, W. J., WOODROW, I. E. & CORK, S. J. (1997) The effects of elevated CO2 atmospheres on the nutritional quality of Eucalyptus foliage and its interaction with soil nutrient and light availability. *Oecologia,* 109**,** 59 - 68.

LEE, T., QUINN, M. S. & DUKE, D. (2006) Citizen, science, highways and wildlife: using a web based GIS to engage citizens in collecting wildlife information. *Ecology and Society,* 11**,** 11.

LEPETZ, V., MASSOT, M., SCHMELLER, D. & CLOBERT, J. (2009) Biodiversity monitoring: some proposals to adequately study species' responses to climate change. *Biodiversity and Conservation,* 18**,** 3185-3203.

LEWIS, S. E. (1995) Roost fidelity of bats: a review. *Journal of Mammalogy,* 76**,** 481 - 496.

LI, H. & REYNOLDS, J. F. (1995) On definition and quantification of heterogeneity. *Oikos,* 73**,** 280-284.

LINDHE NORBERG, U. M., BROOKE, A. P. & TREWHELLA, W. J. (2000) Soaring and non-soaring bats of the family Pteropodidae (Flying foxes, *Pteropus* spp.): wing morphology and flight performance. *The Journal of Experimental Biology,* 203**,** 651 - 664.

LOEBEL, R. (1985) Flying foxes (Chiroptera: Pteropodidae) as orchard pests. . *Australian Mammalogy,* 10**,** 147-150.

LOSEY, J. E., PERLMAN, J. E. & HOEBEKE, E. R. (2007) Citizen scientist rediscovers rare nine-spotted lady beetle, *Coccinella novemnotata*, in eastern North America. *Journal of Insect Conservation,* 11**,** 415-417.

LULY, J., BLAIR, D., PARSONS, J. G., FOX, S. & VANDERWAL, J. (2010) Last Glacial Maximum habitat change and its effects on the grey-headed flying fox (*Pteropus poliocephalus* Temminck 1825). IN HABERLE, S. G., STEVENSON, J. & PREBBLE, M. (Eds.) *Altered Ecologies: Fire,*

Climate and Human Influence on Terrestrial Landscapes,Terra Australis 32. Canberra, The Australian National University, ANU E-Press.

LYONS, S. K. (2003) A quantitative assessment of the range shifts of Pleistocene mammals. *Journal of Mammalogy,* 84**,** 385 - 402.

MAGOME, S., YAMASHITA, T., KOHAMA, T., KANEDA, A., HAYAMI, Y., TAKAHASHI, S. & TAKEOKA, H. (2007) Jellyfish patch formation investigated by aerial photography and drifter experiment. *Journal of Oceanography,* 63**,** 761-773.

MAINA, J. N. (2000) What it takes to fly: The structural and functional respiratory refinements in birds and bats. *The Journal of Experimental Biology,* 203**,** 3045 - 3064.

MANNERT-MASCHKE, M. M. (2008) Convention on Migratory Species. Bonn, Germany, CMS.

MANNING, A. D., FISCHER, J., FELTON, A., NEWELL, B., STEFFEN, W. & LINDENMAYER, D. B. (2009) Landscape fluidity - a unifying perspective for understanding and adapting to global change. *Journal of Biogeography,* 36**,** 193-199.

MARKUS, N. & HALL, L. (2004) Foraging behaviour of the black flying-fox (*Pteropus alecto*) in the urban landscape of Brisbane, Queensland. *Wildlife Research,* 31**,** 345-355.

MARTINEZ-FREIRIA, F., SILLERO, N., LIZANA, M. & BRITO, J. C. (2008) GIS-based niche models identify environmental correlates sustaining a contact zone between three species of European vipers. *Diversity and Distributions,* 14**,** 452-461.

MCCLELLAND, K. (2009) Challenges and recovery actions for the widespread, threatened Grey-headed Flying-fox: A review from a New South Wales policy perspective. *Ecological Management & Restoration,* 10**,** S110-S116.

MCKINNEY, M. L. (2002) Urbanization, Biodiversity, and Conservation. *BioScience,* 52**,** 883-890.

MCKINNEY, M. L. & LOCKWOOD, J. L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution,* 14**,** 450-453.

MCMAHON, J. P., HUTCHINSON, M. F., MIX, H. A. & ORD, K. D. (1995) ANUCLIM user's guide, version 1 Centre for Resource and Environmental Studies, Australian National University, Canberra.

MENKHORST, P. W. & DIXON, J. M. (1985) Influxes of the grey-headed flying-fox *Pteropus poliocephalus* (Chiroptera, Pteropodidae) to Victoria in 1981 and 1982. *Australian Mammalogy,* 8**,** 117-121.

MEYNECKE, J. O. (2004) Effects of global climate change on geographic distributions of vertebrates in North Queensland. *Ecological Modelling,* 174**,** 347-357.

MEYNEEKE, J. O. (2004) Effects of global climate change on geographic distributions of vertebrates in North Queensland. *Ecological Modelling,* 174**,** 347-357.

MICKLEBURGH, S., RACEY, P. A. & HUTSON, A. M. (1992) Old World Fruit Bat Action Plan. Gland, Switzerland., International Union for Conservation of Nature and Natural Resources.

MORRISON, D. W. (1978) Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Animal Behaviour,* 26**,** 852-855.

MUNYENYEMBE, F., HARRIS, J., HONE, J. & NIX, H. (1989) Determinants of bird populations in an urban area. *Australian Journal of Ecology,* 14**,** 549-557.

NELSON, J. E. (1965) Movements of Australian flying foxes (Pteropodidae: Megachiroptera). *Australian Journal of Zoology,* 13**,** 53 - 73. .

ÖCKINGER, E., FRANZÉN, M., RUNDLÖF, M. & SMITH, H. G. (2009) Mobility-dependent effects on species richness in fragmented landscapes. *Basic and Applied Ecology,* 10**,** 573-578.

OLEA, P. P. (2008) Analysing spatial and temporal variation in colony size: an approach using autoregressive mixed models and information theory. *Population Ecology,* 51**,** 161-174.

OLIVER, T., ROY, D. B., HILL, J. K., BRERETON, T. & THOMAS, C. D. (2010) Heterogeneous landscapes promote population stability. *Ecology Letters,* 13**,** 473-484.

PACHAURI, R. K. & REISINGER, A. (2007) Climate Change 2007 Synthesis Report. Contribution of Working Groups I, II and III to the Fourth

Assessment Report of the intergovernmental Panel on Climate Change. Geneva, IPCC.

PALMER, C. & WOINARSKI, J. C. Z. (1999) Seasonal roosts and foraging movements of the black flying fox (*Pteropus alecto*) in the Northern Territory: resource tracking in a landscape mosaic. *Wildlife Research,* 26**,** 823-838.

PARMESAN, C. (1996) Climate and species' range. *Nature,* 382**,** 765-766.

PARMESAN, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics,* 37**,** 637-669.

PARMESAN, C., RYRHOLM, N., STEFANESCU, C., HILL, J. K., THOMAS, C. D., DESCIMON, H., HUNTLEY, B., KAILA, L., KULLBERG, J., TAMMARU, T., TENNENT, W. J., THOMAS, J. A. & WARREN, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature,* 399**,** 579-583.

PARRIS, K. M. & HAZELL, D. L. (2005) Biotic effects of climate change in urban environments: The case of the grey-headed flying fox (*Pteropus poliocephalus*) in Melbourne, Australia. *Biological Conservation,* 124**,** 267 - 276.

PARRY-JONES, K. (2006) A black flying-fox at the Royal Botanic Gardens, Sydney! *Australasian Bat Society Newsletter,* 27**,** 42-43.

PARRY-JONES, K. & AUGEE, M. L. (1991) Food selection by grey-headed flying foxes (*Pteropus poliocephalus*) occupying a summer colony site near Gosford, New South Wales. *Wildlife Research,* 18**,** 111 - 124. .

PARRY-JONES, K. A. & AUGEE, M. L. (1992) Movements of Grey-headed flying foxes (*Pteropus poliocephalus*) to and from a colony site on the central coast of New South Wales. *Wildlife Research,* 19**,** 331-340.

PARRY-JONES, K. A. & AUGEE, M. L. (2001) Factors affecting the occupation of a colony site in Sydney, New South Wales by the grey-headed flying fox *Pteropus poliocephalus* (Pteropodidae). *Austral Ecology,* 26**,** 47-55.

PARSONS, J. G., BLAIR, D., LULY, J. & ROBSON, S. K. A. (2008) Bat Strikes in the Australian Aviation Industry. *The Journal of Wildlife Management,* 73**,** 526 - 529.

PARSONS, J. G., BLAIR, D., LULY, J. & ROBSON, S. K. A. (2009) Flying-fox (Megachiroptera: Pteropodidae) flight altitudes determined via an unusual sampling method: aircraft strikes in Australia. *Acta Chiropterologica,* 10**,** 377 - 379.

PARSONS, J. G., CAIRNS, A., JOHNSON, C. N., ROBSON, S. K. A., SHILTON, L. A. & WESTCOTT, D. A. (2006) Dietary variation in spectacled flying foxes (*Pteropus conspicillatus*) of the Australian Wet Tropics. *Australian Journal of Zoology,* 54**,** 417-428.

PARSONS, J. G., CAIRNS, A., JOHNSON, C. N., ROBSON, S. K. A., SHILTON, L. A. & WESTCOTT, D. A. (2007) Bryophyte dispersal by flying foxes: a novel discovery. *Oecologia,* 152**,** 112-114.

PARSONS, J. G., VANDERWAL, J., ROBSON, S. K. A. & SHILTON, L. A. (2010) The implications of sympatry in the spectacled and grey headed flying-fox, *Pteropus conspicillatus* and *P. poliocephalus* (Chiroptera: Pteropodidae). *Acta Chiropterologica,* 12**,** 301-309.

PATON, D. C. (2009) Bird Risk Assessment Model for Airports and Aerodromes Adelaide, The University of Adelaide.

PEARSON, R. G., RAXWORTHY, C. J., NAKAMURA, M. & PETERSON, A. T. (2007) Predicting species distributions from small numbers of occurence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography,* 34**,** 102-117.

PENNYCUICK, C. J. (1969) The mechanics of bird migration. *Ibis,* 111**,** 525 - 556.

PERRY, A. L., LOW, P. J., ELLIS, J. R. & REYNOLDS, J. D. (2005) Climate change and distribution shifts in marine fishes. *Science,* 308**,** 1912-1915.

PETTORELLI, N., BROÂ€ JÃ¸RGENSEN, J., DURANT, SARAHÂ M., BLACKBURN, T. & CARBONE, C. (2009) Energy availability and density estimates in African ungulates. *The American Naturalist,* 173**,** 698-704.

PEURACH, S. C. (2003) High-altitude collision between an airplane and a hoary bat, *Lasiurus cinereus. Bat Research News,* 44**,** 2-3.

PHILLIPS, S. J., ANDERSON, R. P. & SCHAPIRE, R. E. (2006a) Maximum entropy modeling of species geographic distributions. *Ecological Modelling,* 190**,** 231-259.

PHILLIPS, S. J. & DUDIK, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography,* 31**,** 161 - 175.

PHILLIPS, S. J., DUDIK, M. & SCHAPIRE, R. (2006b) MaxEnt, version 2. AT&T Labs-Research, Princeton University, and the Centre for Biodiversity and Conservation, American Museum of Natural History.

POUNDS, J. A., FOGDEN, M. P. L. & CAMPBELL, J. H. (1999) Biological response to climate change on a tropical mountain. *Nature,* 398**,** 611-615.

R (2008) R: A Language and Environment for Statistical Computing. http://www.R-project.org. *R Foundation for Statistical Computing.*

RATCLIFFE, F. N. (1932) Notes on the fruit bats of Australia. *Journal of Animal Ecology,* 1**,** 32 - 57.

RAUPACH, M. R., BRIGGS, P. R., HAVERD, V., KING, E. A., PAGET, M. & TRUDINGER, C. M. (2008) Australian Water Availability Project (AWAP). CSIRO Marine and Atmospheric Research, Canberra, Australia. .

RAUPACH, M. R., BRIGGS, P. R., HAVERD, V., KING, E. A., PAGET, M. & TRUDINGER, C. M. (2009) Australian Water Availability Project (AWAP). *Final Report for Phase 3, CAWCR Technichal Report No. 013.* Canberra, Australia, CSIRO Marine and Atmospheric Research Component.

REIF, J., VORISEK, P., ST'ASTNY, K., KOSCHOVA, M. & BEJCEK, V. (2008) The impact of climate change on long-term population trends of birds in a central European country. *Animal Conservation,* 11**,** 412-421.

RESIDE, A. E., VANDERWAL, J., KUTT, A. S. & PERKINS, G. C. (2010) Weather, not climate, defines distributions of vagile bird species. *PLoS ONE,* 5**,** e13569.

RICHARDS, G. C. (1990a) The spectacled flying fox, *Pteropus conspicillatus* (Chiroptera: Pteropodidae), in North Queensland 1. Roost sites and distribution patterns. *Australian Mammalogy,* 13**,** 17-24.

RICHARDS, G. C. (1990b) The spectacled flying fox, *Pteropus conspicillatus* (Chiroptera:Pteropodidae), in North Queensland. 2. Diet, seed dispersal and feeding ecology. *Australian Mammalogy,* 13**,** 25-31.

RICHMOND, J. Q., BANACK, S. A. & GRANT, G. S. (1998) Comparative analysis of wing morphology, flight behaviour; and habitat use in flying foxes (Genus: *Pteropus*). *Australian Journal of Zoology,* 46**,** 283-289.

ROOT, T. L., PRICE, J. T., HALL, K. R., SCHNEIDER, S. H., ROSENZWEIG, C. & POUNDS, J. A. (2003) Fingerprints of global warming on wild animals and plants. *Nature,* 421**,** 57-60.

ROSHIER, D. A., DOERR, V. A. J. & DOERR, E. D. (2008) Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. *Oecologia,* 156**,** 465-477.

SCHEEL, D., VINCENT, T. L. S. & CAMERON, G. N. (1996) Global warming and the species richness of bats in Texas. *Conservation Biology,* 10**,** 452-464.

SCHMELITSCHEK, E., FRENCH, K. & PARRY-JONES, K. (2009) Fruit availability and utilisation by grey-headed flying foxes (Pteropodidae: *Pteropus poliocephalus*) in a human-modified environment on the south coast of New South Wales, Australia. *Wildlife Research,* 36**,** 592-600.

SCOTT, G. R. & MILSOM, W. K. (2007) Control of breathing and adaptation to high altitude in the bar-headed goose. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology,* 293**,** R379 - R391.

SHILTON, L. A. (1999) Seed dispersal by fruit bats on the Krakatau Islands, Indonesia. Leeds, UK., University of Leeds.

SHILTON, L. A., LATCH, P. J., MCKEOWN, A., PERT, P. & WESTCOTT, D. A. (2008) Landscape-scale redistribution of a highly mobile threatened species, *Pteropus conspicillatus* (Chiroptera, Pteropodidae), in response to Tropical Cyclone Larry. *Austral Ecology,* 33**,** 549-561.

SHOO, L. P., WILLIAMS, S. E. & HERO, J. (2005) Potential decoupling of trends in distribution area and population size of species with climate change. *Global Change Biology,* 11**,** 1469-1476.

SINCLAIR, E. A., WEBB, N. J., MARCHANT, A. D. & TIDEMANN, C. R. (1996) Genetic variation in the little red flying fox *Pteropus scapulatus* (Chiroptera: Pteropodidae): implications for management. *Biological Conservation,* 76**,** 45-50. .

SIVANPILLAI, R. & LATCHININSKY, A. V. (2008) Can late summer Landsat data be used for locating Asian migratory locust, *Locusta migratoria*

migratoria, oviposition sites in the Amudarya River delta, Uzbekistan? *Entomologia Experimentalis Et Applicata,* 128**,** 346-353.

SNYDER, G. M., PITCHER, K. W., PERRYMAN, W. L. & LYNN, M. S. (2001) Counting Steller sea lion pups in Alaska: An evaluation of medium-format, color aerial photography. *Marine Mammal Science,* 17**,** 136-146.

SPENCER, H. J., PALMER, C. & PARRY-JONES, K. (1991) Movements of fruit-bats in eastern Australia, determined by using radio-tracking. *Wildlife Research,* 18**,** 463-468.

STIER, S. C. & MILDENSTEIN, T. L. (2005) Dietary habits of the world's largest bats: the Philippine flying foxes, *Acerodon jubatus* and *Pteropus vampyrus lanensis. Journal of Mammalogy,* 86**,** 719 - 728.

TAYLOR, R. H. & WILSON, P. R. (1990) Recent increase and southern expansion of adelie penguin populations in the Ross Sea, Antarctica, related to climate warming. *New Zealand Journal of Ecology,* 14**,** 25-29.

THIRIET, D. (2005) The relocation of flying fox colonies in Queensland. *22 EPLJ* 231**,** 231 - 239.

THOMAS, C. D., BODSWORTH, E. J., WILSON, R. J., SIMMONS, A. D., DAVIES, Z. G., MUSCHE, M. & CONRADT, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature,* 411**,** 577-581.

THOMAS, C. D., CAMERON, A., GREEN, R. E., BAKKENES, M., BEAUMONT, L. J., COLLINGHAM, Y. C., ERASMUS, B. F. N., DE SIQUEIRA, M. F., GRAINGER, A., HANNAH, L., HUGHES, L., HUNTLEY, B., VAN JAARSVELD, A. S., MIDGLEY, G. F., MILES, L., ORTEGA-HUERTA, M. A., PETERSON, A. T., PHILLIPS, O. L. & WILLIAMS, S. E. (2004) Extinction risk from climate change. *Nature,* 427**,** 145-148.

THOMAS, C. D. & LENNON, J. L. (1999) Birds extend their range northwards. *Nature,* 399**,** 213.

THOMSON, M. (2007) Placing the wild in the city: "Thinking with" Melbourne's bats. *Society and Animals,* 15**,** 79-95.

THOMSON, S. C., BROOKE, A. P. & SPEAKMAN, J. R. (2002) Soaring behaviour in the Samoan flying fox (*Pteropus samoensis*). *J. Zool., Lond. ,* 256**,** 55-62.

THORPE, J. (2003) Fatalities and destroyed aircraft due to bird strikes, 1912-2002. *The 26th International Bird Strike Committee Meeting.* Warsaw, Poland.

TIDEMANN, C. R. (2003) Displacement of a flying-fox camp using sound. *Ecological Management and Restoration,* 4**,** 224-226.

TIDEMANN, C. R., KELSON, S. L. & JAMIESON, G. I. (1997) Flying-fox damage to orchard fruit in Australia: incidence, extent and economic impact. *Australian Biologist,* 10**,** 177-184.

TIDEMANN, C. R. & NELSON, J. E. (2004) Long-distance movements of the grey-headed flying fox (*Pteropus poliocephalus*). *Journal of Zoology,* 263**,** 141-146.

TIDEMANN, C. R., VARDON, M. J., LOUGHLAND, R. A. & BROCKLEHURST, P. J. (1999) Dry season camps of flying foxes (*Pteropus* spp.) in Kakadu World Heritage Area, north Australia. *Journal of Zoology, London.,* 247**,** 155-163.

TOWNSEND PETERSON, A., SANCHEZ-CORDERO, V., SOBERÓN, J., BARTLEY, J., BUDDEMEIER, R. W. & NAVARRO-SIGÜENZA, A. G. (2001) Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecological Modelling,* 144**,** 21-30.

TRATHAN, P. N. (2004) Image analysis of color aerial photography to estimate penguin population size. *Wildlife Society Bulletin,* 32**,** 332-343.

TSCHAPKA, M. (2004) Energy density patterns of nectar resources permit coexistence within a guild of Neotropical flower-visiting bats. *Journal of Zoology London,* 263**,** 7 - 21.

VAN DER REE, R. & MCCARTHY, M. A. (2005) Inferring persistence of indigenous mammals in response to urbanisation. *Animal Conservation,* 8**,** 309-319.

VAN DER REE, R., MCDONNELL, M. J., TEMBY, I., NELSON, J. E. & WHITTINGHAM, E. (2006) The establishment and dynamics of a recently established urban camp of flying foxes (*Pteropus poliocephalus*) outside their geographic range. *Journal of Zoology,* 268**,** 177-185.

VANDERWAL, J., SHOO, L. P., JOHNSON, C. N. & WILLIAMS, S. E. (2009) Abundance and the environmental niche: Environmental suitability

estimated from niche models predicts the upper limit of local abundance. *American Naturalist,* 174**,** 282-291.

VARDON, M. J., BROCKLEHURST, P. S., WOINARSKI, J. C. Z., CUNNINGHAM, R. B., DONNELLY, C. F. & TIDEMANN, C. R. (2001) Seasonal habitat use by flying-foxes, *Pteropus alecto* and *P.scapulatus* (Megachiroptera), in monsoonal Australia. *Journal of Zoology,* 253**,** 523-535.

VARDON, M. J. & TIDEMANN, C. R. (1999) Flying-foxes (*Pteropus alecto and P. scapulatus*) in the Darwin region, North Australia: patterns in camp size and structure. *Australian Journal of Zoology,* 47**,** 411 - 423. .

WALSH, K. J. E. & RYAN, B. F. (2000) Tropical cyclone intensity increase near Australia as a result of climate change. *Journal of Climate,* 13**,** 3029-3036.

WALTHER, G., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J. C., FROMENTIN, J., HOEGH-GULDBERG, O. & BAIRLEIN, F. (2002) Ecological responses to recent climate change. *Nature,* 416**,** 389 - 395.

WARREN, M. S., HILL, J. K., THOMAS, J. A., ASHER, J., FOX, R., HUNTLEY, B., ROY, D. B., TELFER, M. G., JEFFCOATE, S., HARDING, P., JEFFCOATE, G., WILLIS, S. G., GREATOREX-DAVIES, J. N., MOSS, D. & THOMAS, C. D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature,* 414**,** 65-69.

WEBB, N. J. & TIDEMANN, C. R. (1995) Hybridisation between black (*Pteropus alecto*) and grey-headed (*P. poliocephalus*) flying-foxes (Megachiroptera: Pteropodidae). *Australian Mammalogy,* 18**,** 19-26.

WEBB, N. J. & TIDEMANN, C. R. (1996) Mobility of Australian flying foxes, *Pteropus* spp. (Megachiroptera): evidence from genetic variation. *Proceedings of the Royal Society of London, Series B.,* 263**,** 497 - 502.

WELBERGEN, J. A. (2006) Timing of the evening emergence from day roosts of the grey-headed flying fox, *Pteropus poliocephalus*: the effects of predation risk, foraging needs and social context. . *Behaviour Ecology and Sociobiology,* 60**,** 311 - 322.

WELBERGEN, J. A. (2008) Variation in twilight predicts the duration of the evening emergence of fruit bats from a mixed-species roost. *Animal Behaviour,* 75, 1543-1550.

WELBERGEN, J. A., KLOSE, S. M., MARKUS, N. & EBY, P. (2008) Climate change and the effects of temperature extremes on Australian flying foxes. *Proceedings of the Royal Society of London, Series B.,* 275, 419 - 425.

WESTCOTT, D. A. & MCKEOWN, A. (2004) Observer error in exit counts of flying foxes (*Pteropus* spp.). *Wildlife Research,* 31, 551 - 558.

WILKINSON, G. S. (1992) Information transfer at evening bat colonies. *Animal Behaviour,* 44, 501-518.

WILKINSON, G. S. & BOUGHMAN, J. W. (1998) Social calls coordinate foraging in greater spear-nosed bats *Animal Behaviour,* 55, 337 - 350.

WILLIAMS, G. & ADAM, P. (1994) A review of rainforest pollination and plant-pollinator interactions with particular reference to Australian subtropical rainforests. *Australian Zoologist,* 29, 177-212.

WILLIAMS, S. & MIDDLETON, J. (2008) Climatic seasonality, resource bottlenecks and abundance of rainforest birds: implications for global climate change. *Diversity and Distributions,* 14, 69-77.

WILLIAMS, S. E., BOLITHO, E. E. & FOX, S. (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London Series B-Biological Sciences,* 270, 1887-1892.

WILLIAMS, S. G., MCDONNELL, M. J., PHELAN, G. K., KEIM, L. D. & VAN DER REE, R. (2006) Range expansion due to urbanization: Increased food resources attract Grey-headed flying-foxes (*Pteropus poliocephalus*) to Melbourne. *Austral Ecology* 31, 190-198.

WILLIAMS, T. C., IRELAND, L. C. & WILLIAMS, J. M. (1973) High altitude flights of the free-tailed bat, *Tadarida brasiliensis*, observed with radar. *Journal of Mammalogy,* 54, 807-821.

WOINARSKI, J. C. Z. (2006) Predictors of nomadism in Australian birds: A reanalysis of Allen and Saunders (2002). *Ecosystems,* 9, 689-693.

WOODWARD, F. I. & ROCHEFORT, L. (1991) Sensitivity Analysis of
Vegetation Diversity to Environmental Change. *Global Ecology and
Biogeography Letters,* 1**,** 7-23.

WRIGHT, S. (2010) Some significant wildlife strikes to civil aircraft in the United
States, January 1990 - April2010. Sandusky, USA. , U.S. Department of
Agriculture, Wildlife Services.

Appendix 1

Luly, J.G., Blair, D., **Parsons, J.G.**, Fox, S. and VanDerWal, J. (2010). Chapter 6: Last Glacial Maximum habitat change and its effects on the grey headed flying-fox (*Pteropus poliocephalus* Temminck 1825). In Simon G. Haberle, Janelle Stevenson & Matthew Prebble (editors), *Altered Ecologies: Fire, Climate and Human Influence on Terrestrial Landscapes,* Terra Australis 32. ANU E-Press, Canberra, The Australian National University.