

The Spectacled Flying-fox – a review of past and present knowledge

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ABSTRACT

The Spectacled Flying-fox is listed as vulnerable within its range in Australia despite being recognised as an agricultural pest and there being significant gaps in our knowledge of its ecology. Stakeholders, such as management agencies and fruit farmers, have many questions that we are currently unable to answer. Firstly, I review current knowledge of this species. Of the four large flying-fox species that occur in Australia, the Spectacled Flying-fox has the smallest range, the lowest abundance and appears to be intricately tied to rainforest. Then I describe the aims of my PhD work, using molecular and demographic techniques to describe the population structure of the species. Finally, I summarise the findings of my work and outline how this knowledge can be used by the various stakeholders working with the Spectacled Flying-fox.

Key words: Spectacled Flying-fox; *Pteropus conspicillatus*; vulnerable; molecular analysis; demographics

Introduction

The Spectacled Flying-fox, *Pteropus conspicillatus* Gould 1850 (Andersen 1912), plays an important ecological role throughout its range as a seed and pollen disperser and is recognised as a significant component of the biodiversity of the Wet Tropics World Heritage area of north Queensland, Australia (Westcott *et al.* 2001). However, it is also considered an agricultural pest by fruit farmers due to the loss of fruit from foraging flying-foxes. Its listing in 2002 as a vulnerable species under the Environmental Protection and Biodiversity Conservation Act (EPBC Act 1999), was in part due to a lack of information on the population biology of this species, as well as the conviction of conservationists and scientists that the species was in decline. The paucity of information on even basic population dynamics and ecology of this species has been recognised as a significant obstacle to developing appropriate management or recovery plans (Duncan *et al.* 1999; Westcott *et al.* 2001). An improved understanding of population dynamics would inform management of patterns and processes affecting this species in order to balance the apparently contradictory requirements of pest mitigation and species conservation. A greater knowledge of the species would also answer many questions posed by fruit growers, which may then enable them to implement new and informed mitigation strategies.

Current knowledge of the Spectacled Flying-fox is restricted to diet and feeding ecology (Richards 1990b; Eggert 1994; Parsons 2005), conservation status (Garnett *et al.* 1999; WPSQ 2000; ABS 2001; Tidemann and Vardon 2001; Westcott *et al.* 2001), and roost sites and distribution (Ratcliffe 1932; Richards 1990a). Although current work is being undertaken by the CSIRO on movement patterns in Spectacled Flying-foxes within the Wet Tropics World Heritage area, nothing is known about population structure, broad-scale movement patterns throughout its distribution, or historical and contemporary processes that have affected the current

geographical pattern of colony distribution. Current threats, including shooting by fruit farmers, tick paralysis, habitat loss, barbed wire fences and powerlines, are believed to be aiding the decline of this species, although nothing is known of the effects of these threats on population demographics and therefore whether they are putting the species at risk.

Although previous research has relied on observation techniques, many of the questions posed regarding population structure cannot be resolved with the use of observation alone. Hence, my PhD project was instigated to examine questions of population structure across several spatial and temporal scales, using alternate methodologies to present an inclusive understanding of Spectacled Flying-fox population dynamics. Here, I present a review of current knowledge on the Spectacled flying-fox, and a description of my PhD project and a summary of the results (Fox 2006).

Review of Current Knowledge

The Spectacled Flying-fox is a large fruit bat so named for the straw coloured rings of fur around its eyes (Churchill 1998). Similar straw-coloured fur forms a mantle/ruff on the back of the neck and the shoulders. Elsewhere, the fur is black (Figure 1). *Pteropus conspicillatus* has the smallest distribution of the four Australian *Pteropus* species (Figure 2). Its range primarily covers the Wet Tropics World Heritage Area in north Queensland, between Cardwell in the south and Bloomfield in the north (Figure 3). There is a small population in the Iron Range National Park on the Cape York Peninsula, of which little is known. There are anecdotal reports of *P. conspicillatus* occurring in the McIllwraith Ranges but there have not been any recent reported sightings, even though suitable habitat is available. From the Torres Strait Islands between PNG and Australia, there is only a single record of

P. conspicillatus from Nepean Island (Andersen 1912). Although the distribution of *P. conspicillatus* on Cape York seems distinctly restricted, there are large tracts of land inaccessible to researchers where *P. conspicillatus* camps may yet be discovered. No colonies occur west of the Great Dividing Range. *P. conspicillatus* also occurs on the north and east coasts of PNG and on outlying islands. Animals from PNG are reported to be conspecific with animals from Australia due to similarities in their pelage (Flannery 1995; Churchill 1998). It is unknown whether there is movement of animals between PNG and Australia, although with their known ability to fly 50 km in a single night when in search of food (Shilton and Westcott, unpublished data), movement between PNG and Australia is feasible.

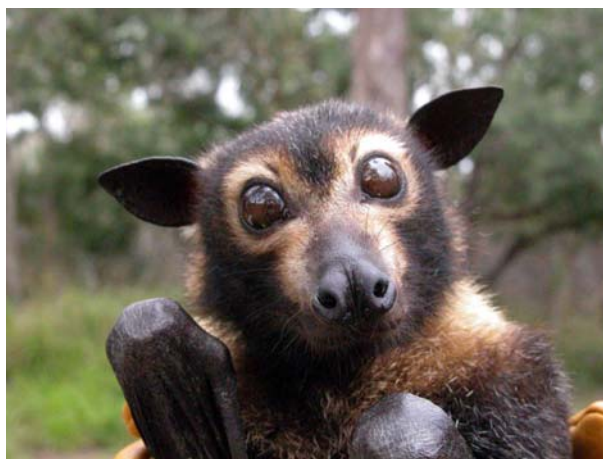


Figure 1. Spectacled Flying-fox, *Pteropus conspicillatus* (Photo: Adam McKeown & Sam Fox).

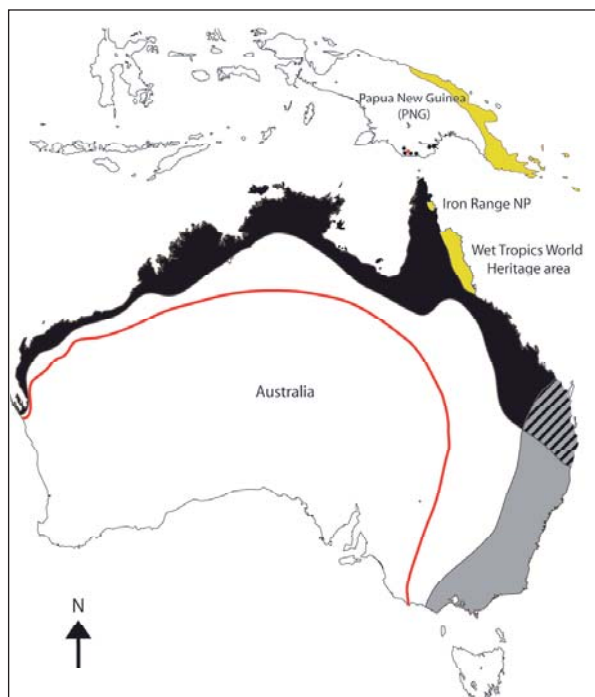


Figure 2. Distributions of the four main *Pteropus* species within Australia. Yellow: Spectacled Flying-fox (*Pteropus conspicillatus*); Red (line forms inner limit of range): Little red flying fox (*Pteropus scapulatus*); Black: Black Flying-fox (*Pteropus alecto*); Grey: Grey-headed Flying-fox (*Pteropus poliocephalus*).

The geographic location of *P. conspicillatus* colonies in the Wet Tropics region is closely associated with that of rainforest vegetation and a high mean annual rainfall. Richards (1990a) reported that colonies were never more than 6.5 km away from rainforest and were located in areas with a mean annual rainfall of 1400 mm or more. Even though these two factors are highly correlated with the location of a *P. conspicillatus* camp, at present we have little understanding of other factors that may influence camp-site choice, with many camp-sites found in locations that are the antithesis of what would be expected. Some permanent *P. conspicillatus* camp-sites are found in city parks or small remnant blocks of forest (pers. obs.). Parsons (2005) suggested that cultural significance of a site may be important to camp-site locality.

Estimates of Spectacled Flying-fox population size have been made every year since 1998 using a visual census conducted by volunteers in the Wet Tropics World Heritage Area (Figure 4). This initiative, started by a group of conservationists and scientists, aimed to establish if this species was in decline. Estimating the size of most mammal populations is difficult, but even more so for a nocturnal, volant mammal such as a flying-fox, where many of the usual methods of estimation, such as mark-recapture, are ineffective (Nelson 1965; Pierson and Rainey 1992). Because of a lack of historical records of population size for *P. conspicillatus* prior to the start of these surveys, it is difficult to say unequivocally whether this species has declined. The only report to mention the number of Spectacled Flying-foxes in the early 1900s is that of Francis Ratcliffe (Ratcliffe 1932) who stated vaguely that he only encountered *P. conspicillatus* in Cairns and on the Atherton Tablelands. The latter area appeared to have five colonies, three of which he visited, and two of which appeared to be 'sometimes large' (meaning >50,000 individuals).

The census approach, however, can only be used as a guide and cannot give an accurate measure of how many Spectacled Flying-foxes there actually are, and therefore, whether they are in decline. Reservations concerning the census data result from the uncertainty of knowing whether all colonies have been located and therefore all animals in the region counted. To test the census methodology, researchers at the CSIRO on the Atherton Tablelands carried out a study to compare counts by volunteers, with that of video based counts. The counters were always within $\pm 15\%$ of the video-based count and more often than not underestimated the count rather than overestimated (Westcott and McKeown 2004). Because Spectacled Flying-foxes in the Wet Tropics region have access to large tracts of rainforest that are inaccessible to people, the problem of 'missing' colonies is always likely to be an issue. The large increase in numbers from 2000 to 2001 (Figure 4) would certainly be a result of this problem.

Project Description

Following the ongoing debate regarding the status and apparent decline of the Spectacled Flying-fox in the Wet Tropics of north Queensland, this project was devised to establish baseline knowledge for this species and through the use of genetic techniques, infer population processes

(Fox 2006). It was believed that by using a different approach to census and observation techniques, this project could offer an alternative and independent assessment of the status of the Spectacled Flying-fox.

By incorporating demographic and genetic data, this study aimed to investigate population structure in the Spectacled Flying-fox across varying geographic scales throughout its distribution.

Molecular study

To determine the genetic structure of a population, it is important to understand the extent of genetic variation in

the species by evaluating the genotypes of individuals (Slatkin 1994). By comparing these genotypes across different spatial scales, genetic diversity, gene flow and degree of inbreeding can be determined, as well as relatedness patterns, dispersal ability and the mating system. Understanding the extent of gene flow between populations is important in determining the independence of each individual population. If there is extensive gene flow between populations they may act as a single unit and the genetic structure within each population will be similar. With reduced rates of gene flow, each population acts more independently and the genetic structure could be markedly different between

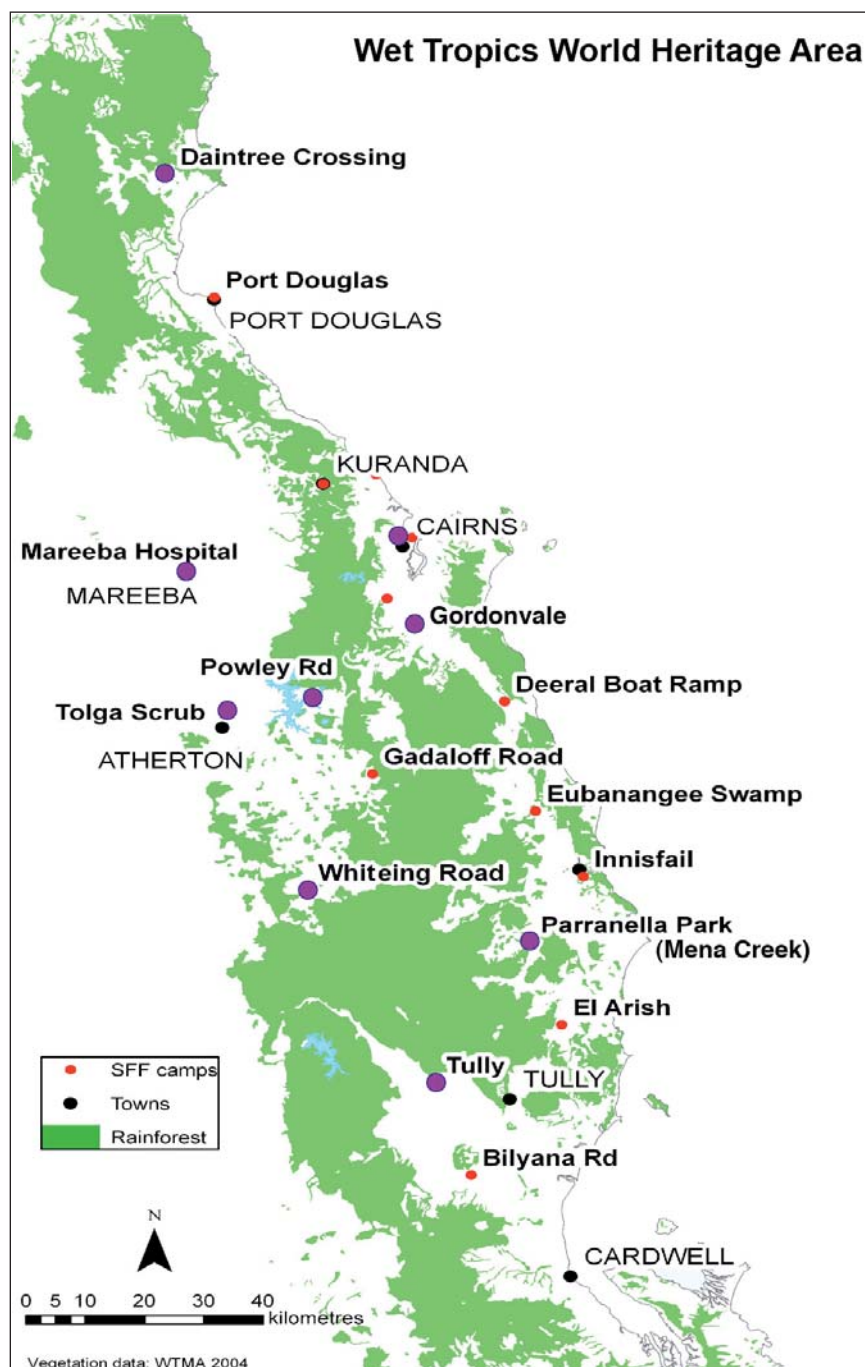


Figure 3. Known colony locations of *Pteropus conspicillatus* (Spectacled Flying-fox) in the Wet Tropics region, principal area of its range in Australia. Red dots are camps not sampled in this study, purple dots are camps that were sampled.

populations (Slatkin 1994). If different temporal scales are also investigated, historical events that shaped the contemporary structure can be established. For example, mtDNA datasets can be analysed to determine whether the population has been through an historical bottleneck or population expansion.

Two classes of genetic markers that are extensively used by population geneticists to cover multiple spatial and temporal scales are various genes of the mitochondrial genome, and multilocus genotypes based on microsatellites in the nuclear genome. Mitochondrial DNA gives a broad-scale picture, as well as permitting historical population structure to be determined, while microsatellites allow fine-scale variability to be detected and measured. By using these two classes of markers together, population structure, and many of the processes that are currently affecting it, and have affected it historically, can be identified.

Genetic analysis of populations has become an important component of improving strategies for the conservation and management of threatened species. The realisation that genetics can inform management on important aspects of a species' ecology and biology, such as its probable capacity to cope with stochastic environmental events (genetic diversity), its distinctiveness from other closely related species (phylogeny), reasons for reduced reproductive output and less fit offspring (inbreeding depression), evidence of past reduction in population size (historical bottleneck), and the likely effects of relocating populations (gene flow, introgression, genetic diversity), has meant that a range of genetic techniques is now an important tool used in conservation biology. Many aspects of a species' biology that are critical to its effective conservation are often unknown, or difficult and time consuming to determine directly (Frankham *et al.* 2002). Hence, the inclusion of genetic analysis in conservation and management of threatened species, although relatively recent, is now standard.

Mitochondrial DNA

Mitochondrial DNA (mtDNA) is a circular genome located in the cytoplasm of cells (Awise 2000), which is transmitted maternally. mtDNA has a rate of mutation approximately 5–10 times greater than nuclear DNA (Brown *et al.* 1979) and is highly variable (Frankham *et al.* 2002). Because of its clonal mode of inheritance, mtDNA typically reflects the maternal lineage, and together with nuclear markers can be used to infer female-biased dispersal. The characteristics of mtDNA, especially its rapid rate of sequence evolution, make it a valuable tool for studying both inter- and intra-specific relationships and it is commonly used in studies of phylogeny, phylogeography and population genetics in animals. Molecular surveys of mtDNA frequently detect phylogeographic patterns that record the effects of long-standing population structure (Awise 2000).

Microsatellites

Microsatellites have become the genetic marker of choice for many population geneticists investigating contemporary gene flow within and between populations (Beaumont and Bruford 1999; Balloux and Lugon-Moulin 2002). Consisting of short tandemly repeated sequences (e.g. AT₁₁), an advantage of microsatellites is that they are highly polymorphic due to variability in the number of repeats (Queller *et al.* 1993). Microsatellites are relatively abundant and uniformly distributed throughout the non-coding regions of the genome (Hancock 1999). Microsatellites are particularly useful because repeats are often lost or gained via slippage during DNA replication or recombination (Hancock 1999), creating a great deal of variation in the number of repeats at each locus. Microsatellites are generally considered to have a rate of mutation several orders of magnitude higher than other nuclear DNA markers (Nikitina and Nazarenko 2004), making them useful in both inter- and intrapopulation studies (Goldstein and Schlotterer 1999). Microsatellites are biparentally inherited codominant markers, therefore providing

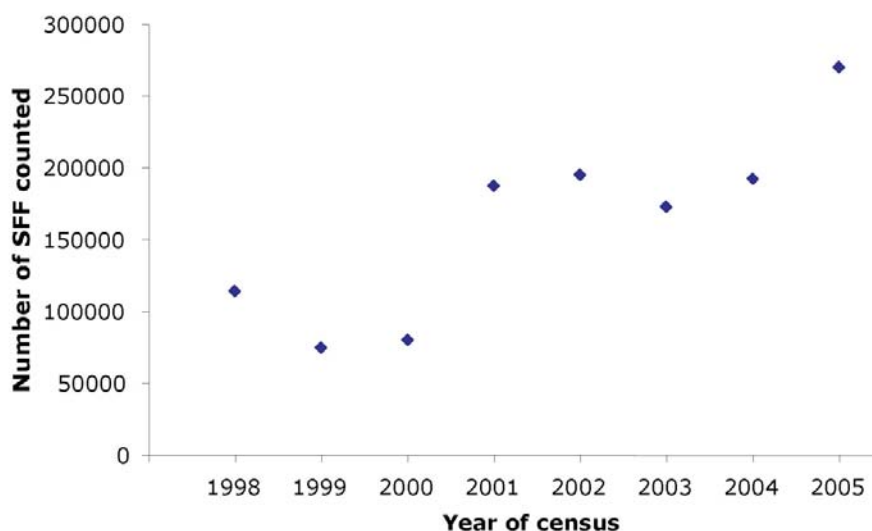


Figure 4. Census results for 1998–2005; counts of Spectacled Flying-fox (SFF) colonies in the Wet Tropics region during December. Data from Queensland Parks and Wildlife Service.

genetic information for both males and females. Their widespread occurrence in the genome, along with their extremely high among-individual polymorphism, has meant that microsatellites have become the dominant marker used in population genetic studies in recent years (Queller *et al.* 1993).

Microsatellites are used to investigate many aspects of population structure, including; gene flow (Girman *et al.* 2001), genetic diversity (Gautschi *et al.* 2003; Baucom *et al.* 2005; Jedrzejewski *et al.* 2005), inbreeding (Eldridge *et al.* 1999; Bjorklund 2003; Andersen *et al.* 2004), bottlenecks (Leijts *et al.* 1999; Miller and Hedrick 2001; Al-Rabah'ah and Williams 2004), relatedness and kinship (Bentzen *et al.* 2001; Burland *et al.* 2001; Gerlach *et al.* 2001; Kerth *et al.* 2002; Garner and Schmidt 2003), as well as mating systems (Heckel and Von Helversen 2003), reproductive success (Ortega *et al.* 2003), social structure (Storz *et al.* 2000), and divergence between populations and species (Petren *et al.* 2005). While gene flow considers the broad-scale, between-population questions relating to migration, dispersal and extent of vagility, genetic diversity considers the smaller within-population factors such as population resilience, fitness and inbreeding. Relatedness can be considered at both spatial scales depending on whether the mating system of species is being considered (broad-scale) or whether single groups of individuals are being assessed for kinship (small scale).

Whereas mtDNA is used principally to infer historical events at broad spatial scales, microsatellites are used to examine more contemporary events over smaller spatial scales. Use of these two markers together allows for robust genetic analysis of processes that affect population structure.

Demographic study

Other components determining population structure are demographic factors such as sex ratios, age structure, mating strategy, birth and death rates, longevity and reproductive output. Census and observation may provide information on some demographic factors, although factors such as age estimation often require long term handling of animals or destructive sampling.

The age structure of individuals in a colony highlights a number of processes that may be occurring currently within the colony. A colony of relatively young individuals may indicate a growing population or a species that has a short maximum lifespan. A colony with a greater proportion of old individuals may indicate little recruitment to the colony or a species that has an extended lifespan. A population with a bimodal age structure may indicate years of decline in population size and the following recovery. This knowledge is important in assessing a populations'/species' capacity for growth in the form of reproductive output. No studies have been undertaken on the age structure of flying-fox colonies.

Although the mating system of a species is considered to be a demographic factor, it has important consequences for gene flow, relatedness of individuals and ultimately, genetic diversity in a population. Because of this, knowledge of a species' mating system can be invaluable when determining the effective population size (Nunny

and Elan 1994). A population of randomly mating individuals may lead to a panmictic population exhibiting a greater degree of heterozygosity and genetic diversity. Alternately, species that exhibit extreme polygynous behaviour (where a single resident male mates with a large harem of females, for example southern elephant seals, *Mirounga leonina* (Fabiani *et al.* 2004)) may have a greater degree of relatedness in offspring and reduced genetic diversity due to a smaller proportion of the adult male population reproducing. Polygyny would also affect the population dynamic in that the sex ratio of adults found in a single population may be skewed. In this case, a population of reproducing individuals may have a large number of females and a much smaller number of males, while non-breeding populations may solely consist of bachelor males and possibly non-breeding females, creating a local skew in sex ratios. Some mating systems may lead to a greater risk of inbreeding depression and reduced heterozygosity and genetic diversity, while other mating systems have strategies to avoid inbreeding depression such as dispersal of male or female offspring (Stow and Sunnucks 2004). The above examples show how a single demographic parameter, the mating strategy, can influence gene flow, relatedness of individuals, genetic diversity, effective population size, sex ratio, population growth rate, inbreeding and dispersal in a species.

Apart from individual colony structure attributes such as population size and sex ratios (Richards 1990a; Hayden 1992; Bull 1993) no data on demographic factors in the Spectacled Flying-fox exist. Many of the demographic factors suggested to occur in Spectacled Flying-foxes have been inferred from the same factors observed in other Australian flying-fox species. In many instances this is reasonable as traits such as number of reproductive events per year (one), gestation time (6 months) and the number of young born (one) are uniform across flying-fox species (Hall and Richards 2000). Other traits such as age structure, sex ratios, reproductive output and population growth that are more fluid within populations and are affected by intrinsic as well as extrinsic factors, may vary from population to population, as well as from species to species. Flying-foxes are believed to be long lived based on the observation that they are known to live long in captivity (Hall and Richards 2000), and that they have other life history traits (such as slow growth; late sexual maturation; only produce a single, large young each time; high maternal investment in young (Tuttle and Stevenson 1982; Kurta and Kunz 1987; Read and Harvey 1989; Austad and Fischer 1991; Barclay *et al.* 2004) that are associated with extended longevity. However, average longevity has never been assessed empirically in wild flying-foxes, and as this trait is linked to other important factors such as reproductive output and population growth, it needs to be understood in light of general life history traits as well as informing conservation and management.

In many ways, demographic and genetic elements work together in explaining patterns. By only considering either the demographic or genetic processes, or a few of the factors that contribute to these processes, results and their interpretations, are limited. In addition, combined datasets provide information that may be used to

understand current and historic population processes. Although the demographic aspects of population structure are reflected in the current time frame (such as sex ratios seen in a colony during the breeding season), some genetic factors reveal a signature of historical events and processes that may have contributed to the contemporary structure (such as an historical bottleneck of a species with low vagility due to habitat fragmentation, which has resulted in reduced genetic diversity). Genetic analysis across differing spatial scales provides insight into the different impacts on a broad spatial scale compared to a local spatial scale.

The specific aims of the project are to:

1. Investigate the historical population structure of the Spectacled Flying-fox using mtDNA.
2. Examine the genetic relatedness of Spectacled Flying-foxes across their range to determine movement patterns, gene flow and genetic diversity across the three core areas of their distribution
3. Investigate the level of relatedness of individuals within a colony during the pupping season to determine whether there is any social structure within colonies occurring
4. Investigate aspects of the life history of a wild population of Spectacled Flying-foxes and, through the use of life tables, investigate rates of population growth, mortality and reproductive output

Summary of Results and Conclusions

Distance analysis found significant isolation in Spectacled Flying-fox populations between PNG and Australia, and Iron Range and the Wet Tropics region, suggesting that there is currently little gene flow between these regions (Fox 2006). Haplotypic diversity in mtDNA and genetic diversity at microsatellite loci are significantly lower in PNG than in Australia. The PNG data demonstrated similar diversity to Wet Tropics colonies with almost half the number of samples. These results all suggest an extended period of separation of Spectacled Flying-foxes from PNG and Australia.

Analysis of mtDNA in the Spectacled Flying-fox indicated a close historical relationship with the Black Flying-fox (*P. alecto*) through hybridisation or incomplete lineage sorting, or possibly both (Fox 2006). The age of the species may indicate whether incomplete lineage sorting was occurring – species of recent origin would exhibit incomplete lineage sorting. Hybridisation could be ruled out if there was reproductive isolation, but this does not appear to be the case with these two species. The mating period, distribution and feeding areas overlap. Hybrid offspring of the two species are also believed to be fertile (H. Spencer, pers. comm.). This result would be more clearly understood with a greater geographic distribution of Black Flying-fox samples and the inclusion of the third large *Pteropus* species, *Pteropus poliocephalus*.

A pattern of high haplotype diversity and low nucleotide diversity in the mtDNA data is indicative of an historical population expansion. This same pattern of molecular

diversity was observed in the Mexican free-tailed bat (Russell *et al.* 2005), which was found to have undergone a population expansion. The unimodal distribution of pair-wise nucleotide differences in the mismatch analysis, and neutrality tests strongly support this assertion. Conversely, the microsatellite data suggested that Spectacled Flying-foxes throughout the Wet Tropics region have been through a diffuse bottleneck that may have permitted the retention of many alleles likely to be lost under an intense bottleneck model. The slow contraction and expansion of rainforest during the last glacial maximum is a likely candidate for the cause of the bottleneck in Wet Tropics Spectacled Flying-foxes, while historical migration events from Indonesia or PNG may explain the pattern of expansion in the mtDNA data.

In Australia, *Pteropus conspicillatus* is principally found in the Wet Tropics region of north Queensland. The highly gregarious nature of this species, along with a patchy landscape of food resources, means there is considerable movement of individuals between colonies. A high degree of movement does not automatically confer abundant gene flow unless matings, and therefore offspring, result from these journeys. However, the lack of structure in the mtDNA and microsatellite data, suggest that high gene flow does occur among colonies throughout the region. This implies that mating is random with regard to geographic location or colony, and that there is no bias in the dispersal of offspring from a colony (i.e. no evidence for female philopatry). This is in agreement with the two previous studies on gene flow using allozyme markers in the other three *Pteropus* species found on mainland Australia (Sinclair *et al.* 1996; Webb and Tidemann 1996).

Iron Range appears distinct from the other Australian colonies (Fox 2006). It has the lowest population-by-population pairwise relatedness value compared to almost every other colony. The measure of allelic richness, which removes the bias as a result of sample size, revealed Iron Range had the second highest allelic richness of all colonies. From limited field observations of this colony, it appears to be very small in size, at most comprising several hundred individuals. It is difficult to determine if this is an unusual colony, or whether small sample size and a random sampling of alleles is biasing these diversity measures. However, when a comparison of the effective number of alleles was made by randomly subsampling the two Atherton Tableland populations with large sample sizes, with the total dataset, there was little difference. This may suggest that increasing the sample size in the Iron Range population would not change the results or the allelic diversity outcome. The high allelic diversity suggests that this colony has not been isolated for an extended length of time, as random processes, such as genetic drift, appear not to have affected it.

Female philopatry is common in mammals (Prugnolle and de Meeus 2002), and especially in female Microchiroptera (Wilkinson 1992; Worthington-Wilmer *et al.* 1994; Petri *et al.* 1997; Entwistle *et al.* 2000; Burland *et al.* 2001; Castella *et al.* 2001; Kerth *et al.* 2002; Miller-Butterworth *et al.* 2003). No female philopatry has been reported in the Megachiroptera due to a lack of genetic studies on colony inter-relatedness. This study found no evidence of female philopatry in

Spectacled Flying-foxes (Fox 2006). However, preliminary evidence that sub-adults travel with their mothers to forage was observed. The need to travel long distances to forage for patchy food resources provides impetus for this behaviour. In doing this, sub-adults would learn the location of valuable food resources at different times of year. The requirement for constant movement between colonies depending on the location of current food sources provides many opportunities for inter-colony matings. This study suggests such matings are common. In addition, despite the observation of family groups containing closely related sub-adults and mature females, there is no evidence of inbreeding or obvious within kin-group matings.

As the age structure of the Tolga Scrub colony indicates a population of mainly young animals, and the reproductive output of this colony is low, the ability of this population to achieve positive growth is low unless mortality rates are reduced. Although the year analysed (2002) was a relatively bad tick paralysis season (equating to approximately 5% loss of individuals from Atherton Tablelands colonies—J. Maclean, pers. comm.), the difference between the instantaneous mortality rate and annual mortality rate gives an indication of the effect of tick paralysis. The annual mortality rate (without the effect of tick paralysis), although in keeping with mortality rates for mammals in general, is higher than this species can realistically sustain, considering their short life span and low reproductive output (Fox 2006).

Considering the short period of time over which this study was undertaken, it is difficult to make any statement about year-to-year variation in recruitment and mortality. Both reproductive output (birth) and mortality rate (death) are likely to vary from year to year, and these two processes are critical influences on current population size trends. Thus, it is important to have a detailed and comprehensive understanding of these demographic components. However, mortality rate is a difficult parameter to ascertain directly. Determining the ages of individuals through the use of cementum layers in teeth, although time consuming, may be the only realistic method of determining age structure for a flying-fox colony, and therefore, mortality rate and population growth. However, new methods for aging animals using non-destructive techniques, such as the rate of telomere erosion throughout an organisms life, are now becoming available (Gan *et al.* 2001; Haussmann and Vleck 2002).

As flying-fox colonies have such a fluid nature, the use of life tables to estimate demographic processes may be inappropriate, as the assumptions of these tables may not be met. Although it can be argued that the life table results from this study cannot be extrapolated to other colonies due to their fluid nature, other factors suggest that sampling flying-foxes at this time of the year may be as close to random as can be hoped. That the sex ratio of samples taken was 1:1, and the movement of individuals between colonies is large-scale and apparently random, it could be argued that the sample taken would likely be an average across the Wet Tropics. This would need to be proven one way or the other by sampling across several colonies throughout the range of the Spectacled Flying-fox at the same time.

Application of Conclusions

The initial impetus for this study came from a need to provide basic information on the general biology and ecology of the Spectacled Flying-fox to facilitate informed decisions regarding this species. For the management agencies these decisions involved creating management plans, for the fruit farmers it was how best to protect their crops without having to cull animals on a nightly basis. To conservationists, it was how best to help the species stabilise in light of their alleged decline.

To management agencies, the level of gene flow and connectivity between colonies observed in this study emphasises the need to manage the Spectacled Flying-fox as a single management unit throughout the Wet Tropics region. It also highlights the fact that there appear to be very few barriers to movement in this region, and that their current distribution is not a reflection of their incapacity to move further afield, but likely due to other limiting ecological aspects, such as food resources.

The loss of individuals to tick paralysis each year is known to management agencies. However, these results reveal the effect of this loss on the population growth rate. There is a critical need to reduce the mortality rate, especially that due to tick paralysis, to improve population growth rates to a more sustainable level. The clarification of the age at first reproduction in females, and determining the reproductive output on an annual basis, will advise management of the capacity of this species to recover from a population decline.

The high connectivity of colonies found in the Wet Tropics region will answer many questions posed by fruit farmers. These results show that the removal of a single colony neighbouring a fruit farm would have no effect on mitigating the impact of foraging flying-foxes, as individuals foraging on fruit crops would have come from colonies throughout the Wet Tropics region. The removal of a colony from the panmictic Wet Tropics population would have no immediate effect on genetic diversity in the species, although it would have an effect on demographic factors such as overall reproductive output, which in the long term would likely affect genetic diversity.

This study also highlights that Spectacled Flying-foxes are incapable of a boom and bust reproductive system, dismissing the 'flying rodents' claim made by many fruit farmers. As the majority of females give birth for the first time between the ages of three and four, produce a single young per year, and most likely only live to six or seven years of age (Fox *et al.* 2006), this species follows a typical 'slow' life history trait scenario, without the long life span to compensate for the low reproductive output. It appears possible that in many years their mortality rate overshadows their reproductive output, resulting in either zero or even a negative population growth rate.

The high genetic diversity within Wet Tropics colonies will confirm for conservationists that the Spectacled Flying-fox has the genetic capability to cope with environmental change. High gene flow and connectivity of colonies ensure that loss of individuals through a localised mortality event will not have an immediate effect on genetic diversity within the population,

although it will affect reproductive capacity and total population size.

Considering the aspects of population structure that appear to be most important to the conservation of this species, I believe the most important future research that could be completed on this species is to determine whether the mortality rates and population growth rates estimated in this study are applicable to the rest of the Wet Tropics population. Once this has been resolved, the degree of urgency for remedial action can be established.

The population of Spectacled Flying-foxes occurring in the Iron Range National Park area appears to be an outlier within Australia and little is known about this population. The movement of the entire colony out of the park during the winter months and the fact that this was

known only by local Aboriginal people before August 2004, highlight the need for intensive field-based research, as well as more genetic samples, to accurately assess the status of this population.

While this study has concentrated on Australian populations of Spectacled Flying-fox, it has highlighted the lack of knowledge on the populations in PNG. Little is known of the colonies of Spectacled Flying-fox that occur in PNG, where only a couple of larger colonies close to towns can be verified as still in existence. As little is known about flying-foxes in PNG in general, this would be a worthwhile, if ambitious, project in adding knowledge on the evolution of flying-foxes in the Australo-Pacific region, a so-called hotspot of diversity for the Megachiroptera.

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