

**THE SPECTACLED FLYING FOX, *PTEROPUS CONSPICILLATUS*,
IN THE CONTEXT OF THE WORLD HERITAGE VALUES
OF THE WET TROPICS WORLD HERITAGE AREA.**

A Report for: Environment Australia



D. A. Westcott, A. J. Dennis,

A. McKeown, M. G. Bradford, C. R. Margules

CSIRO, Sustainable Ecosystems and the Rainforest Cooperative Research Centre.

PO Box 780, Atherton, Qld, 4883, Australia



June 2001



Ref: VM1/0301-15

**THE SPECTACLED FLYING FOX, *PTEROPUS CONSPICILLATUS*, IN THE
CONTEXT OF THE WORLD HERITAGE VALUES OF THE WET
TROPICS WORLD HERITAGE AREA.**

A Report for Environment Australia

D. A. Westcott, A. J. Dennis, A. McKeown, M. Bradford, C. R. Margules

CSIRO, Sustainable Ecosystems and the Rainforest Cooperative Research Centre.

PO Box 780, Atherton, Qld, 4883, Australia

With a contribution from Professor Jamie Kirkpatrick

School of Geography and Environmental Studies

University of Tasmania

June 2001

Cover photos with permission from Stanley Breeden

Left - *Ficus racemosa*

Centre - Spectacled flying-fox camp

Top Right - Spectacled flying-fox eating the fruit of *Ficus watkinsiana*

Bottom Centre - Spectacled flying-fox showing pale nape, shoulders and eye rings.

EXECUTIVE SUMMARY

Our review of the knowledge of *Pteropus conspicillatus* and its relationship with World Heritage values has identified a real lack of direct information on the species. To some extent this information gap has been covered through the use of unstructured observational data and data derived from other species. Our review draws on available literature on *P. conspicillatus* and other *Pteropus* and also on unpublished information from a range of relevant experts (Section 2; Appendix A).

Pteropus conspicillatus has suffered a significant loss of habitat, particularly on productive soils (Section 3.10.1), which is likely to have led to a historical decline in population size. It is also experiencing mortality from a suite of other human-induced factors that may affect population persistence (Section 3.10). These novel factors include killings at orchards, deaths from collisions with powerlines and fences, camp disturbance, and possibly paralysis tick envenomation. Attempts to quantify a level of decline in recent decades suffer from a lack of rigorously collected data or any means of understanding the error of the estimates (Section 3.11). Recent counts to estimate population size provide a better measure with some understanding of the errors involved (Section 3.11). At this stage however, estimates are available for only three years, which is insufficient to draw any conclusions about population trends. Mathematical models suggest that mortality greater than 20% could push the population into decline (Section 3.11). Unfortunately, the data are not available to determine if mortality levels are below or beyond this figure. In summary, while a decline can be inferred from the loss of habitat, insufficient data are available to quantify a historical or recent population trend. Despite this, if population counts are continued, count methodology and population model parameterisation improved and accurate measurement of current mortality factors is undertaken, a better understanding of likely population trends can be quickly derived.

We find that *P. conspicillatus* is a significant component of World Heritage values in its own right and also contributes to two ecological processes that are important to the maintenance of other World Heritage values and the ongoing evolution of the Wet Tropics World Heritage Area (Sections 3.7, 3.8 and 5). *Pteropus conspicillatus* is representative of the mixing of Australian and Asian biota and represents a unit of biodiversity in the World Heritage Area (Section 5.2). It has a disjunct distribution

associated with tropical rainforests in Australia and New Guinea, with the largest of the two Australian populations occurring in the Wet Tropics World Heritage Area (WTWHA; Section 3.2).

Pteropus conspicillatus contributes to the dispersal of seeds within rainforest and between patches of rainforest (Section 5.3.4). Because it moves freely across ecological boundaries both within and without the WTWHA (Section 3.4), it also contributes to the dispersal of seeds from rainforest into other vegetation communities and land uses. It probably also has aided the spread of some Asian flora into Australia (Section 5.2). Some of the plant species it is known to include in its diet, and therefore probably disperses or pollinates, are themselves listed specifically as having World Heritage value under criteria I and II (Section 5.3.4). Seed dispersal in general also contributes to the maintenance of other World Heritage values including plant diversity and distribution, population and genetic structuring and the ongoing evolution of community structure (Section 5.3.1, 5.3.2). While the fact that *P. conspicillatus* contributes to these processes is clear, its level of contribution has yet to be measured. Therefore, the extent of impact of a population decline or loss of the species on these World Heritage values cannot be quantified. Given the nature of the seed dispersal services it is known to provide, *P. conspicillatus* is likely to be especially important for large fruited plants, particularly when they are isolated in small fragments of forest. Although less well supported by data, its pollination services are also likely to be particularly important for plants in isolated fragments (Section 5.3.4).

Pteropus conspicillatus clearly contributes to, and helps maintain the World Heritage values of the Wet Tropics World Heritage Area. This benefit means that under the *Environmental Protection and Biodiversity Conservation Act* and the *Operational Guidelines for the Implementation of the World Heritage Convention* threats to the species persistence within the World Heritage Estate require management action, be it within or outside the Estate (Section 9.1). In particular, the Act requires such action even when full scientific certainty regarding threats is lacking. Despite a paucity of data regarding many aspects of *P. conspicillatus*' biology and the lack of full quantification of the extent and impact of both recent and current threats to the species, there is a clear need for careful management to ensure its future and the long-term integrity of the Wet Tropics World Heritage Area.

TABLE OF CONTENTS

Executive Summary	2
Table of Contents	4
1 Introduction	6
2 Methods	8
3 Spectacled flying-fox Ecology and Biogeography	9
3.1 Origins and Taxonomy	9
3.2 Distribution	10
3.3 Habitat	11
3.4 Movement Patterns	11
3.5 Camp site selection	14
3.6 Life history attributes	16
3.6.1 Birth sex ratios	16
3.6.2 Adult sex ratios	16
3.6.3 Breeding Seasonality	17
3.6.4 Age at first breeding.	18
3.6.5 Mating system	18
3.6.6 Fecundity	19
3.6.7 Longevity and Mortality	19
3.6.8 Rate of Population Growth	19
3.7 Diet and Foraging Behaviour	20
3.8 Ecological interactions	21
3.8.1 Localised high biomass and nutrient input	21
3.8.2 Carriers of wildlife disease	22
3.8.3 Seed dispersal	22
3.8.4 Pollination	24
3.9 Human interactions and values	24
3.9.1 Disease	24
3.9.2 Human appreciation	25
3.9.3 Traditional uses	25
3.9.4 Orchard pests	25
3.10 Threats and Conservation.	26
3.10.1 Habitat clearing	26
3.10.2 Paralysis Ticks	27

3.10.3	Control in Orchards	28
3.10.4	Camp disturbance and destruction	29
3.10.5	Hunting and Traditional Use	29
3.10.6	Competition	29
3.10.7	Powerlines and barbed-wire fences	29
3.10.8	Cyclones	30
3.11	Population Sizes and Trends	30
4	Summary of data limitations on knowledge of the ecology and behaviour of <i>Pteropus conspicillatus</i> .	34
4.1	Summary points with a high degree of certainty	35
4.2	Summary points with a moderate level of certainty for <i>P. Conspicillatus</i>	38
5	Spectacled Flying-foxes and World Heritage Values	40
5.1	World Heritage Convention and the Wet Tropics	40
5.2	Contributions as a species to World Heritage Values	41
5.3	Contributions to World Heritage Values through participation in Ecological Processes.	42
5.3.1	Seed dispersal as a determinant of the distribution of species and vegetation types.	42
5.3.2	Is seed dispersal important to the maintenance of rainforests plant diversity?	43
5.3.3	Population genetic consequences of Seed and Pollen dispersal.	45
5.3.4	What is the role of Spectacled Flying-foxes in seed dispersal and pollination in Australia	45
6	The likely consequences of threats to <i>P. conspicillatus</i> on the World Heritage values of the WTWHA.	50
6.1	Significant conclusions and their relationship to world heritage values.	52
6.1.1	List of significant conclusions	52
6.1.2	Significance of conclusions for World Heritage values	53
7	Summary	56
8	Reference List	57
9	APPENDIX A Experts consulted	67
10	Appendix B Natural criteria against which the Wet Tropics of Queensland was inscribed on the World Heritage List in 1988.	68
11	Appendix c Summary of external reviewers comments	73

1 INTRODUCTION

Old World fruit bats, Pteropodidae, are a prominent part of the global tropical fauna from Africa through to Australia and Oceania. Fruit bats are pollinators of many tropical forest trees (Start & Marshall 1976; Kress 1985; Marshall 1983, 1985; McCoy 1990; Eby 1991; Fujita & Tuttle 1991; Parry-Jones & Augée 1991; Elmqvist et al 1992; Cox et al 1992; Eby 1998; Hall & Richards 2000). They disperse seeds within rainforests and also onto cleared land and into other habitats (Docters van Leeuwen 1935; van de Pijl 1957; Thomas 1982; Utzurrum 1985; Brautigam 1988; Whittaker & Jones 1994; Richards 1990 a).

Pteropus are considered to be important seed dispersers and pollinators through out their range, and they are also significant agricultural pests (Mickleburgh et al. 1992; Fujita & Tuttle 1991). In Australia, as elsewhere, *Pteropus* are the focus of conflicting concerns; on the one hand is the issue of their conservation status, on the other the cost of the damage they inflict in orchards. In the Wet Tropics region of north-eastern Australia *Pteropus conspicillatus* has been the focus of significant community debate over these issues. This debate is not simply over the management of *P. conspicillatus*, a single species. It is also a debate about the consequences of management actions for the forests of the Wet Tropics World Heritage Area (WTWHA). This situation arises because *P. conspicillatus* move freely across the WTWHA boundaries. Thus, management decisions both inside and outside the boundaries of the WTWHA which impact on *P. conspicillatus* have the potential to impact on the World Heritage values of the WTWHA (Hitchcock, 2001).

Here we review knowledge of *P. conspicillatus* in the context of the World Heritage values of the WTWHA. Our task was

- i) to gather available data and the input of experts in relevant fields to review current knowledge of *P. conspicillatus* and to assess the scientific value and limitations of this knowledge
- ii) to provide a scientific evaluation of *P. conspicillatus* in the context of World Heritage values of the WTWHA
- iii) to consider the likely consequences of threats to *P. conspicillatus* for the World Heritage values of the WTWHA.

The review of current knowledge comprises Section 3 of the report. Within each subsection an assessment of the scientific value and limitations of the knowledge relevant to that subsection appears in a box entitled "Assessment of existing data". Section 4 summarises the limitations in general terms and provides a list of main points, while Section 5 provides a scientific evaluation of *P. conspicillatus* in the context of World Heritage values of the WTWHA. Section 6 examines the likely consequences of threats to *P. conspicillatus* for the World Heritage values of the WTWHA. First, it discusses consequences of threats, then lists the significant conclusions of the report, each with a coded assessment of the strength and nature of the conclusion. It then goes on to provide a discussion of the significance of our conclusions for World Heritage values and responsibilities by Professor Jamie Kirkpatrick.

We were not asked and do not attempt to review management techniques, make management recommendations or assess the conservation status of the species. Thompson (in prep.) and Kofron (in prep.) deal with these issues.

2 METHODS

The data for this review were obtained in three ways. First, a thorough literature search was conducted using the search terms 'Pteropus', 'Pteropidae', 'Pteropus conspicillatus', 'flying fox', and 'fruit bat' using the Web of Science bibliographic database (ISI, 2001).

Second, we identified researchers with expertise in the following fields: Pteropids generally as well as *P. conspicillatus* specifically, plant pollination and vegetation dynamics, vertebrate conservation and management, and World Heritage (Appendix A). Contact with these experts was attempted and those that were available within our time frame were asked to provide an assessment of the status of *P. conspicillatus* in the context of the World Heritage values of the WTWHA (listed in Appendix B). They were asked to address this issue within the terms of reference provided by Environment Australia and to identify data and publications relevant to the task.

Third, we contacted other individuals with experience with the species, eg, managers and animal carers, and asked them to contribute. Some of these people provided verbal rather than written input (Appendix A).

Finally, we asked the experts to provide or summarise any unpublished data that they felt was relevant to this review and assessment of *P. conspicillatus* in the context of world Heritage Values. We provided substantial quantities of our own unpublished data on *P. conspicillatus* and its ecology.

The report was then sent to three independent reviewers for their professional review of the document; two within Australia with expertise in World Heritage, conservation and management, and one internationally, with bat and Pteropid expertise. A summary of the reviews and how they were dealt with is attached in Appendix C.

3 SPECTACLED FLYING-FOX ECOLOGY AND BIOGEOGRAPHY

3.1 ORIGINS AND TAXONOMY

The origin of bats is poorly understood with the first fossil Chiropterans appearing in the Eocene (60 mybp) as fully developed fliers. The Megachiroptera, Old World flying foxes (Pteropidae), first appear in the fossil record 35 mybp. No Megachiroptera appear in the extensive fossil deposits of Riversleigh or Murgon, covering the periods 3–23 mybp suggesting that they are a recent addition to the Australian fauna (Hall & Richards 2000). There has been debate on the relationships of the Microchiroptera and Megachiroptera (Smith & Madkour 1980; Pettigrew 1986; Pettigrew et al. 1989; Pettigrew 1991; Baker et al 1991), although recent work suggests that all bats are monophyletic (D. Wilson pers. comm. 2001). The single megachiropteran family, Pteropidae, consists of some 41 genera and around 200 species (Nowak 1997; Fujita 2000). Approximately 60 species are included in the genus *Pteropus* making it the largest genus in the family (Mickleburgh et al. 1992; Nowak 1997; Tidemann & Vardon 2001). The exact number is unclear due to the uncertain taxonomic status of some species (Tidemann & Vardon 2001). Over 90 % of *Pteropus* species have some or all of their distribution on islands (Mickleburgh et al. 1992) suggesting that while members of the genus have been effective colonisers of oceanic islands such events have been rare enough to allow divergence after colonisation.

P. conspicillatus is comprised of two described sub-species, *P. c. conspicillatus* from Australia and *P. c. chrysauchen* from New Guinea and surrounding islands (Mickleburgh et al. 1992). However, neither Flannery (1995a, b) nor Bonaccorso (1998) recognise this sub-specific division. In addition, three closely related species, have been shown to have only minor genetic and morphological differences to *P. conspicillatus* suggesting that divisions at the subspecific level may be of little import. Flannery (1995 b) noted that *P. conspicillatus* in New Guinea and Indonesia are morphologically very similar to *P. tonganus* and that electrophoretic studies had indicated few differences. In their examination of putative hybridizations between *P. alecto* and *P. conspicillatus*, Webb & Tidemann (1995) also noted many morphological similarities and surprisingly few genetic differences between the species (only one fixed allele difference). While no *P. alecto* x *P. conspicillatus* hybrids were identified, *P. alecto* x *P. poliocephalus* hybrids (with two fixed allele differences) were found. This suggests that in the absence of pre-mating isolating mechanisms it is likely that *P. conspicillatus* could hybridize with *P. alecto* (Webb & Tidemann 1995). As might be expected given these morphological and genetic

similarities, the four species in this group, *P. alecto*, *P. poliocephalus*, *P. conspicillatus* and *P. tonganus*, share many behavioural, physiological and ecological traits. This makes it reasonable to use data from these other species as a guide when appropriate information for *P. conspicillatus* is unavailable.

3.2 DISTRIBUTION

The historical Australian range of *P. conspicillatus* is not known for certain. Its current distribution is in association with rainforest from Ingham to Cooktown and in the McIlwraith and Iron Range of Cape York (Ratcliffe 1932; Clague et al. 1999). Clague et al. (1999) suggest that the abandonment of a camp near Ingham and possibly others in the Cardwell area indicate a decline in extent of occurrence in the south of its range with no evidence of replacement camps being established. However, bats injured in orchards in the Ingham area, which were sent to Tolga Bat Hospital (J. Maclean pers. comm. 2001), a seasonal camp at Broadwater (Whybird, pers. comm. 2001) and two new camps discovered near Cardwell (Whybird unpubl.), indicate that *P. conspicillatus* is foraging in the area at least. In addition, Spencer (pers. comm. 2001) has noted temporary range contractions in the past associated with low rainfall. This might mean that the disappearance of the camp at Ingham is a response to climate.

Outlying records of the species are surprisingly rare. For example, there is only a single report from the Torres Strait (Andersen 1912) and records of one or two animals at Chillagoe and Brisbane (Richards 1990 b). However, the morphological similarity between *P. conspicillatus* and *P. alecto*, means that movements, particularly if infrequent and involving small numbers of animals, will easily go unnoticed (Tidemann & Vardon 2001). In addition, small satellite camps of one species of *Pteropus*, within main camps of a congener, can be particularly difficult to detect (see Tidemann et al., 1999; Tidemann & Vardon, 2001).

Outside Australia, *P. conspicillatus* is recorded from New Guinea and some of its offshore islands (Flannery 1995 a, b). While it appears uncommon in this part of its range (Mickleburg et al. 1992; Flannery 1995a, b) camps at any particular site are often comprised of thousands of individuals (Flannery 1995a, b). It is not clear whether or not these populations are genetically isolated but each could be considered to constitute unique management or conservation units.

Assessment of existing data

The data describing the distribution of the species is relatively good and consists primarily of museum data and the observations of reliable eyewitnesses. Given the highly dynamic nature of both *Pteropus* generally and *P. conspicillatus* camp use in particular (see below), it seems reasonable that conclusions about contractions in the southern part of the range should be viewed as preliminary but regarded as a serious possibility. Searches for replacement camps should be conducted to allow confirmation of this decline.

3.3 HABITAT

While *P. conspicillatus* will forage and roost outside rainforest there is no doubt that rainforest is an important habitat type for the species. Its distribution is apparently limited to areas with sufficient rainforest coverage (Richards 1990b). The 55 camps from across its Australian distribution recorded by Richards (1990b) were all within 7 km of wet tropical rainforest. The morphology of the teeth and tongue indicate specialisation for fruit (Birt et al. 1997) a fact that in Australia also suggests a rainforest specialist.

Assessment of existing data

The association with rainforest is clear and reliable.

3.4 MOVEMENT PATTERNS

There has been considerable interest in the movement of *Pteropus* in Australia. Two general movement patterns are described for most species. The first of these are movements out from camps to foraging sites and back. For the three Australian *Pteropus* species examined in any detail, these distances ranged up to approximately 40 km. These estimates have been confirmed both indirectly and directly (*Pteropus alecto*: indirectly Vardon & Tidemann 1999; Vardon et al. 2001, directly using radio-telemetry Palmer & Woinarski 1999; Palmer et al 200. *Pteropus poliocephalus*: indirectly Nelson 1965a,b; Webb & Tidemann 1996; Tidemann 1999; directly using radio-telemetry Eby 1991; Spencer et al. 1991, *Pteropus scapulatus*: indirectly Nelson 1965a,b; Sinclair et al., 1996; Vardon et al., 1997; Vardon & Tidemann, 1999; Vardon et al., 2001).

The second scale of movement is inter-colony movement. Both seasonal and dramatic changes in colony size have long been noted (Anonymous 1890; Ratcliffe 1931). Ratcliffe (1931) suggested that these occurred in response to changes in resource distribution. This has been supported by observations of camp size changes (Nelson 1965a; Vardon &

Tidemann 1999), banding programs (Tidemann 1999) and from radio-telemetry studies (Eby 1991). Recent satellite radio-telemetry studies on *Pteropus* (presumably *P. poliocephalus*) report movements by an individual bat of 1740 km (Nelson & Tidemann 2000).

There are limited data available on *P. conspicillatus* movement in the literature. There are no published data on foraging movements, though these are generally assumed to be of the same order of magnitude as those of other *Pteropus* species. Published information on movements between camps is richer. Ratcliffe (1932), Richards (1990b), Bonaccorso (1998), and Garnett et al. (1999) all reported changing temporal patterns of camp occupation by *P. conspicillatus*. In particular, Richards (1990b) shows changes in camp occupancy along the North Johnstone catchment that are highly suggestive of inter-camp movements through the year. Both Richards (1990b) and Bonaccorso (1998) describe seasonal disappearances from particular areas.

While well documented, these patterns of inter-camp movement are not necessarily regular or predictable over time. Garnett et al. (1999), state that “There is evidence that the flying foxes move camp both within and between years, and will camp at levels of aggregation that can vary by several orders of magnitude”. Richards (1990b) reported that during the 1980s *P. conspicillatus* vacated upland areas such as the Atherton Tablelands in favour of camps in the lowlands. In all but one of the last five years, however, *P. conspicillatus* have remained throughout the year, in undetermined numbers, on the Atherton Tablelands (Westcott & Dennis, pers. obs.; J. Maclean, pers. comm. 2001). At some point in the mid-1990s *P. conspicillatus* abandoned camps at Ingham and Mareeba and were reported as having been absent for several years (Garnett et al. 1999; Clague et al. 1999). Subsequently, at least one of these camps has been re-occupied, at least briefly (J. Maclean, pers. comm.; Westcott & Dennis, unpubl. data).

In late 2000 and early 2001, Westcott & Dennis (unpubl. data) radio-tagged eight *P. conspicillatus*. The results of this work, while very preliminary, indicate that within their range, the movement patterns of *P. conspicillatus* are similar to those of other Australian *Pteropus*. Our initial monitoring sought simply to document camp use by these animals (Table 1) and indicated frequent, sometimes daily, changes in the camps used. Straight-line distances between camps averaged 39 km (range 15–85 km). A limited number of nights of continuous telemetric observation have been conducted on several bats.

Although preliminary, these data indicate that *P. conspicillatus* foraging movements occur on a scale similar to that observed for other *Pteropus*. The best data currently available comes from ♀2 (Table 1). Over five nights of continuous tracking from prior to departure from the roost until her return to the roost, ♀2 travelled an average of 54.3 km (range 31.7 - 67.6 km) within a range that over the five nights encompassed 3 819 ha and as much as 2 163 ha in any one night's foraging in forest fragments and on agricultural land.

Table 1. The number of different camps occupied by eight radio-collared *P. conspicillatus* in short periods of observation.

Bat	Observation Period	Observation Days	# of Camps Occupied
♂1	21/9/00 - 11/10/00	21	3
♂2	28/11/00 - 8/12/00	12	3
♀1	9/01/01 - 12/01/01	4	2
♀2	6/02/01 - 25/3/01	48	4
♀3	6/02/01 - 23/3/01	46	4
♀4	6/02/01 - 23/3/01	46	4
♀5	6/02/01 - 23/3/01	46	2
♀6	6/02/01 - 23/3/01	46	2

Assessment of existing data

Most published data on *P. conspicillatus* movements are composed of inferences based on observations of changes in camp sizes. Given that similar observations in other *Pteropus* species (Ratcliffe 1932; Nelson 1965a) were later confirmed using radio-telemetry studies it is likely that these inferences are reasonable.

Direct documentation of movement, both foraging and inter-camp movements, is still preliminary. Despite this caution, the work supports the inference made about *P. conspicillatus*' movement patterns and is broadly similar to the data obtained for other species. These movement data confirm that *P. conspicillatus* feeds in both rainforest and on agricultural lands.

Pteropus conspicillatus, like other species of *Pteropus*, has a complex range of behaviours with regard to camp size and the use of the landscape. What drives this is not known though the inference that it is a response to food is reasonable given the abundance of data from around the world on the influence of resource distribution on animal populations.

We conclude that the information to date is reliable but that the full extent and pattern of movements between colonies and while foraging is not yet fully known

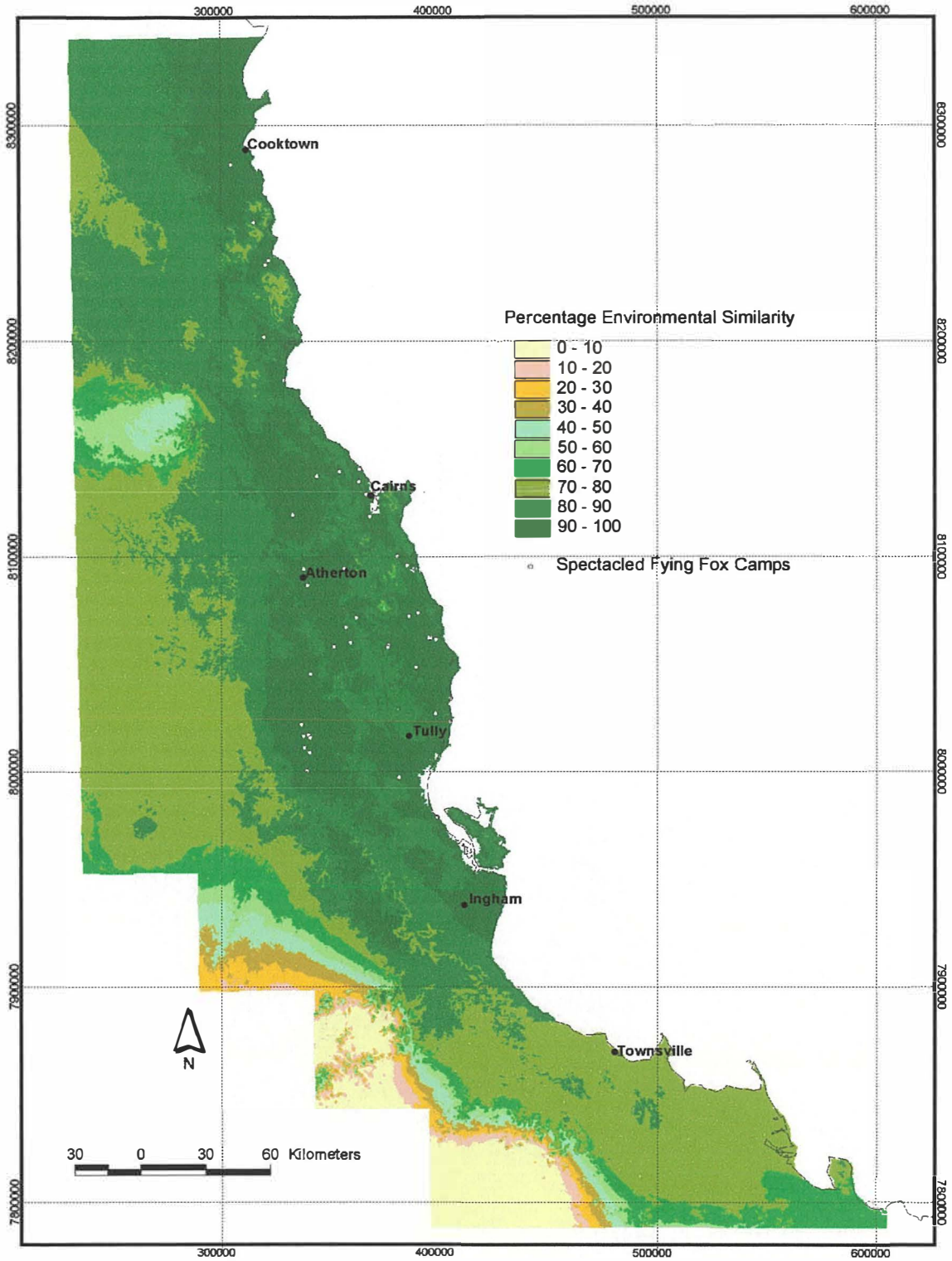
3.5 CAMP SITE SELECTION

Like other *Pteropus*, *P. conspicillatus* is highly social and generally spends the day in “camps” occupied by up to tens of thousands of individuals, not all of which may be conspecifics. The species is not selective of the type of vegetation in which it camps, a characteristic it shares with many other *Pteropus* species (Tidemann, 1999; Tidemann et al., 1999). Richards (1990b) recorded *P. conspicillatus* camps in a wide range of vegetation types, from riverine and other rainforests, paperbark (*Melaleuca* spp.) swamps, mangroves and eucalypt forest. Flannery (1990a) recorded *P. conspicillatus* in swamps and rainforests in New Guinea and Indonesia while Bonaccorso (1998) found it in both primary and secondary rainforest. *P. conspicillatus* camps in New Guinea have also been recorded in plantations of coconut (*Cocos nucifera*), she-oaks (*Casuarina* spp.) and hoop-pine (*Araucaria cunninghamii*) (Tidemann & Vardon 2001).

The wide range of camp habitats recorded suggests that appropriate vegetation types for camp-sites are unlikely to be limiting for *P. conspicillatus* (Tidemann & Vardon 2001). In addition, a simple analysis of the climatic envelope associated with the camps listed in Garnett et al. (1999) suggests that those same climatic conditions are common throughout the species Wet Tropics range (Figure 1; Hilbert, Garnett & Westcott, unpubl. data). This apparent abundance of potential campsite climates and habitats reflects the pattern known for *P. alecto* (Tidemann et al. 1999; Vardon et al. 2001). What has yet to be examined is micro-habitat selection.

Figure 1. (next page)

Climatic similarity from DOMAIN using all 35 climate variables (Hilbert & Garnett, unpubl. data). The locations of camps reported in Garnett et al. (1999) of *P. conspicillatus* were entered into a regional geographic information system. Each location has a specific climatic environment defined by a large number of climatic variables. The spatial distributions of these variables were estimated across the humid tropics on a 320 metre grid using the ANUCLIM software (McMahon et al. 1995), weather data from a large number of stations (c. 200) and a digital elevation model. Thirty five variables are estimated that relate to the temperature, rainfall, radiation, and available water. The similarity index mapped is the highest environmental similarity found by comparing all locations in the humid tropics with all known camps using DOMAIN (Carpenter et al. 1993).



Assessment of existing data.

Attempts to describe *P. conspicillatus* camp habitat have been limited to a relatively coarse level only (Richards 1990 b; Hilbert & Garnett unpubl data). The preference for dense vegetation types, particularly rainforest, is clear (Richards 1990b) and is similar to the preferences of other *Pteropus* species (Pierson & Rainey 1992; Hall & Richards 2000). The huge variation in gross characteristics of camps would suggest that finer scale investigation of similar parameters would yield no greater detail.

What remains to be examined in *P. conspicillatus* camp site choice are camp site characteristics below the level of gross environmental characteristics (Richards 1990 b) and climate (Hilbert & Garnett, unpubl. data; Garnett et al. 1999). These might include whether access to a range of microclimates, proximity to food resources, social memory or other characteristics are important for campsite choice. Camp choice and use may also be affected by the reproductive cycle as is the case for *P. alecto* (Vardon et al 2001).

3.6 LIFE HISTORY ATTRIBUTES

3.6.1 Birth sex ratios

The only data available for *P. conspicillatus* comes from the sex ratios of pups on females treated for ticks, being male: female ratio of 1:1 (J. Maclean, pers. comm., 2001). This matches captive colony birth sex ratios found for *P. alecto* and *P. poliocephallus* (L. Martin, pers. comm. 2001; Martin & McIlwee, 2001).

Assessment of existing data

Empirical data on birth sex ratios have been derived from pups on females treated for ticks. The data are likely to be reliable but could possibly be biased if there is differential investment in male and female offspring.

3.6.2 Adult sex ratios

J. Maclean (pers. comm. 2001) reports a male:female sex ratio of 1:4 and Tidemann & Vardon (2001) 1:2 in *P. conspicillatus* treated for tick envenomation. Hayden (1992) reported a male biased sex ratio from the Powley Rd camp of 3.5:1 in November 1992. Surveys the following March at the same camp (Bull 1993) showed a female biased sex ratio of 1:1.6, perhaps suggesting non-random camp use associated with the reproductive cycle. Sex ratio data from other Australian *Pteropus* also indicate a female bias: *P. alecto*, 1:1.7 (Vardon & Tidemann 1999); *P. scapulatus*, 1:1.5 (Nelson 1965b; Vardon & Tidemann 1999), 1:1.7 (Vardon et al. 1997); *P. poliocephalus*, 1:1.6 in camps with 100%

P. poliocephalus (Eby et al. 1999), 1:1.4 in camps with 95-98% *P. poliocephalus* and the remainder *P. alecto* (Eby et al. 1999). Nelson (1965a) also reported that camps of this species showed a strong female bias from September to October. This bias decreased toward equality up to December. He doesn't record whether it reached equality. Female biased sex ratios were shown to be a result of earlier maturation of females in *P. melanotus* (Tidemann 1985). This has also been suggested for *P. alecto* (Vardon & Tidemann 1998). Given the data presented for all *Pteropus*, it seems reasonable to infer a female biased sex ratio in *P. conspicillatus*. The record of a male biased camp (Hayden 1992) however, suggests the possibility of some degree of sexual segregation between camps.

Assessment of existing data

Empirical data drawn from tick victims that may involve bias if genders respond differently to tick bite or have different levels of exposure. The former may occur if females carrying young are more susceptible or collapse more frequently at camps than males. The latter may occur if lactating females forage differently to males. Other data are from a sample of one camp, which is a small sample.

3.6.3 Breeding Seasonality

Most *Pteropus* are seasonal breeders, having defined times of mating and parturition (O'Brien 1993). Observations made by wildlife carers on the Atherton Tablelands suggests that the peak in *P. conspicillatus* births occurs between October and December of each year and that this timing is relatively stable across years (n= 10 years, J. Maclean, pers. comm., 2001). While there are rare reports of neonates as late as January there is no indication of the frequency of births outside the October – December period and these probably represent the tail of the distribution (J. Maclean, pers. comm., 2001). In New Guinea Bonoccorso (1998) reports births occurring between July and August. Some geographical plasticity in breeding is noted for *P. alecto* (Vardon and Tidemann 1998) and for *P. poliocephalus* (Tidemann 1999). It seems probable that *Pteropus* species can conceive soon after abortion or neonate death (see Tidemann and Vardon 2001; L. Martin, pers. comm. 2001), which may account for some births outside the normal season.

Assessment of existing data

Based on limited observational data, predominantly from tick victims brought in for care. Data appear reliable for the Atherton Tablelands. No data were available for other areas within the Wet Tropics Region.

3.6.4 Age at first breeding.

Age at first breeding is unknown for wild animals but some free-living, captive-reared animals breed in their second year (J. Maclean, pers. comm., 2001). Maclean suggests that this may be earlier than wild animals, perhaps the result of a better nutritional status of captive-reared animals (pers. comm., 2001). Garnett et al. (1999) report that *P. conspicillatus* is mature at one year old, which is similar to *P. melanotus* (Tidemann 1985). The patterns of skull fusion in *P. conspicillatus* and *P. melanotus* are similar but different from *P. alecto*, *P. poliocephalus* and *P. scapulatus* suggesting different developmental schedules (Tidemann, pers. comm. 2001). Wild *P. alecto* and *P. poliocephalus* are mature at 18 months of age (Nelson 1965 a; Vardon and Tidemann 1998; Tidemann 1999). In contrast, successful reproduction appears to begin at 24 months in captive colonies in *P. poliocephalus* and *P. alecto* (Martin & McIlwee 2001). While animals may be capable of reaching physiological sexual maturity at 18 months, whether in the wild this translates into significant numbers of successful breeding attempts is the subject of debate (L. Martin, pers. comm. 2001; Tidemann & Vardon 2001; M. Vardon, pers. comm. 2001; H. Spencer pers. comm. 2001).

Assessment of existing data

Limited observational data and inference suggest a low level of certainty about exact age but reasonable level of certainty that they become successfully reproductive by the age of 24 months.

3.6.5 Mating system

There are no data on the mating system of *P. conspicillatus* though some form of polygyny could be expected given the female biased sex ratios reported for *P. conspicillatus* (Bull 1993; J. Maclean pers. comm. 2001) and other species (Nelson 1965b; Eby et al. 1999; Vardon & Tidemann 1999). The uncertainty associated with the number and breeding status of animals away from camps limits the conclusions that can be drawn here.

Assessment of existing data

Speculation based on limited empirical data on sex ratios, therefore, carries a low level of certainty.

3.6.6 Fecundity

Females give birth to one pup per year (Maclean, pers. comm. 2001) though in captivity other species do occasionally produce twins and even triplets (L. Martin, pers. comm. 2001). In captivity, *P. rodricensis* can conceive soon after neonate death and abortion, and it is possible that this occurs in other *Pteropus* as well (see Tidemann and Vardon 2001; L. Martin pers. comm. 2001). Hayden (1992) reported 66% of females at the Powley Rd camp as having young in November while in March at the same camp Bull (1993) reported 44% of females as having juveniles, with 47 % of all juveniles presented as being independent.

Assessment of existing data

There is limited empirical data here. However, that females generally do have one young per year has a high level of certainty whereas the proportion of females giving birth in each year has a low level of certainty.

3.6.7 Longevity and Mortality

There are no data from the wild though captive animals are reported to have lived for up to 17 years (Hall 1983). Presumably, most wild animals do not live as long. Mark-recapture studies of *P. poliocephalus* found the average age at recapture was 3.4 years, with a maximum of eight years (Tidemann 1999), although since then one 12 year old individual has been recovered (M. Vardon, pers. comm. 2001). Estimated longevity of adult female *P. alecto* was seven years (Vardon and Tidemann 2000). Juvenile mortality rates for *P. alecto* are high (0.43-0.80; Vardon and Tidemann 2000). However, this study was done at a time of food scarcity and may vary considerably between years. No longevity or juvenile mortality data are available for *P. conspicillatus*.

Assessment of existing data

The data comes from captive animals and is probably best interpreted as indicating maximum ages.

3.6.8 Rate of Population Growth

Garnett et al. (1999) estimated potential rate of increase for *P. conspicillatus* of 1.3 – 1.5 based on an estimated female reproductive success of 50 to 80% and a sex ratio of 1:2. Martin & McIlwee (2001) estimated rates of increase as falling between –12 to 25% under survival and fecundities which varied from 70-100% and 0.45-0.5 respectively and a sex

ratio of 1:1 (Table 3 in Martin & McIlwee 2001). Allowing for both adult and juvenile mortality reduced rates of increase to 13% and below. Modelling by Tidemann & Vardon (2001) for *P. alecto* and *P. poliocephallus* using simple matrix models for females only estimated rates of increase falling between 9 – 23% under survival, fecundities, and age at first parturition that varied between 50 – 90%, 45%, and 1-2 years respectively. Rates of 15% and 23% were obtained only with ages at first parturition of <24 months, a situation which these authors suggest is the case for *P. conspicillatus*. The frequency of successfully rearing young to independence from such early births is contentious (L. Martin, pers. comm. 2001). Rates of population increase for other *Pteropus* species as reported in Tidemann & Vardon (2001) are: 40% for *P. giganteus* (Dolbeer et al. 1988), 40% for *P. alecto* (Vardon & Tidemann 2000), 33% for *P. tonganus* (Brooke et al. 2000), and 27% in a captive colony of *P. rodricensis* (West & Redshaw 1987). It is not certain from these references how the figures for *P. alecto* or *P. rodricensis* were calculated. The figure for *P. tonganus* appears to be calculated from data presented by Brooke et al. (2000) on camp surveys and as such cannot exclude immigration as well as reproduction contributing to population growth.

Assessment of existing data

Discrepancies between the estimated rates of increase for *P. conspicillatus* (and thus also for the consequences of different mortality regimes) appear to result primarily from a reliance on differences in the estimates for life history parameters, primarily age at first parturition. Under realistic assumptions, i.e. allowing for some adult and juvenile mortality, the different models produce estimates within roughly similar ranges when similar parameters are considered. While the appropriate figures used to parameterise the models are currently debated, reliable empirical data are needed to resolve this debate.

3.7 DIET AND FORAGING BEHAVIOUR

All species of *Pteropus* feed primarily on nectar, flowers and fruit (van der Pijl, 1957; Marshall, 1983, 1985; Mickleburgh et al. 1992). While no *Pteropus* species appears to be an obligate consumer of any one of these forage types, the degree of dietary specialisation varies between species (Marshall 1983). Many species, perhaps all, will consume leaves and sometimes insects, particularly when fruit and blossom are in short supply (Lowry, 1989; Funakoshi et al., 1993; O'Connor and Kerr, 2000). In the case of *P. conspicillatus* diet appears to be biased toward fruit. However, both flower and foliage feeding do occur and their relative contribution to the diet has not been examined. To date, there are records

of *P. conspicillatus* consuming the fruits of 48 native plant species, the flowers parts and products of 18 native species, and the foliage of one native species (Richards 1990a, Eggert 1994; Westcott & Dennis, unpubl. data). *Pteropus conspicillatus* is also known to feed on the fruits of 12 exotic species, some of which are of commercial importance or are considered weeds (Westcott & Dennis, unpubl. data).

This count of species occurring in the diet of *P. conspicillatus* is preliminary and it is to be expected that many more species will be added with further research. As noted by Law (2001) there has yet to be any attempt to quantify the relative importance of the different food types in *P. conspicillatus*' diet, nor has there been any attempt to quantify the reliance of *P. conspicillatus* on different vegetation types for foraging. While the fruits identified in the species' diet are primarily rainforest species, four of the flowers fed upon are from sclerophyll forest species. This suggests that at least at some periods of the year non-rainforest resources are likely to be important (Garnett et al. 1999; H. Spencer pers. comm. 2001), as is the case with *P. alecto* in the Northern Territory (Palmer and Woinarski 1999; Vardon and Tidemann 1998, 1999; Palmer et al. 2000; Vardon et al. 2001).

Assessment of existing data

Our knowledge of *P. conspicillatus*' diet can only be considered preliminary. With thousands of species of fleshy fruited and flowering plants available within the Wet Tropics region *P. conspicillatus* will be found to feed on many more.

Both the association between camps and rainforest (Richards 1990 b) and the documented diet of the species to date suggest a reliance on rainforest for foraging. However, all researchers to date have focused on the *P. conspicillatus* in rainforest (Richards 1990 a; Eggert 1994; Westcott & Dennis, unpubl. data) making it impossible to assess the extent of the species reliance on other resources. All workers are comfortable with the assertion that rainforest species form the major portion of the diet, simply on the basis of the species' distribution being so tightly linked to rainforest.

3.8 ECOLOGICAL INTERACTIONS

3.8.1 Localised high biomass and nutrient input

High numbers of animals in restricted areas, as occurs in *Pteropus* camps, must provide high levels of biomass and nutrient in the form of waste and dead animals. The flow on effects of this are unknown and may vary depending on soil type and camp location. In addition, *P. conspicillatus* are known to be food for many predators, particularly at camps (Ratcliffe 1932).

Assessment of existing data

Nutrient input qualitative speculation. Prey for wide range of predators is reliable observation.

3.8.2 Carriers of wildlife disease

There is no data on the role of *P. conspicillatus* as hosts or vectors of diseases affecting other wildlife with the exception of one record of a *P. conspicillatus* testing positive for Australian Bat Lyssa virus (Kofron 2001). They may also carry other diseases. See Human Interactions below.

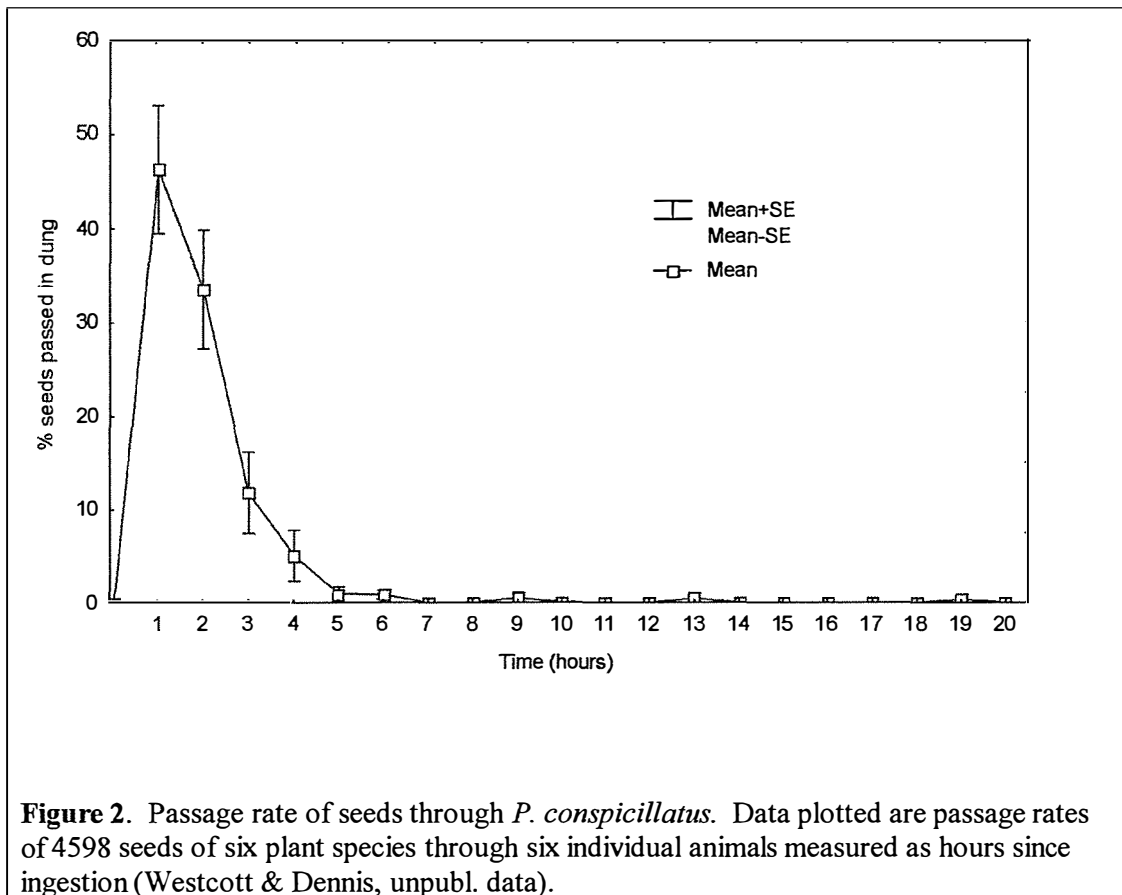
Assessment of existing data

Limited to one reliable record.

3.8.3 Seed dispersal

The role of bats and Pteropidae in general as seed dispersers is clearly demonstrated and accepted (van de Pijl 1957; Marshal 1983, 1985). The first direct evidence of such a role for *P. conspicillatus* came from Richards (1990 a). Like other *Pteropus* and because of its means of foraging and morphology, *P. conspicillatus* exhibits two distinct modes of seed dispersal. In consuming small-seeded fruits *P. conspicillatus* chews the fruit and then compresses the pulp against its palate and sucks out the juice. The remaining pulp and fibre are then spat out. The majority of seeds are spat out with the fibre. However, some proportion can be swallowed along with the juice. The exact proportion probably varies depending on the fruit characteristics and seed size. Seeds of up to 7.3 x 5.6 mm have been recorded from *P. conspicillatus* dung in Atherton Tableland camps (Westcott & Dennis, unpubl. data). These dimensions are slightly greater than the maximum size predicted by Tedman & Hall (1985) based on the morphology of the lumen and probably indicate either individual differences in size or the capacity of the lumen to stretch. For ingested seeds the distance that they are dispersed will be a function of how far the animals move in the time that the seeds remain in the gut. We documented the gut passage rates of 4598 seeds of six plant species through six individual *P. conspicillatus* (Figure 2; Westcott & Dennis unpubl. data). Slightly fewer than 50% of these seeds appeared in the dung within an hour of ingestion with approximately 90% appearing within three hours. A small proportion (<10%) appeared as much as 19 hours after consumption. Given the rates of

movement reported above (Westcott & Dennis, unpubl. data) dispersal distances for small seeds of as much as 15 km could be common and tens of kilometres are possible.



The second mode of seed dispersal exhibited by *P. conspicillatus* is external transportation. This appears to occur when one animal displaces another from a forage tree (Richards 1990a). When displaced, an individual may depart holding a fruit (Richards 1990 a; Hall & Richards 2000). The distances such fruits are carried are not known though it might be expected that displaced bats would settle in an adjacent or nearby tree. In areas, such as Cairns suburbs and Tableland paddocks, where the distances between trees can be large, reports of mangoes and mandarins being dropped 100 m from the nearest source tree have been made (R. Sing, pers. comm. 2000; Hall & Richards2000).

Assessment of the data

The data supporting the claim that *P. conspicillatus* acts as a seed disperser is clear and unequivocal.

3.8.4 Pollination

To date, the flower parts and products of 18 species have been recorded in the diet of *P. conspicillatus* (Richards 1990 a; Eggert 1994; Westcott & Dennis, unpubl. data; Weber, in Werren 2001). Further investigation will no doubt find additional species in the diet, e.g. B. Law (pers. comm. 2001) suggests that all canopy *Syzygium* may eventually be found to be pollinated by *P. conspicillatus*. This flower foraging opens up the opportunity for pollen, captured on the body at one flower, to be transferred to another. As is the case for seed dispersal, *Pteropus* generally are recognised as acting as pollinators throughout their range (Marshall 1983, 1985; Mickleburg et al. 1992; Fujita & Tuttle 1991). Pollination by Australian *Pteropus* has been demonstrated for *Eucalyptus* (McCoy 1990) and for the exotic ornamental, *Ravenala madagascariensis* (Calley et al. 1993). Pollination of *Ceiba pentandra* by *P. conspicillatus*' close relative *P. tonganus* has been documented in Samoa (Elmqvist et al. 1992). In this example *P. tonganus*, though the primary disperser of *C. pentandra*, destroyed 50% of flowers. Given the foraging and morphological similarities between *P. tonganus* and *P. conspicillatus* it might be expected that *P. conspicillatus* would also destroy many flowers but in the process disperse pollen.

Assessment of data

The role of *P. conspicillatus* in pollination is inferred from observations of flower feeding by this species. Given that other studies have confirmed pollination under similar circumstances by closely related species this is probably a reliable inference. While there are few data available, additional pollinators are known for all but one species identified in *P. conspicillatus*' diet to date (B. Jackes 2001), though the relative importance of these pollinators compared to *P. conspicillatus* is unknown.

3.9 HUMAN INTERACTIONS AND VALUES

3.9.1 Disease

Pteropus generally are implicated or known to be involved in the spread of three diseases to humans and/or domestic animals in Australia (Hooper 2001). Of 746 flying foxes brought in for care and tested for Australian bat Lyssavirus between 1996 and 1999, 50 (7%) were positive and one of these was a *P. conspicillatus* (H. E. Field, Qld Dept. Primary Industry, in Kofron 2001). Australian bat Lyssavirus is the only disease which flying foxes are known to transfer directly to humans, with one case reported to date. *Pteropus* are natural hosts for Hendra virus, which appears to have been transmitted to humans from *Pteropus* via horses (Halpin et al. 2000). Menangle virus is widespread in

Pteropus in Australia and appears to be transmitted to humans via pigs (Kirkland et al. 2001; Love et al. 2001). There has been discussion of a link between *Pteropus* and Ross River virus and reports of a higher incidence of Ross River virus in mosquitoes in the vicinity of flying fox camps (Harley et al. 2000). However, in a more recent epidemiological study no association has been found between a person's proximity to flying foxes and their risk of disease (D. Harley, pers. comm. 2001).

Assessment of existing data

Evidence for *P. conspicillatus*' role as a human disease carrier is solid for Australian Bat Lyssa virus though the risk is minimal.

3.9.2 Human appreciation

While some people who live near *P. conspicillatus* camps appreciate their presence, some communities have expressed concern over associated human health risks, the noise and the smell of the colonies (Kofron 2001).

P. conspicillatus camps, and particularly their flyouts, are impressive and are included in wildlife tours, foreign education programs and as a must see for some independent ecotourists to the region (Westcott & Dennis, pers. obs.).

3.9.3 Traditional uses

Pteropus are known to have been important culturally and as a resource in some Aboriginal cultures. They are currently eaten in other parts of Australia (Tidemann & Vardon 1999). The time limits imposed on us have meant that we have not discussed the cultural or resource significance of *P. conspicillatus* with the Traditional Owners in the WTWHA. This is a gap that should be filled.

3.9.4 Orchard pests

Pteropus have long been considered as orchard pests in Australia and there is a long history of vigorous and imaginative approaches to protecting crops from their activities (Anonymous 1890; Anonymous 1987; Tidemann & Vardon 1997). The cost of such depredation varies both regionally and in relation to the type of crop (Tidemann et al. 1997). Crop damage by *P. conspicillatus* has been reported from many commercial fruit

crops grown within its range (Kofron 2001). Growers currently use a range of both non-lethal and lethal control methods to protect their crops. No method has yet been developed that satisfies all growers or appears cost effective in all cases. Rigden et al. (2000), who report on grower experiences with different forms crop protection, conclude that non-lethal methods can be highly effective.

Assessment of existing data

There is good evidence that *P. conspicillatus* damages a wide range of fruit crops but there has been no independent quantification of any aspect of *P. conspicillatus* damage in fruit orchards.

3.10 THREATS AND CONSERVATION.

3.10.1 Habitat clearing

While reliant on rainforest, the exact habitat requirements of *P. conspicillatus* are unknown. The inclusion of non-rainforest species in the diet suggest that habitats adjacent to rainforest, e.g. some eucalypt and melaleuca woodlands and mangroves, are important to this species (H. Spencer, pers. comm. 2001). The extent and timing of clearing has varied across the Wet Tropics region both geographically and with different vegetation types (Winter et al. 1987; Collins 1994; Garnett et al. 1999; Figure 3, Hilbert, unpubl. data). In some habitats, particularly those on the richer and most productive soils, levels of clearing have been extremely high (Garnett et al. 1999). While clearing must have reduced, and to a decreasing extent continues to reduce, the carrying capacity of the region for *P. conspicillatus* it is impossible to estimate the extent of this effect from the data at hand.

The extent to which commercial orchards have replaced lost rainforest resources is unknown (Garnett et al. 1999). However, it is not likely to be significant as exotic tropical fruits tend to ripen during the peak in native fruit availability, whereas it is the loss of resources during a bottleneck that is important to maintaining population size.

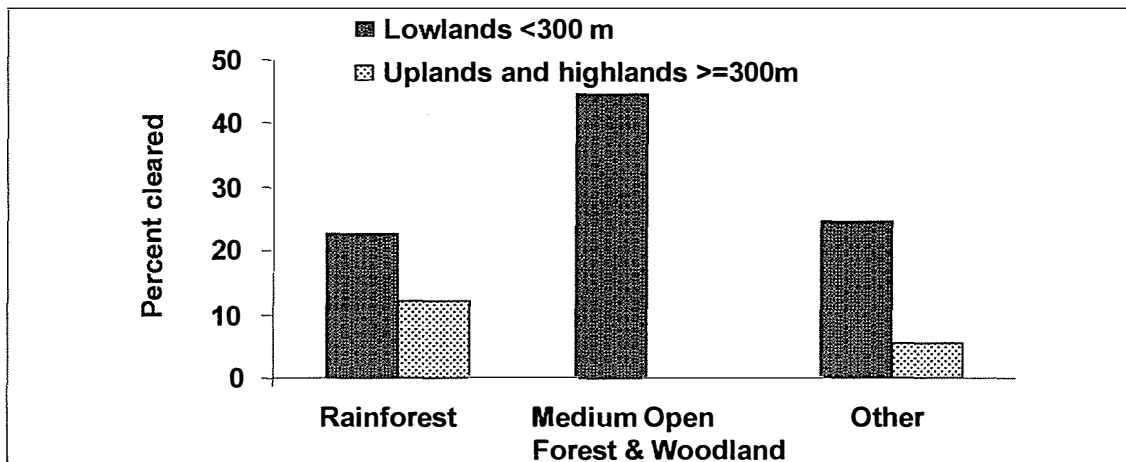


Figure 3. Estimates of the percentages of forest types that have been cleared in the humid tropics of North Queensland (D. Hilbert, unpubl. data). Rainforest includes all closed forests with vines. Medium Open Forest and Woodland are a sclerophyll type often dominated by paperbarks (*Melaleuca* spp.), especially in the lowlands. "Other" refers to a variety of sclerophyll forests and woodlands as well as coastal complexes that are a fine grained mosaic of rainforest and sclerophyll types. The range of species recorded in *P. conspicillatus*' diet suggests that all of these forest types are likely to be used by the species. The potential distributions of forest types in areas that are now cleared were predicted using an artificial neural network model (Hilbert and van den Muyzenberg 1999). The areas of these modelled distributions were added to the present extent of forests according to the vegetation mapping of Tracey and Webb (1975) to estimate the total pre-settlement areas for each forest class. Tests with independent, fine-scale mapping of forest fragments in the Atherton Tableland indicate that the modelling is highly accurate (c. 85% accuracy at a one hectare resolution) for the uplands and highlands. Qualitative assessments for the coastal lowlands suggest that the model may underestimate the original extent of rainforest while overestimating Medium and Open Forest and Woodland.

3.10.2 Paralysis Ticks

P. conspicillatus show little resistance to the toxin of the paralysis tick *Ixodes holocyclus* and can be paralysed before the tick is fully distended (Eggert 1994). Paralysed bats fall to the ground and can die from the effects of the venom, from fly strike, or vertebrate predation (Spencer et al. 1992; Eggert 1994; Garnett et al. 1999). With appropriate treatment many will survive (Johnson 1994; J. Maclean, pers. comm. 2001) and juveniles so treated can subsequently survive to maturity after release (Williamson 1995) suggesting that recovery is complete. An estimate of the proportion of animals that become victims of paralysis ticks was 6% at Zillie Falls (Eggert 1994). Elsewhere on the Atherton Tableland, and in different years, estimates vary below and above this figure (J. Maclean pers. comm. 2001). At lower altitudes and in some Tableland colonies, tick attack appears to be rare

(Eggert 1994). With the absence of reports of *P. conspicillatus* falling victim to ticks prior to 1986 it has been suggested that this is a recent phenomenon associated with a change in diet to include the weed wild tobacco, *Solanum mauritanium* (Spencer et al. 1992), an hypothesis that was supported by Eggert's (1994) comparison of diet data from the early 1980s (Richards 1990 a) with those of the early 1990s.

3.10.3 Control in Orchards

While non-lethal methods of flying fox control in orchards are available (Hall & Richards 1987; Fleming & Robinson 1987; Leu 1993, 1994; Turner 1994; Tidemann & Vardon 1997) their cost and/or in some cases, limited effectiveness (Anonymous 1987; Rigden 2000), means that many growers still rely to some extent on lethal methods to protect their crops from *P. conspicillatus*. The most common lethal methods used are shooting and electrocution (McHold & Spencer 1998). Both methods require a Damage Mitigation Permit. Between 1996 and 2000 between 11-13 growers used permitted electric grids to protect their crops while in 2000 some 46 growers in total held Damage Mitigation Permits allowing them to kill flying foxes (Kofron 2001).

A reliable figure for the number of *P. conspicillatus* killed by orchardists is impossible to determine from the available data. In 2000 growers held 46 Damage Mitigation Permits authorising the destruction of 5 071 *P. conspicillatus*, a figure representing 6.3% of the estimated population in November of that year (data in Kofron 2001). However, the events leading to the current action before the Federal Court indicate that some growers kill *P. conspicillatus* without permits and that some exceed their permits (Booth 2000). The data presented by Booth (2000), e.g. that 73 *P. conspicillatus* killed on 800 m of grid on the 23rd of November, suggest that the real numbers will be very much higher than those estimated by the Queensland Parks and Wildlife Service (Kofron 2001). Some growers may also claim to have killed more individuals than they actually did so as to preserve their ability to do so in the future (Garnett et al. 1999). Booth's (2000) data suggests that unlicensed killings will be much greater than under reported killings.

3.10.4 Camp disturbance and destruction

Attempts to reduce the number of pest bats and/or the annoyance of colonies have often resulted in camp disturbance or destruction. Mortality can occur as a direct result of the methods used to disturb the camp, eg through shooting (Pierson 1984). It is thought also to occur indirectly, through the death of juveniles after disturbance of maternity camps (Garnett et al. 1999). Both Clague et al. (2000) and Spencer (2001) report high levels of camp abandonment in the last two decades, in many cases in response to disturbance or destruction of camps. These authors presented no data on mortality associated with these instances of disturbance. However, some instances did involve the destruction of animals (H. Spencer, pers. comm. 2001). B. Thompson (pers.comm. 2001) has collated records of six camps where camp destruction focused on the killing of the bats rather than the destruction of the camp site.

3.10.5 Hunting and Traditional Use

Pteropus are hunted for food throughout most of their range (Mickleburgh et al. 1992), including in parts of Australia (Tidemann & Vardon 1997; B. Law pers. comm. 2001). No such use of *P. conspicillatus* is currently known within the Wet Tropics region (Garnett et al. 1999; Kofron 2001). Some shooting for entertainment may occur.

3.10.6 Competition

It has been suggested that competition with *P. alecto*, particularly in woodland areas in the southern part of the range, may be contributing to a reduction in the southern range of *P. conspicillatus* (Garnett et al. 1999).

3.10.7 Powerlines and barbed-wire fences

Deaths of *P. conspicillatus* through electrocution on powerlines and collisions with barbed-wire fences appear to be common (Garnett et al. 1999). Unfortunately, the numbers dying in this manner are unknown.

3.10.8 Cyclones

Pteropus conspicillatus are reported to move out of the path of cyclones. Following cyclones they split into small groups and move to areas where the foliage and food supply has not been badly affected (Richards 1990a). On Pacific islands, cyclones have been shown to impact heavily on the local *Pteropus* population, both through initial mortality, and due to an increase in hunting and a decrease in food availability (Pierson & Rainey 1992; Grant et al. 1997; Brooke et al. 2000).

Assessment of existing data

There is little doubt that these threats all continue to impact on *P. conspicillatus* populations. In almost all cases there is still insufficient data to allow the quantification of this impact.

The extent of habitat loss is well documented but the impact of this loss on *P. conspicillatus* is not. In addition, the relative impact of the differential loss of forests on productive soils and at certain altitudes has not been examined. While orchards and suburban fruit trees may compensate for lost habitat to some extent, they are unlikely to match the seasonality and abundance of native fruits. Orchards are also a source of mortality.

While deaths from paralysis ticks, control at orchards, disturbance at colonies and powerlines and barbed-wire fences are all causes of mortality, none have been measured with sufficient accuracy for a confident prediction of their effects on population size to be made. The latter four factors are clearly of recent origin and constitute additional, non-natural mortality factors that could contribute to a decline in population size. Deaths from paralysis ticks may also be recent and non-natural.

3.11 POPULATION SIZES AND TRENDS

Historical population sizes are difficult to determine for several reasons. First, while many residents remember large fly-outs, few noted the species involved. Indeed, even Francis Ratcliffe's writings are vague on the subject (Ratcliffe 1932). He reported several very large *Pteropus* camps on the Atherton Tablelands without identifying which species were involved. In addition, he writes "The evidence collected indicated that the three larger species, *Pt. poliocephalus*, *gouldi*, and *conspicillatus*, do not of themselves form really large camps as frequently as reports would lead one to believe. When a well known camp of one or other of these species has been reported to attain unusual size, enquiries often discovered the fact that *Pt. scapulatus* was present as well." (Ratcliffe 1932, 47). Elsewhere Ratcliffe reported that *P. conspicillatus* camps were uncommon and required much time to find (Garnett et al. 1999; S. Garnett pers. comm. 2001). Similarly, Harrison

(1962) considered *P. conspicillatus* camps to be small and scattered through the rainforest. Although, camp abandonment is considered to have been severe in recent decades (Spencer 2001; Clague et al. 2000), there is no data on the natural extent of camp abandonment with which to compare this, particularly during the century or so during which camp disturbance was uncontrolled.

The abandonment of camps has been inferred to indicate massive population declines in *P. conspicillatus*. For example, according to Clague et al. (2000), a loss of “15 permanent camps with a total population of 610 000 bats in the last 15 years... This indicates an approx 78% population decline in just 15 years...” Data provided by Clague et al. (2000) and Spencer (2001) indicate the loss of large numbers of camps, many following destruction of habitat. Neither of these authors recorded the formation of similar numbers of new camps, although elsewhere, Whybird (unpubl.) reports that more camp sites are located each year during censuses. Considered alone, the loss of these camps may indicate a population decline but can neither confirm nor quantify a decline for the following reasons. First, while data is presented on the loss of camps, no data is presented on the fate of the animals, some or all of which could have relocated at the time of camp abandonment. In addition, estimating total population size from camp size estimates assumes that all camps were occupied and counted simultaneously. Given that the population estimates supplied are assigned to decades, this is not likely to be the case.

Since 1998 there has been a concerted effort to systematically estimate the population size of *P. conspicillatus* in the Wet Tropics based on fly-out counts (Garnett et al. unpubl. a; Garnett et al. unpubl. b; Whybird and Garnett unpubl; Garnett and Whybird unpubl.; Whybird unpubl.). To the extent possible these counts are performed using accepted methodologies (explained in Garnett et al. 1999). The results over the last three years provided estimates for the camps counted of 113 960 (\pm 14 100) in November 1998, 74 400 (\pm 8 650) November 1999, and 79 980 (\pm 9 045) in November 2000 (Whybird unpubl.). Again, these results have been interpreted in some quarters as indicating a population decline. The accuracy of the counts has been severely criticised in others, particularly by fruit growers, and strong qualifications were put on the count data by its authors (Garnett et al. 1999).

The major criticisms of the counts fall into two main areas. The first is over the ability of counters to count accurately. Factors influencing the accuracy of the counts at individual

camps include: i) the effect of environmental conditions on counter's abilities to detect bats, ii) the capacity to estimate bat numbers particularly at times of heavy flow, iii) variation within and between individuals in counter accuracy, iv) the recording of only a single count for each exit stream, v) the necessity to sometimes use single counts rather than averages over several nights (Garnett et al. 1999; Garnett, 2001; R. Sing, pers comm., 2000). While all these factors can, and no doubt do, influence the accuracy of counts at each camp the errors, i) might be expected to fall on both sides of the actual figure (Garnett 2001), ii) are unlikely to be out by more than an order of magnitude (Garnett et al. 1999; Garnett 2001), and, iii) are likely to be similar to those estimated in counts of other species. Observer error was approximately 10% for counts of *P. poliocephalus* (Eby et al. 1999) and *P. alecto* (Tidemann & Vardon 2001). The errors discussed here are acceptable and within the range required to detect population trends.

The second and most serious area of concern centres around the question of whether the same population is actually counted. There are several issues here. First, while every attempt is made to identify all camps in the region, large areas of the WTWHA are not searched and some areas with known camps were not counted (Garnett et al. 1999; Garnett pers. comm. 2001). Second, even large camps can be missed. For example, a camp in the southern end of the range was overlooked during the November 2000 counts and more camps are being found and counted each year (Whybird unpubl.). Over looking camps will be more likely in the many parts of the species range which are remote and difficult to access. This is a problem if the proportion of the population in these "unknown" or uncounted camps varies significantly between counts. The propensity of *Pteropus* in general (Nelson 1965a; Eby 1991; Martin 1987; Tidemann et al. 1999; Palmer 1999; Parry-Jones & Augee 1992) and *P. conspicillatus* in particular (Table 1; Westcott & Dennis, unpubl. telemetry data) to change camps and exhibit high levels of mobility suggests that variation in counts could stem from movements to and from uncounted camps. The high levels of night-to-night variance in exit counts also suggest this (see Tidemann and Vardon 2001; Garnett et al. unpubl.; Garnett and Whybird unpubl.). The potential for moving to uncensused areas and the species mobility between camps make it difficult to assume that the same proportion of the population is being counted and therefore any interpretation of limited numbers of counts uncertain. This could mask a serious decline or suggest a decline when one is not occurring. These issues mean that the small number of counts available at present cannot be interpreted with regards to population trends.

However, over a longer period, counts could be expected to both over and under-estimate the population so any consistent population trend can be considered a good indication of the actual population trend.

Population models developed by Martin & McIlwee (2001) suggest that *P. conspicillatus* populations will begin to decline when annual mortality is greater than 20% and fecundity 40% and lower. There is no data on annual mortality and recruitment rates for *P. conspicillatus* to determine where the population currently sits in relation to these models. The levels of mortality associated with one farm's electrocution grids reported by Booth (2000) are extremely high, eg. 73 dead bats were sighted on one part of the farm on November 23rd after the lines were cleared on the evening of the 22nd. If this is general across the farm, season and wet tropics, then such mortality must have the potential to push the population into decline.

Assessment of existing data

An historical decline can be inferred from the loss of habitat and resources. The data presented however are not adequate to estimate the magnitude of the decline.

Count data probably provides a relatively good estimate of the combined population sizes of the camps counted. Whether it is sufficiently precise to show a decline of between 35 000 – 40 000 animals is unlikely due to sampling errors in the counting of fly-outs at camps, the counting of all camps, and the mobility of the animals. It is common in cases where counts are known to involve error, to use the data to indicate population trends rather than actual sizes. In this case, the uncertainty in determining whether the same population is being counted and the fact that only three years of count data are at hand make this inappropriate. The count data probably reflect the approximate population size of the camps counted but what is counted is not necessarily the same proportion of the entire population across counts. The counts need to be continued and extended and a method of detecting all camps needs to be developed to improve confidence in interpretation of count results.

The limited mortality data from one orchard, when considered with the population model suggest that such control measures have the potential to significantly impact on populations and could drive a decline. The modeling effort needs to be extended to include scenarios that represent the range of population parameters reported in the literature for this and other species. Varying sex ratios and age at first breeding as well as fecundity and survival rates will give a broader picture of the sensitivity of the species to different levels of mortality. More importantly, actual data on the population parameters needed to model population trends for this species should be collected from the wild.

4 SUMMARY OF DATA LIMITATIONS ON KNOWLEDGE OF THE ECOLOGY AND BEHAVIOUR OF *PTEROPUS CONSPICILLATUS*.

Pteropus conspicillatus has been the subject of surprisingly few direct studies. These have focused on distribution and gross features of camp site selection (Richards 1990 b), diet and seed dispersal (Richards 1990 a; Westcott & Dennis, unpubl. data), movement (Westcott & Dennis, unpubl. data), population estimation and status (Garnett et al. 1999) and general natural history in New Guinea (Bonaccorso 1998). The empirical data from the published works appear reliable and the conclusions reasonable given these data. In general any limitations stem from the extent rather than the quality of data. The unpublished data of Westcott & Dennis presented here are the results to date of ongoing research. We cannot guarantee that subsequent data collected will closely reflect those described here. These data are presented because they substantially support or clarify questions and issues raised in this review.

Much of the data available come from unstructured observations. Much of these data are excellent. Some, however, have been collected in a manner that makes their interpretation difficult. Unfortunately, some of the issues of greatest interest in the ongoing debate over the management of this species fall into this category, e.g. historical declines. These declines are likely to be real, at least in part, but the data are inadequate to rule out alternative explanations or indicate the size of the decline. Similarly, many of the basic life history parameter estimates used in population modelling are based on extremely limited observation or derived primarily from other species and captive studies. While we can and should, in the absence of specific data, use data from related species, we cannot be completely confident about the conclusions drawn from them but can use them to illustrate the likely range of outcomes for the species in question. Finally, although threats such as habitat clearing are well documented, and must have had an impact on the population size, the consequences of this threat are not documented.

Our review of the knowledge of *P. conspicillatus* has identified a real lack of direct information on the species. To some extent this information gap has been covered through the use of unstructured observational data and data derived from other species. While this approach has sufficed to date, the need for appropriate and defensible management decisions requires a more rigorous approach.

We suggest a number of areas that should be marked for immediate investigation:

- Count methodology – counts will remain the only means of monitoring population trends, if not actual sizes, in censused areas.
- Camp documentation – identifying the number and location of uncensused camps and how these vary in time will be key to estimating actual population sizes. In an area such as the WHWTA this can be achieved through the development of appropriate remote sensing methods.
- Landscape use – fundamental to understanding how *P. conspicillatus* use and respond to resource availability and distribution, to understanding the reliance of *P. conspicillatus* on different vegetation types including orchards, to determining extent and timing of movements to uncensused camps.
- Ecology and Behaviour – increasingly the management debate will focus on basic population parameters. Given the current data this will be a relatively barren debate, strenuous efforts should instead be directed to actually measuring these parameters. Movement and sex ratio data to hand suggest that there are complex ecological and social forces determining the spatial and temporal distribution of animals and their camp use. Importantly, it appears that females and males may be responding to different pressures.
- Orchards – under what ecological circumstances are orchards used, what are the costs associated with orchard use and what is the pattern of damage across the region.
- Impact of threats – an independent assessment of mortality associated with the various threats. Any assessment of the impacts of culling should be done as a collaboration with growers.

4.1 SUMMARY POINTS WITH A HIGH DEGREE OF CERTAINTY

Introduction

- Fruit bats, including *Pteropus*, are pollinators of many tropical forest trees and disperse seeds within rainforests and from rainforest into other habitats
- *Pteropus* species are considered agricultural pests throughout their range

Origins and taxonomy

- *Pteropus conspicillatus* is a distinct species but whether Australian animals represent a distinct subspecies is uncertain

Distribution

- *Pteropus conspicillatus* occurs in Australia and New Guinea
- Current distribution of *P. conspicillatus* in Australia is associated with rainforest in the following two regions:
 - Ingham to Cooktown
 - Mcilwraith and Iron Range, Cape York
- Records of occurrence outside this distribution are rare

Habitat

- Rainforest is important habitat for *P. conspicillatus*
- Distribution of *P. conspicillatus* is limited to areas with rainforest coverage
- Known camps are all in rainforest or within 7 km of rainforest
- Dentition and tongue characteristics are consistent with a rainforest fruit specialist
- *P. conspicillatus* feeds and camps in both rainforest and surrounding vegetation types and on agricultural lands

Movement patterns

Pteropus species

- Foraging range of three *Pteropus* species is up to 40 km from camps
- Both seasonal and large changes in camp size have been observed for *Pteropus* species due to intercamp movement

Pteropus conspicillatus

- Camp occupation by *P. conspicillatus* varies temporally
- *Pteropus conspicillatus* exhibits seasonal disappearances from some areas
- Inter-camp movements of *P. conspicillatus* also occur throughout the year and are neither regular or predictable
- Abandoned camps may be subsequently reoccupied
- Changes in camp occupancy of *P. conspicillatus* may vary by up to several orders of magnitude
- In a period of 48 days and less, five *P. conspicillatus* individuals used 2-4 camps, these camps had an average inter-camp distances of 39 km..

Camp characteristics

- A single camp of *P. conspicillatus* may include up to tens of thousands of individuals
- Not all *Pteropus* individuals within a camp are necessarily conspecific
- *P. conspicillatus* camps occur in a range of vegetation types [rainforest, sclerophyll, riverine, wetland, mangrove]
- Dense vegetation types are the most common camp habitat

- The climatic characteristics of known campsites are widespread and not likely to be limiting within the Wet Tropics

Life History characteristics

- The annual birth peak occurs between October and December
- Timing of the annual birth peak is stable between years
- Reproductive females produce one pup per year

Diet

- All *Pteropus* species feed on nectar, flowers and fruit
- Dietary specialisation varies between *Pteropus* species
- *Pteropus conspicillatus* diet is biased towards fruit, but includes flowers and leaves
- Limited available data on components of *P. conspicillatus* diet includes:
 - Fruits (48 native species - mostly rainforest, 12 exotic species)
 - Flowers (18 native species - including 4 sclerophyll species)
 - Foliage (1 native species)

Ecology

Seed dispersal

- *Pteropus Conspicillatus* disperses seeds
- 2 modes of seed dispersal have been recorded
 - Ingested and eventually excreted seeds all of which are small
 - Carried seeds (all sizes)
- Seed dispersal distances may range from metres to tens of kilometres
- Dispersal distances will depend on the mode of seed dispersal
- *Pteropus conspicillatus* can disperse fruit and seeds of all sizes (only three other animals can do this)

Pollination

- *Pteropus* generally are recognised as pollinators throughout their range
- *Pteropus conspicillatus* feeds on flowers

Threats and conservation

Human induced threats include:

- Significant habitat loss (particularly on productive soils), which has occurred in the past and continues at a slower rate
- Control at fruit orchards, currently poorly quantified
- Camp disturbance or destruction, which are ongoing
- Collisions with power lines and barbed wire fences, currently unquantified

- Tick paralysis, causes high levels of mortality on the Atherton Tableland and is likely to be human induced

Population dynamics

- A historical decline can be inferred from loss of habitat but its magnitude cannot
- Recent population size estimates (based on fly-out counts over 3 years) include
 - 1998 114 000 (± 14 000)
 - 1999 74 000 (± 9 000)
 - 2000 80 000 (±9 000)
- Interpretation of population trends from this data is confounded by the uncertainty associated with the proportion of the population being counted. This uncertainty is derived from the:
 - High mobility of *P. conspicillatus*
 - High variability in camp occupancy and use and the current ability to detect all camps
 - These problems could equally mask a serious decline or suggest a decline when one is not occurring

4.2 SUMMARY POINTS WITH A MODERATE LEVEL OF CERTAINTY FOR *P. CONSPICILLATUS*

Distribution

- Extent of occurrence may vary from year to year

Movement patterns

- Foraging movement patterns of *P. conspicillatus* are similar to other *Pteropus* species
- Change in *P. conspicillatus* camp size is often due to movement between camps
- Movement between camps may be driven by responses to food availability

Life History characteristics

- Birth sex ratio is 1:1
- Adult sex ratio is likely to be female biased
- Females are likely to begin successful reproduction at the age of 24 months
- *Pteropus conspicillatus* is likely to have a potential rate of increase below 25%

Ecology

Nutrients

- Camps may result in localised concentrations of high nutrient levels

Pollination

- Flower feeding implies a role in pollination

Threats and conservation

- Mortality from paralysis tick is novel
- Current levels of mortality at fruit orchards have the potential to impact on the population
- The combined novel mortality agents affecting *P. conspicillatus* could contribute to a decline in population size

Population dynamics

- Continuing population counts can provide a measure of population trends
- Mortality of greater than 20% can cause a population decline

5 SPECTACLED FLYING-FOXES AND WORLD HERITAGE VALUES

5.1 WORLD HERITAGE CONVENTION AND THE WET TROPICS

The Convention Concerning the Protection of the World Cultural and Natural Heritage (UNESCO 1972), generally referred to as the World Heritage Convention (hereafter the Convention), forms the basis for listing of places of significant global heritage by the World Heritage Commission of UNESCO. While the Convention recognises both cultural and natural heritage, the WTWHA is currently listed in recognition of its natural heritage only.

The Convention (Article 2, UNESCO 1972) defines Natural Heritage as follows:

“natural features consisting of physical and biological formations or groups of such formations, which are of outstanding universal value from the aesthetic or scientific point of view;

geological and physiographical formations and precisely delineated areas which constitute the habitat of threatened species of animals and plants of outstanding universal value from the point of view of science or conservation;

natural sites or precisely delineated natural areas of outstanding universal value from the point of view of science, conservation or natural beauty.”

Thus, listing under the Convention is limited to land or places rather than to moveable or temporal entities such as species. This means that application of the Convention to particular species can only be achieved via the species' habitat. Hitchcock (2001) reports that while he could identify no World Heritage Area as having been established entirely for the protection of a particular species, flagship species had been the focus of some nominations, e.g. the Komodo dragon (Komodo National WHA in Indonesia), the Okapi (Okapi Wildlife Reserve WHA in Democratic Republic of Congo), Arabian Oryx (Arabian Oryx Sanctuary WHA in Oman) and Wood Buffalo (Wood Buffalo National Park WHA in Canada). Similarly, a single species of plant appears to have been the primary interest in establishment of the very small Vallée de Mai Nature Reserve WHA in the Séychelles.

In the case of the WTWHA listing was achieved against all four criteria for natural heritage (Australian Government, 1987) specified in the Convention's Operational Guidelines (UNESCO 1997). These four criteria are:

- i) outstanding examples representing the major stages of the earth's evolutionary history
- ii) outstanding examples representing significant ongoing geological processes, biological evolution and man's interaction with his natural environment
- iii) contain unique, rare or superlative natural phenomena, formations or features of exceptional natural beauty
- iv) contain the most important and significant habitats where threatened species of plants and animals of outstanding universal value from the point of view of science and conservation still survive.

The specific values used in the initial listing are included in Appendix B.

The status of *P. conspicillatus* in the context of the World Heritage values of the WTWHA must be assessed in two arenas: i) its contribution as a species to the four recognised World Heritage criteria, and ii) its interaction and involvement in ecological processes from which the WTWHA's World Heritage values are derived and sustained.

5.2 CONTRIBUTIONS AS A SPECIES TO WORLD HERITAGE VALUES

Criterion (i) - major stages in the earth's evolutionary history

The mixing of the continental biota of the Australian and Asian continental plates;

The apparently recent arrival of Megachiropterans in Australia is indicated by their centre of radiation occurring outside Australia and the absence of fossil data on the continent (Hall & Richards 2000). Thus *P. conspicillatus* contributes to the World Heritage values of the WTWHA under Criterion 1 as one of the bat species whose entry into Australia illustrates the faunal exchange since connections with the Asian Plate were established. In addition, their role in seed dispersal means that they were probably important in the initial spread of Asian plant species to the Australian continental plate.

Criterion (ii) – outstanding examples representing ongoing...biological evolution...;

Pteropus conspicillatus represents one unit in the overall mammal diversity of the region.

Criterion (iii) contain unique, rare or superlative natural phenomena...;

While not listed as a World Heritage value in the original listing, *P. conspicillatus* fly-outs can be spectacular natural phenomenon and are often included in wildlife tours.

Criterion (iv) - contain the most important and significant habitats where threatened species of plants and animals ... survive.

Pteropus conspicillatus represents a unit of the WTWHA biological diversity and would represent one of the WTWHA's values under the Environment Australia's (2001) phrasing of Criterion (iv).

5.3 CONTRIBUTIONS TO WORLD HERITAGE VALUES THROUGH PARTICIPATION IN ECOLOGICAL PROCESSES.

Pteropus conspicillatus exists as a component of forest ecosystems and their processes. In such roles it also has the potential to contribute to the World Heritage values of the WTWHA. Seed and pollen dispersal are important processes in the life history of plants, and are widely believed to be important in structuring plant populations and communities, including rainforests, and in ongoing biological evolution. Before discussing the specific role of spectacled flying-foxes in the process of seed and pollen dispersal in tropical rainforests it is important to clarify whether or not seed and pollen dispersal is important in maintaining and sustaining the types of values that led to the World Heritage listing, including maintaining and promoting species richness and maintaining and structuring plant populations and influencing their distributions.

5.3.1 Seed dispersal as a determinant of the distribution of species and vegetation types.

For fleshy-fruited plants, dispersal away from the parent plant is generally achieved through the agency of an animal disperser. To the extent that a disperser crosses the plant species distributional boundaries it can alter the range of that plant species. This can lead to range expansion when conditions are appropriate for germination and survival. The history of vegetation distributions in the Wet Tropics region over the last 18 000 years is

one of repeated, climate driven expansions and contractions of rainforest and associated vegetation types (Hopkins *et al.* 1990; Nix and Switzer 1991; Hilbert *et al.* 2000). The process of rainforest expansion into adjacent sclerophyll forests is one that continues today (Harrington and Sanderson 1994). *Pteropus conspicillatus*' habit of moving across vegetation boundaries, and in particular foraging in both rainforest and associated vegetation types (see above) suggests that it has the potential to play an important role in this process, albeit an as yet unquantified one.

Numerous studies have also examined the importance to plants of dispersing into suitable sites for germination and growth. Many plant species require soil, light and/or moisture conditions to be within an acceptable range for germination and recruitment, and, within that range, some conditions promote greater vigour than others (Augspurger 1983; Augspurger and Kelly 1984; Dirzo and Dominguez 1986; Howe and Schupp 1985; Osunkoya *et al.* 1993; Osunkoya 1994; Sork 1987). These conditions are often unpredictable in space and time (Herrera 1985) making it important for plants to have their propagules widely dispersed to increase the chance of placing a seed in an appropriate site for establishment. Here again seed dispersal plays an important role in maintaining diversity by assisting species to find appropriate microsites in space and time.

Disturbance has also been demonstrated to be an important factor in the dynamics of rainforests (see Connell 1979). It occurs at a range of intensities and extents from isolated treefall gaps to widespread storm damage and is particularly important to pioneer species with light controlled dormancy (e.g. Hopkins *et al.* 1990; Hopkins and Graham 1987; Vazquez-Yanes and Orosco-Segovia 1986). Like suitable microsites, disturbance is often patchy in space and time and requires the widespread dispersal of seeds for a species to take advantage of opportunities. Studies demonstrated the seed shadows created by bats are temporally, spatially and numerically important in the recolonisation of a wide range of disturbances including, strip cut forests (Gorchov *et al.* 1993), the colonisation of recently formed river bends (Foster *et al.* 1986), in recolonising pasture in the Neotropics (Medellin & Gaona 1999) and after volcanic eruptions (Whittaker & Jones 1994).

5.3.2 Is seed dispersal important to the maintenance of rainforests plant diversity?

Much international literature examines various aspects of seed dispersal and how this process contributes to the maintenance of diversity and spatial heterogeneity in tropical

rainforest plants. The available data demonstrate that seed dispersal processes do contribute to the maintenance of plant diversity through several generalised functions. The following very brief discussion outlines some of the ways that seed dispersal contributes to the maintenance of tropical plant diversity. It is important to keep in mind that 70 to 95% of rainforest trees are animal dispersed (Dennis 1997 and references therein).

Janzen (1970) and Connell (1971) describe a process by which seed dispersal allows propagules to escape distance and density-dependent mortality beneath parent plants. Dispersal away from such effects gives dispersed seeds a higher probability of survival than non-dispersed seeds. This process has been demonstrated to occur for numerous rainforest plants throughout the world, including in Australia (Dennis 1997, references in table 1.2). For other species the process has been demonstrated not to be important (Dennis 1997 references in table 1.3). Decreased survival close to the parental tree increases the probability of allospecific establishment under the parental tree and should lead to increased diversity.

Hubbell (2000) has recently demonstrated that the probability of an individual rainforest tree's survival is linked to that of its neighbours. This neighbourhood effect occurs because of the contagion associated with many sources of mortality. If a tree becomes diseased or is attacked by herbivores its neighbours are far more likely to fall victim to the same fate. Similarly, it is immediate neighbours that are most likely to be damaged or killed by the fall of a tree. Thus while an adult tree cannot escape its neighbours in space, dispersal allows its offspring to escape it in time by being removed by dispersers.

Finally, vertebrates acting as seed dispersers do not distribute seed evenly across the available habitat (Wenny & Levey 1998; Harms et al. 2000). The failure of seeds to arrive at potential recruitment sites is termed recruitment limitation and may arise for a variety of reasons including non-random movement of dispersers within a habitat (Wenny & Levey 1998; Wenny 2001). Non-random arrival of seeds at any given location results in an increase in the number of competitive environments available given a set number of co-existing species (Harms et al. 2000) and this in turn translates into an increase in diversity through an increase in the range of competitive environments available in a habitat (Muller-Landau et al. 2000; Nathan & Muller-Landau 2000).

5.3.3 Population genetic consequences of Seed and Pollen dispersal.

Both seed and pollen dispersal influence the spatial arrangements of plant genotypes in relation to each other. For both seed and pollen dispersal it is expected that an increase in dispersal distance should result in a decrease in the relatedness of neighbours resulting in a decrease in population structuring and an increase in heterozygosity. These predictions have been met for both seed dispersal (Hamrick et al. 1993; Loiselle et al. 1995) and for pollen dispersal (Nason et al 1998).

5.3.4 What is the role of Spectacled Flying-foxes in seed dispersal and pollination in Australia

The evidence that *P. conspicillatus* is a seed disperser in the WTWHA is clear and unequivocal (see above). However, opinion varies as to its importance in this role. Richards (1990 a) and others suggest that “Species of *Pteropus*, particularly *P. conspicillatus*, must therefore be considered as possibly being the only dispersal agent for many species of rainforest tree...” (Richards 1990 a, p30). On the other hand, Tidemann & Vardon (2001) suggest that levels of redundancy in terms of dispersal agents (41 species of bird and mammal are known to be seed dispersers, Westcott & Dennis unpubl. data) are likely to be adequate to compensate for the absence of *P. conspicillatus*. The issues here are i) the nature of seed dispersal provided by *P. conspicillatus*, ii) whether there are additional dispersers and their relative contributions to dispersal, and, iii) whether *P. conspicillatus*' food plants are intrinsic to the World Heritage values of the WTWHA. What must remain clear here is that just because multiple species are dispersing the propagules of a plant does not mean that all but one are redundant. Their effects are additive and it may only take a proportional loss of dispersal services to affect the outcome of the dispersal process.

The dispersal service provided by *P. conspicillatus* falls into two distinct modes (Richards 1990a; Hall & Richards 2000). Small seeds may be swallowed incidentally along with fruit juice and pulp and dispersed internally. The distances involved in this mode of dispersal are potentially large, on the order of tens of kilometres (Shilton et al. 1998; Westcott & Dennis, unpubl. data). Given that *P. conspicillatus* forages and moves across landscape boundaries dispersal for these seeds will potentially occur in between patches and into uncolonised habitat. The second mode of dispersal, involving large fruits and

seeds, is through external carriage and occurs when individuals are displaced during intraspecific encounters (Richards 1990a). In this mode of dispersal seeds are probably moved relatively short distances only, estimated at up to c. 100 m (Hall & Richards 2000). If so, then this mode of dispersal probably occurs most frequently within, rather than between patches, ie at a neighbourhood rather than a landscape scale.

Dispersal services provided by *P. conspicillatus* are not known to be provided by other *Pteropus* species. While *P. conspicillatus* is not the only *Pteropus* to forage in the rainforests of the WTWHA (H Spencer, pers. comm. 2001; J Winter, pers. comm. 2001), it appears to be the only species that commonly does so. Spotlighting observations of *Pteropus* foraging in rainforest are rarely recorded. John Winter (pers. comm. 2001) has 33 records of identified *Pteropus* species feeding in rainforest. Of these only one was of *P. alecto*, the remainder being *P. conspicillatus*. These data are in line with the impressions of other workers with extensive spotlighting experience (Whybird, pers. comm. 2001; A Dennis, pers. obs.). Thirty *Pteropus* observed feeding in *Melia azanderach* in April 2001 were all *P. conspicillatus* despite *P. alecto* being known to be camping nearby (Westcott & Dennis, unpubl. data).

Do other vertebrate dispersers provide the same service? The fruit of forty-eight plant species have been recorded from *P. conspicillatus*' diet. Additional dispersers are known for 39 of the 48 species (Figure 4, Westcott & Dennis, unpubl. data). Seven of the remaining nine species are figs and, given that such a wide range of species generally feed on figs (Nason et al 1998), are likely to have a variety of undetected dispersers. Plant species with fruits smaller than 25 mm can have as many as 13 dispersers, whereas larger fruits have only been recorded with a maximum of three dispersers. In general, within forest patches the dispersal service provided by *P. conspicillatus* to small seeded species is likely to be replicated by a variety of bird species such as fruit doves, *Ptilonopus spp.*, bowerbirds, Ptilonorhynchidae, and also the small megachiropterans. Landscape scale or long distance dispersal similar to that provided by *P. conspicillatus* to seeds ≤ 5 mm from fruits < 30 mm in diameter may also be provided by bird species such as the fruit pigeons, eg topknot pigeons, *Lopholaimus antarcticus*, and metallic starlings, *Aplonis metallica*, which also forage and move across landscape boundaries. However, there are no data on the movement patterns of these birds so the extent of overlap with *P. conspicillatus* in dispersal service is unknown. Generally, larger seeded plant species have a smaller suite

of dispersers comprised of the musky-rat kangaroo, *Hypsiprymnodon moschatus*, the southern cassowary, *Casuarius casuarius*, (Westcott & Dennis unpubl. data) and perhaps also the giant white-tailed rat, *Uromys caudimaculatus* (Theimer, 2001) as well as *P. conspicillatus*. Each of these four species provides slightly different deposition patterns with varying levels of clumping, scattering, and burial (Dennis 1997; Thiemer 2001; Moore 1991). Though unquantified and currently under investigation (Westcott & Dennis, work in progress) these observations suggest that while *P. conspicillatus* contributes to the dispersal of seeds from a local to a landscape scale, the service it provides is not necessarily unique. Currently identifiable exceptions to this conclusion will be those circumstances in which *C. casuarius* and *H. moschatus* are absent, such as in small and isolated fragments (Dennis 1997). A feeding *P. conspicillatus* displaced from a tree which moved with fruit into open habitat would also provide a unique rehabilitation or recolonisation service as these habitats are less likely to be visited by *C. casuarius* and *H. moschatus* (Richards 1990).

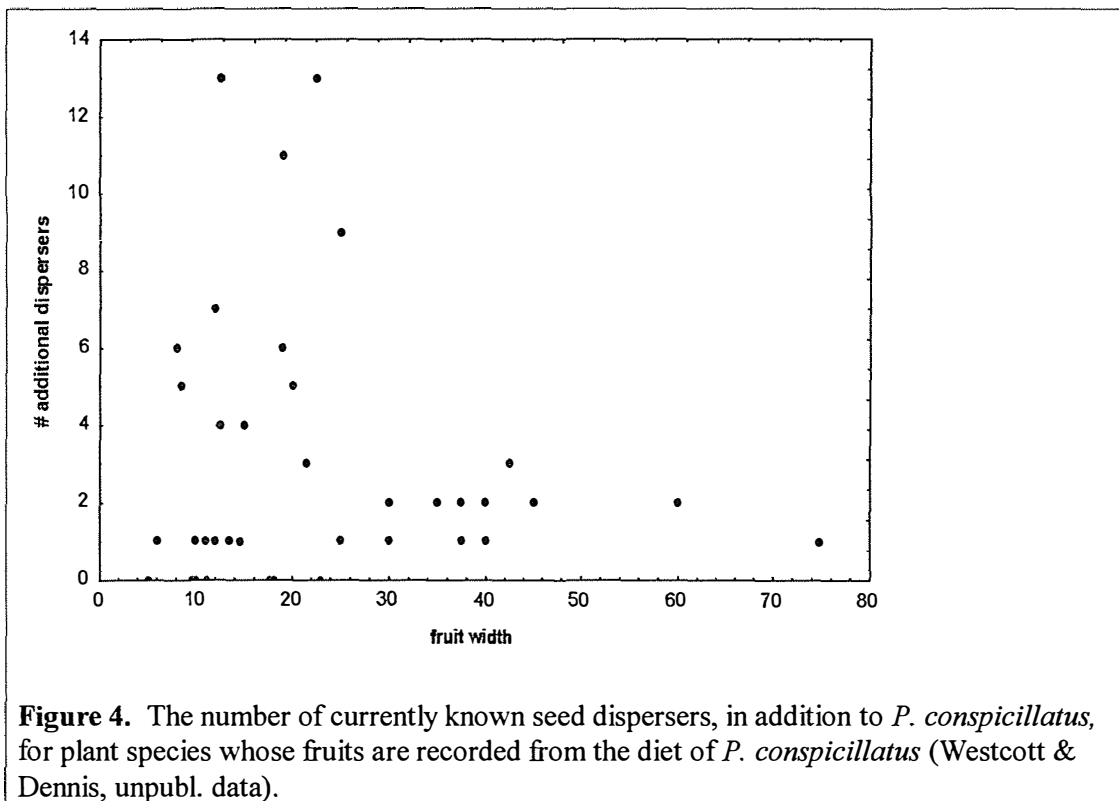


Figure 4. The number of currently known seed dispersers, in addition to *P. conspicillatus*, for plant species whose fruits are recorded from the diet of *P. conspicillatus* (Westcott & Dennis, unpubl. data).

In some contexts, *P. conspicillatus* appears to be abundant (Westcott & Dennis, unpubl. data), and the value of its contribution to ecosystem levels of dispersal may stem in large part from this abundance. At the same time, *P. conspicillatus* deposit relatively high proportions of handled seeds at the feeding site. In the case of small seeded fruits, some seeds will be spat out with the fibre, while the dispersal of large seeded fruits following displacement appears to occur rarely relative to the number of fruits handled (Richards 1990a; Hall & Richards 2000). Ultimately, however, it is the number of seeds dispersed, not the proportions that are important. At this stage, there are no data available to quantify this.

The role of *P. conspicillatus* in seed dispersal in the rainforests of the WTWHA suggests that it plays an as yet unquantified but potentially significant role in the maintenance of the plant biodiversity listed as one of the World Heritage values of the WTWHA under criterion (ii). Our limited foraging records indicate that *P. conspicillatus* feeds on the fruits of nine species for which no other disperser is currently known, as well as three plant families (Annonaceae, Myrtaceae, Rutaceae) and two genera (*Melia* and *Canthium*) listed as World Heritage values under criterion (i), and two genera (*Elaeocarpus* and *Planchonella*) listed as World heritage values under criterion (ii). In addition, *P. conspicillatus* has been recorded feeding on the fruit of one WTWHA plant species currently listed under the Qld. Nature Conservation Act, and therefore relevant to criterion (iv). Given the scant data on *P. conspicillatus*' diet it is reasonable to expect that these figures are preliminary only. The contribution that such feeding makes to the populations of the forage species is undocumented but are generally predicted to be positive.

Much less can be said about their role as pollinators in the World Heritage Area. Clearly, sclerophyll forest trees are an important resource for *P. conspicillatus* and the bats may well be important in the pollination of some of these trees. In addition, the fact that they fly from rainforest to forage in sclerophyll forests increases the chances that small seeds will be dispersed from one vegetation type to another. *Pteropus conspicillatus* may also have a role in the pollination of a number of rainforest plants (Jackes 2001; Weber in Werren 2001). As with their role in seed dispersal, pollination by *P. conspicillatus* may be most important for plants in small and/or isolated fragments. This will be particularly important for plants whose additional pollinators are invertebrates that do not fly readily between

fragments of forest. *Pteropus conspicillatus* has the potential to ensure widespread genetic mixing through pollination for some species.

Assessment of existing data

That *P. conspicillatus* is a seed disperser is clear and unequivocal. That it is a pollen disperser is reasonably inferred from observations of flower foraging and highly probable given data from other *Pteropus* (see section 3.8.4).

The roles of seed dispersal in the origin and maintenance of rainforest diversity and of seed and pollen dispersal in determining plant population genetic structure have long been postulated. There is a recent and growing body of empirical evidence validating these hypotheses. Such processes will influence the World Heritage values of the WTWHA at both the levels of rainforest diversity and of single plant species, genera and families listed as providing World Heritage values.

That *P. conspicillatus* contributes to these processes is clear, however, the relative contribution of *P. conspicillatus* remains to be quantified. There are both ecological contexts and some species for which the contribution is likely to be important.

6 THE LIKELY CONSEQUENCES OF THREATS TO *P. CONSPICILLATUS* ON THE WORLD HERITAGE VALUES OF THE WTWHA.

By their very nature threats to *P. conspicillatus* can be expected to impact on the species through a reduction in population size. This reduction may act directly on the species, or indirectly, e.g. through loss of habitat. Given the uncertainty associated with the role of *P. conspicillatus* in maintaining many of the World Heritage values of the WTWHA, identifying likely consequences of threats to the species can be done only with qualification.

The greatest certainty can be ascribed to the biodiversity and species richness contributions that *P. conspicillatus* makes to the World Heritage values. *Pteropus conspicillatus* contributes to these values of the WTWHA in this manner under Criterion (i), (ii), and (iii). Threats that result in significant declines or even possible extinction of *P. conspicillatus* reduce the diversity and the values the WTWHA was established to protect, conserve and present. Article 4 of the Convention stipulates:

“Each State Party to this Convention recognizes that the duty of ensuring the identification, protection, conservation, presentation and transmission to future generations of the cultural and natural heritage referred to in Articles 1 and 2 and situated on its territory, belongs primarily to that State. It will do all it can to this end, to the utmost of its own resources and, where appropriate, with any international assistance and co-operation, in particular, financial, artistic, scientific and technical, which it may be able to obtain.”

Thus adequate management of threats to the species, on or off the World Heritage estate, would appear to form part of the State Party’s obligations under the Convention (Hitchcock 2001).

The likely threats to World Heritage values of the WTWHA resulting from the loss or diminution of *P. conspicillatus*’ role in ecological processes such as seed and pollen dispersal are less well established. A significant reduction in these services might be expected to eventually result in an increase in clumping of plant species, resulting in reduced species richness at local scales. For individual plant species, a reduction in the quantity and/or the distance of the average dispersal might be expected to reduce the opportunity of the species to colonise new or degraded habitat, to find appropriate germination and recruitment opportunities, decrease levels of heterozygosity and increase genetic structuring in populations.

The extent to which any of these potential outcomes result from the impact of threatening processes on *P. conspicillatus* will be determined by the extent to which the ecological services provided by *P. conspicillatus* contribute to the total service provided by all dispersers. This is a question that is as yet unresolved for single plant species or communities. As noted for seed dispersal systems across the tropics, mutualisms between plants and their dispersers are only rarely tightly coevolved and exclusive (Howe 1993). From the limited data currently available (Westcott & Dennis, unpubl data) we are able to identify additional dispersers for all but nine species of the forty-eight recorded in *P. conspicillatus*' diet. The quantity of dispersal provided by *P. conspicillatus* relative to other species remains to be determined. The fact that *P. conspicillatus* is an abundant disperser in some habitats and relatively insensitive to habitat boundaries may make its contribution especially important in those contexts, e.g. small and isolated fragments.

Even in the presence of additional dispersers, the importance of the contribution made by *P. conspicillatus* may lie in the species providing a unique form of dispersal, e.g. in terms of dispersal distance, deposition mode, or quantity dispersed. Again, the importance of this is currently unquantified and can only be speculated on. For small seeds, dispersal by *P. conspicillatus* probably results in distances and deposition patterns similar to that produced by a variety of birds. Large seeds will be dispersed by *P. conspicillatus* similar distances and in a spatial pattern (Hall & Richards 2000) similar to that of the musky rat-kangaroo, *H. moschatus*, but never buried as is sometimes the case for *H. moschatus* (Dennis 1997). The other major disperser of large fruits, *C. casuarius*, probably provides greater dispersal distances for their seeds but deposits them in clumps (Westcott & Bradford 2000), perhaps exposing them to greater levels of competition and predation (Moore 1991).

Discussion of the relative quantity and quality of dispersal provided by *P. conspicillatus* remains speculative. Though currently under investigation, these services are unquantified for the WTWHA. Even once quantified, their flow on effects for the World Heritage values of the WTWHA will occur over long time scales and in complex plant communities making them difficult to document and detect in the short term. What is clear, however, is *P. conspicillatus*' involvement in these basic ecosystem processes. Any threats to the species will be felt within the ecosystem. How and to what extent is not known.

6.1 SIGNIFICANT CONCLUSIONS AND THEIR RELATIONSHIP TO WORLD HERITAGE VALUES.

The following section lists some of the main points derived from this review and discusses their implications for world heritage values. It describes how each general conclusion is drawn (E - Empirical evidence; I - Inference; S - Speculation) and ranks the strength of data supporting the conclusion (1 - very strong to 5 - weak). Most importantly, Professor Jamie Kirkpatrick presents a brief interpretation of what these conclusions may mean in the context of World Heritage values and responsibilities.

6.1.1 List of significant conclusions

P. consicillatus:

1. is representative of the mixing of Australian and Asian biota (E, 1)
2. is involved in seed dispersal (E, 1) that has aided the spread of Asian flora into Australia (I, 3)
3. represents a unit of biodiversity (E, 1)
4. is an agent of two important ongoing ecological processes in WTWHA in general - seed dispersal (E,1) and pollination (I, 1)
5. is an agent of seed dispersal and pollination of plants in families and genera listed as having World Heritage value under criteria I and II (E, 1)
6. through its seed dispersal affects plant - species diversity (I,3)
 - population structure (I,3)
 - spatial distribution (E, 2)
 - ongoing evolution of community structure and distribution (I, 1)
 - genetic structuring of populations (I, 2)
7. through its pollen dispersal affects plant - fecundity (I,3)
 - genetic structuring of populations (I, 2)
8. has a distribution associated with tropical rainforests (E, 1)

9. has an extra-limital range in New Guinea (E, 1)
10. is a wide ranging species within its range and crosses ecological boundaries (E, 1)
11. makes important use of areas both inside and outside World Heritage boundaries for both camp and foraging habitat (E, 1)
12. has an expected population decline if mortality is greater than 20% (I, 3)
13. is a significant cultural and food resource to traditional owners (I,2)
14. has suffered a significant loss of habitat, particularly on productive soils (E, 1)
15. is susceptible to recent and/or ongoing novel mortality factors that may affect population persistence including:
 - killings at orchards (E, 1)
 - deaths from collisions with powerlines and fences (E,3)
 - camp disturbance (E, 4)
 - paralysis tick (E, 3)
16. has suffered a population decline (I, 2)
17. has suffered a range contraction (I, 5)

6.1.2 Significance of conclusions for World Heritage values

This section was contributed by Prof. Jamie Kirkpatrick (University of Tasmania) as an interpretation of the World Heritage consequences of our conclusions regarding the biology of *P. conspicillatus*.

The World Heritage Convention makes the Government of Australia responsible for the protection and conservation of the values of World Heritage Areas. The *Environmental Protection and Biodiversity Conservation Act 1999* (EPBC) provides the Australian legal framework for such protection and conservation. One of the objects of the Act (Section 3.1.b) is 'to promote ecologically sustainable development through the conservation and ecologically sustainable use of natural resources'. One of the principles of ecologically sustainable development (EPBC, Section 3A.b) is that 'if there are threats of serious or irreversible environmental damage, lack of full scientific certainty should not be used as a

reason for postponing measures to prevent environmental degradation'. Under the provisions of Part 3 of the EPBC the World Heritage values of a declared World Heritage property are protected. Although there is no explicit statement in the EPBC that actions outside World Heritage properties that affect the values of these properties are subject to the Act, the EPBC requires consistency with the World Heritage Convention, and the *Operational Guidelines for the Implementation of the World Heritage Convention* produced by the Intergovernmental Committee for the Protection of the World Cultural and National Heritage of UNESCO are clear that a World Heritage Area can be listed as endangered as a result of actions outside the boundaries of that World Heritage Area (e.g. 79(i)(c)).

The conclusions of the present report indicate that *P. conspicillatus* contributes to the World Heritage values of the WTWHA under natural criteria (i) (ii), (iii) and (iv) with a generally high degree of scientific certainty (see conclusions 1-8 above), in that *P. conspicillatus* is a highly significant species in on-going ecological processes (the distributional dynamics of rainforest), constitutes a superlative natural phenomenon and is both an important element of biodiversity and may be important for the future of threatened plant species important for both science and conservation.

Some degree of uncertainty exists in relation to the current conservation status of *P. conspicillatus*. There is the highest degree of scientific certainty that there has been a significant loss of its most productive habitat (conclusion 14), that it uses habitat both inside and outside rainforest (conclusions 10 and 11) and that it is susceptible to potential decline in population through mortality related to orchard protection (conclusion 15). It is interesting to note in this context that most systems for deciding whether species should be listed as threatened include loss of habitat at a particular threshold as sufficient for listing, as they do predicted declines. The uncertainty in the present situation relates to the impact of novel forms of mortality and past loss of habitat on population decline (conclusion 16) and range (conclusion 17). Nevertheless, the inference from scientific evidence is relatively strong that a population decline has occurred, and a constant range does not necessarily imply the maintenance of population numbers. The degree of uncertainty, as a whole, that *P. conspicillatus* is in a state of decline is relatively low, well within the bounds of even the weakest form of application of the uncertainty principle.

There is also some degree of scientific uncertainty on the possible implications for World Heritage values related to other organisms and to the rainforest ecosystem of the decline or extinction of *P. conspicillatus* (conclusions 5-7). Given that that *P. conspicillatus* contributes to World Heritage value in itself, this does not affect the desirability of actions that could be taken to arrest its likely decline. However, it seems substantially more likely that the loss of *P. conspicillatus* would lead to a diminution of other biological world heritage values than otherwise.

Thus, there is a strong case for concluding that mitigation of the recognised threats to the future of *P. conspicillatus* also form part of the State Party's obligations under the Convention. Further research on the species directed towards reducing uncertainties related to the interactions of these threats with population levels would obviously also be desirable, both to monitor the effects of mitigatory actions and to increase the certainty that these actions are required.

7 SUMMARY

Failure to reach decisions based on unequivocal information that is available to all stakeholders helps destroy public faith in management actions. However, it must be stressed that in ecological studies without appropriate and focused sampling, levels of certainty are often below that of unequivocal. It is for this reason that use of the precautionary principle has been incorporated into decision making for management actions at all levels of government. Our review of the knowledge of *P. conspicillatus* has identified a real lack of direct information on almost all aspects of the ecology of the species. Many of the basic life-history parameters used to model population dynamics are based on very few observations or derived from studies of other species. Similarly, apparent historical declines are based on opportunistic observations and may be real in full or in part. Unfortunately, the data are insufficient to quantify declines but some decline must be inferred from loss of habitat alone. In the absence of anything else, these data can provide some guidance but we cannot be confident about the conclusions drawn from them. While this approach has sufficed to date, the need for appropriate and defensible management decisions requires a more rigorous and scientific approach to be taken in the future.

The relative quantity and quality of dispersal services provided by *P. conspicillatus* to the rainforest ecosystem of the WTWHA remains speculative as these services are not yet quantified. What is clear is that *P. conspicillatus* does contribute to these basic and essential ecosystem processes. Any threats to the species constitute threats to the ecosystem. What is not clear is the magnitude of these threats and their significance for the long-term viability of the world heritage values of the WTWHA.

The conclusion that *P. conspicillatus* contributes to World Heritage values, both directly and through its participation in ecological process, presents a strong case for Governmental responsibility in the careful management of the species. Ultimately management decisions will be imposed on groups with highly divergent interests. The diametrically opposed positions adopted by these groups and the distrust of the data used to argue their respective cases can too easily obfuscate management solutions that have the potential to achieve the goals of both groups. Steering a course that meets the real management needs of both industry and conservation is the challenge for the future.

8 REFERENCE LIST

- Anderson, K. (1912) Catalogue of the Chiroptera in the collection of the British Museum.; Volume i: Megachiroptera. Second edition, British Museum (Natural History), London
- Anonymous (1890) Orchard Pests: *New South Wales Agriculture Gazette* (1) pp105-107
- Anonymous (1987) Growers experiences with fruit crop protection: *Old Fruit and Vegetable News* Nov. 19 1987 pp15-17.
- Augspurger, C. K. (1983b) Seed dispersal of a tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens.: *Journal of Ecology*. (71) pp. 759-71
- Augspurger, C. K. and Kelly C. K. (1984a) Pathogen mortality of tropical tree seedlings: experimental studies of the effect of dispersal distance, seedling density and light conditions.: *Oecologia*. (61) pp. 211-217
- Australian Government (1987) Nomination of the Wet Tropical Rainforests of North-eastern Australia ; Dept. of Arts, Sport, the Environment, Tourism and Territories, Canberra
- Baker, R. J., Novacek, M. J., and Simmons, N. B. (1991) On the monophyly of bats: *Syst. Zool.* (40) pp. 216-31
- Birt, P., Hall, L. S., and Smith, G. C. (1997) Ecomorphology of the tongues of Australian Megachiroptera (Chiroptera: Pteropodidae): *Australian Journal of Zoology*. (45) pp. 369-84
- Bonaccorso, F. J (1998) Bats of Papua New Guinea: Conservation International, Washington, D.C.
- Booth, C. J. (2000) Affidavit to the Federal Court of Australia, Brisbane
- Brautigam, A. (1998) Flying-foxes in danger: *Species*. (11) pp. 11-2
- Brooke, A. P., Solek, C., and Tualualei, A. (2000) Roosting Behaviour of Colonial and Solitary Flying Foxes in American Samoa (Chiroptera : Pteropodidae): *Biotropica*. (32) pp. 338-50
- Bull, C. H. (1993) Colony structure, population estimates and roost fidelity of selected colonies of Spectacled Flying-foxes (Chiroptera: *Pteropus conspicillatus*) on the Atherton tablelands, Queensland, Australia; Centre for Rainforest Studies, Yungaburra, Queensland
- Calley, M., Braithwaite, R. W., and Ladd, P. G. (1993) Reproductive-Biology of *Ravenala madagascariensis* (Gmel) as an Alien Species: *Biotropica*. (25) pp. 61-72
- Carpenter, G., Gillison, A.N. & Winter, J. (1993) DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation* 2, 667-80.
- Clague, C., Freeman, A., Garnett, S., Spencer, H., Whybird, O., and Richards, G (1999) Spectacled Flying-fox, *Pteropus conspicillatus*. Pages 44-45 in The Action Plan for Australian Bats, A Duncan, G B Baker and N Montgomery (eds) Environment Australia, Canberra
- Clague, S., Whybird, O. and Clague, C. (2000) Spectacled Flying-fox - the need and justification for listing; Unpublished submission to Queensland Parks and Wildlife Service.

- Collins, M. J. (1994) Patterns and rates of rainforest conversion on the Atherton and Evelyn tablelands, North eastern Queensland. 1978-88: *Proceedings of the Royal Society of Queensland*. (104) p. 1
- Connell, J. H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and rain forest trees. Centre for Agricultural Publication and Documentation, Osterbeek Wageningen, The Netherlands.
- Connell, J. H. (1979) Tropical rain forests and coral reefs as open non-equilibrium systems.: Blackwell Scientific Publications, Oxford, England
- Cox, P. A., Elinqvist, T., Pierson, E. D., and Rainey, W. E. (Flying-foxes as pollinators and seed dispersers in Pacific Island Ecosystems. *In* Wilson, D. E. & Graham G. I. *Pacific island Flying-foxes: proceedings of an international conservation conference*, Guam.
- Dennis, A. J. (1997) Musky Rat-kangaroos, *Hypsiprymnodon moschatus*: cursorial frugivores in Australia's wet-tropical rain forests: PHD thesis, James Cook University, North Queensland
- Dirzo, R. and Dominguez C. A. (1986) Seed shadows, seed predation and the advantages of dispersal. Dr W. Junk Publishers, Dordrecht
- Docters van Leeuwen, W. M. (1935) The dispersal of plants by fruit eating bats: *Gardens Bull. Straits settlements*. (9) pp. 58-63
- Dolbeer, R. R., Fielder, L. R., and Rasheed, H. (1984) Management of fruit bat and rat populations in the Maldiv Islands, Indian Ocean: *In* Crabb, A. C. and Marsh, R. E. *Proceedings of the Thirteenth Vertebrate Pest Conference*, University of California, Davis
- Eby, P. (1991) Seasonal movements of gray-headed flying-foxes, *Pteropus poliocephalus* (Chiroptera, Pteropodidae), from two maternity camps in Northern New-South-Wales: *Wildlife Research*. (18) pp. 547-59
- Eby, P. (1998) An analysis of diet specialisation in frugivorous *Pteropus poliocephalus* (Megachiroptera) in Australian subtropical rainforest: *Australian Journal of Ecology*. (23) pp. 443-56
- Eby, Peggy, Richards, Greg, Collins, Linda, and Parry-Jones, Kerry (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) pp. 240-53
- Eggert, Cathy (1994) Is tick paralysis in the spectacled flying-fox, *Pteropus conspicillatus*, related to a change in the foraging behaviour of *P. conspicillatus*: Honours thesis, Southern Cross University, Lismore
- Elmqvist, T., Cox, P. A., Rainey, W. E., and Pierson, E. D. (1992) Restricted pollination on oceanic islands - pollination of *Ceiba pentandra* by Flying Foxes in Samoa: *Biotropica*. (24) pp. 15-23
- Flannery, T. (1995a) Mammals of New Guinea: Reed Books, Chatswood, NSW
- Flannery, T (1995b) Mammals of the south-west Pacific and Moluccan Islands: Reed Books, Chatswood, NSW
- Fleming, P. J. S. and Robinson, D. (1987) Flying-fox (Chiroptera: Pteropodidae) on the north coast of New South Wales: damage to stonefruit crops and control methods:

- Australian Mammalogy*. (10) pp. 143-45
- Foster, R. B. Javier Arce B. and Wachter T. S. (1986) Dispersal and sequential plant communities in an Amazonian Peru floodplain.: Dr W. Junk Publishers, Dordrecht
- Fujita, M. S. (2000) Flying-fox (Chiroptera: Pteropodidae) pollination, seed dispersal and economic importance: A tabular summary of current knowledge.: Bat Conservation International, Austin (Texas)
- Fujita, M. S. and Tuttle, M. D. (1991) Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance: *Conservation Biology*. (5) pp. 455-63
- Funakoshi, K., Watanabe, H., and Kunisaki, T. (1993) Feeding Ecology of the Northern Ryukyu Fruit Bat, *Pteropus Dasymallus-Dasymallus*, in a Warm-Temperate Region: *Journal of Zoology*. (230) pp. 221-30
- Garnett, S., Whybird, O., and Spencer, H. (1999) The conservation status of the spectacled flying-fox *Pteropus conspicillatus* in Australia: *Australian Zoologist*. (31) pp. 38-54
- Garnett, S., Whybird, O., and Spencer, H. (no date) Results of the First Spectacled Flying Fox Census - a report to participants. Unpublished Report.
- Garnett, S., Whybird, O., and Spencer, H. (no date) Report on the Census of Spectacled Flying-foxes 13-26 November 1998. Unpublished Report
- Garnett, S. and Whybird, O. (no date) Report on the Census of Spectacled Flying-foxes November 1999. Unpublished Report
- Garnett, S. (2001) submission to review for Environment Australia;
- Gorchov, D. L., Cornejo F., Ascorra C., and Jaramillo M. (1993) The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon.: *Vegetatio*. (107/108) pp. 339-49
- Grant, G., Craig, P. and Trail, P. (1997) Cyclone induced shift in foraging behaviour in flying foxes in American Samoa. *Biotropica* (29-2) pp. 224-228.
- Hall, L. S. (1983). Spectacled Flying-fox. *In* The Australian Museum Complete Book of Australian Mammals, R Strahan, ed, p 282. Angus and Robertson Publishers, Sydney.
- Hall, L. and Richards, G (2000) Flying-foxes, fruit and blossom bats of Australia: University of NSW Press Ltd, Sydney
- Hall, L. S. and Richards, G. C. (1987) Crop protection and management of flying-foxes (Chiroptera: Pteropodidae): *Australian Mammalogy*. (10) pp. 137-9
- Halpin, K., Young, P. L., Field, H. E., and Mackenzie, J. S. (2000) Isolation of Hendra virus from Pteropid bats: a natural reservoir of Hendra Virus: *Journal of General Virology*. (81) pp. 1927-32
- Hamrick, J. L., Murawski, D. A., and Nason, J. D. (1993) The influence of seed dispersal mechanisms on the genetic structure of tropical tree populations: *Vegetatio*. (108) pp. 281-97
- Harley, D, Ritchie, S, Phillips, D, and Van den Hurk, A (2000). Mosquito isolates of Ross River virus from Cairns, Queensland, Australia. *American Journal of Tropical Medicine and Hygiene* (62) pp561-565.

- Harms, K. E., Wright, S. J., Calderon, O., Hernandez, A., and Herre, E. A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest: *Nature*. (404) pp. 493-5
- Harrington, G. N. and Sanderson, K. D. (1994) Recent contraction of wet sclerophyll forest in the wet tropics of Queensland due to invasion by rainforest: *Pacific Conservation Biology*. (1) pp. 319-27
- Harrison, J. L. (1962) Mammals of Innisfail. I. Species and distribution: *Australian Journal of Zoology*. (10) pp. 45-83
- Hayden, S. (1992) Population estimates and sex ratios of a spectacled flying-fox (*Pteropus conspicillatus*) camp on the Atherton Tableland of north Queensland, Australia. Centre for Rainforest Studies, Yungaburra, Queensland.
- Herrera, C. M. (1985) Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates: *Oikos*. (44) pp. 132-41
- Hilbert, D.W., A. Graham, and T. Parker. 2000. Forest and woodland habitats of the Northern Bettong (*Bettongia tropica*) in the past, present, and future. Report to the Queensland Parks and Wildlife Service, March, 2000.
- Hilbert, D. and van den Muyzenberg, J. (1999) Using an artificial neural network to characterise the relative suitability of environments for forest types in a complex tropical vegetation mosaic.: *Diversity and Distributions*. (5) pp. 263-274
- Hitchcock, P. (2001) submission to review for Environment Australia.
- Hooper, P. T. and Williamson, M. M. (2000) Hendra and Nipah virus infections: *Veterinary Clinics of North America-Equine Practice*. (16) p. 597
- Hopkins, M. S., Graham, A. W., Hewett, R., Ash, J., and Head, J. (1990) Evidence of late Pleistocene fires and eucalypt forest from a north-Queensland humid tropical rainforest site: *Australian Journal of Ecology*. (15) pp. 345-347
- Hopkins, M. S. and Graham A. W. (1989) Community phenological patterns of a lowland tropical rainforest in north - eastern Australia.: *Australian Journal of Ecology*. (14) pp. 399-413
- Howe, H. F. (1993) Specialised and generalised dispersal systems: where does 'the paradigm' stand?: *Vegetatio*. (107/108) pp. 3-13
- Howe, H. F. and Schupp E. W. (1985) Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*): *Ecology*. (66) pp. 781-91
- Hubbell, Stephen P. (Speciation, dispersal and the structure of ecological communities on local to biogeographic spatial scales: The perspective from neutral theory: *In 3rd International Symposium - workshop on Frugivores and Seed dispersal*, Sao Pedro, SP Brazil
- ISI (2001) Web of Science: www.webofscience.com
- Jackes, B. (2001) submission to review for Environment Australia;
- Janzen, D. H. (1970) Herbivores and the number of tree species in tropical forests.: *The American Naturalist*. (104) pp. 501-28
- Johnston, A. (1994) Flying-foxes in coolite boxes.: *North Queensland Naturalists Club*. (197) pp. 18-21

- Kirkland, P. D., Love, R. J., Philbey, A. W., Ross, A. D., Davis, R. J., and Hart, K. G. (2001) Epidemiology and Control of Menangle Virus in Pigs: *Australian Veterinary Journal*. (79) pp. 199-206
- Kofron, C. (2001) submission to review for Environment Australia;
- Kress, J. W. (1985) Bat pollination of an Old World *Heliconia*.: *Biotropica*. (17) pp. 302-8
- Law, B. (2001) submission to review for Environment Australia;
- Leu, A. (1993) Birds and bats in orchards: a background document. Queensland Dept. of Environment and Heritage; Brisbane
- Leu, A. (1994) Winged vertebrate pests in orchards: A background document; Queensland Dept. of Environment and Heritage, Brisbane
- Loiselle, B. A., Sork, V. L., and Graham, C. (1995) Comparison of genetic variation in bird-dispersed shrubs of a tropical wet forest: *Biotropica*. (27) pp. 487-94
- Love, R. J., Philbey, A. W., Kirkland, P. D., Ross, A. D., Davis, R. J., Morrissey, C., and Daniels, P. W. (2001) Reproductive disease and congenital malformations caused by Menangle virus in pigs: *Australian Veterinary Journal*. (79) pp. 192-8
- Lowry, J. B. (1989) Green-leaf fractionation by fruit bats; is this feeding behaviour a unique feeding strategy by herbivores?: *Australian Wildlife Research*. (16) pp. 203-6
- Marshall, A. G. (1983) Bats, flowers and fruit: evolutionary relationships in the Old World: *Biological Journal of the Linnean Society*. (20) pp. 115-35
- Marshall, A. G. (1985) Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zoological Journal of the Linnean Society* (83) pp. 351-369.
- Martin, L., and A McIlwee (2001). On the intrinsic capacity for increase of Australian flying foxes (*Pteropus* spp., Megachiroptera). Submitted to the Australian Zoologist.
- Martin, L., Towers, P. A., McGuckin, M. A., Little, L., Luckoff, H., and Blackshaw, A. W. (1987) Reproductive biology of flying-foxes (Chiroptera: Pteropodidae): *Australian Mammology*. (10) pp. 115-8
- McCoy, M. (1990) Pollination of eucalypts by flying-foxes in northern Australia.: *In* Slack, J. M *Flying-fox workshop proceedings*,
- McHold, M. and Spencer, H. (1998) Assessment of control measures by exotic fruit farmers against crop attack by Flying-foxes: *Australian Tropical Research Foundation*. (10) p. in press
- McMahon, J.P., Hutchinson, M.F., Nix, H.A. & Ord, K.D. (1995) ANUCLIM user's guide, version 1. Centre for Resource and Environmental Studies, Australian National University, Canberra.
- Medellin, R. A. and Gaona, O. (1999) Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico: *Biotropica*. (31) pp. 478-85
- Mickleburg, S. P., Hutson, A. M. and Racey, P. A. (1992) Old world fruit bats. An action plan for their conservation; IUCN, Gland, Switzerland.
- Moore, G. J. 1991. Seed dispersal by male toothbilled bower birds, *Scenopoeetes dentirostris* (Ptilinorhynchidae), in northeast Queensland rainforests: processes and

- consequences. Pages 267. *Zoology*. James Cook University of North Queensland, Townsville.
- Muller-Landau, H. C., Wright, S. J., Calderon, O., Hubbell, S. P., Condit, R., and Foster, R. B. (2000) Recruitment limitation of tree species on Barro Colorado Island, Panama: *In 3rd International Symposium- Workshop on Frugivores and Seed dispersal*, Sao Pedro, SP Brazil
- Nason, J. D., Herre, E. A., and Hamrick, J. L. (1998) The breeding structure of a tropical keystone plant resource: *Nature*. (391) pp. 685-7
- Nathan, R. and Muller-Landau, H. C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment *Trends in Ecology and Evolution* (15 - 7): pp. 278-285
- Nelson, J. and Tidemann, C. R. (2000) Satellite tracking of flying-foxes - A world first: *Australasian Wildlife Management Newsletter* p. 10
- Nelson, J. E (1965a) Movements of Australian flying foxes (Pteropodidae: Megachiroptera): *Australian Journal of Zoology*. (13) pp. 53-73
- Nelson, J. E. (1965b) Behaviour of Australian Pteropodidae (Megachiroptera): *Animal Behaviour*. (13) pp. 544-7
- Nix, H. A. and Switzer, M. A. (1991) Rainforest animals: atlas of vertebrates endemic to Australia's wet tropics: Australian National Parks and Wildlife Service, Canberra
- Nowak, R. M. (1997) Mammals of the World: Johns Hopkins Press, Baltimore
- O'Brien, G. M. (1993) Seasonal reproduction in flying foxes, reviewed in the context of other tropical mammals. *Reproduction Fertility and Development* (5) pp. 499-521
- O'Connor, J. I. and Kerr, G. (2000) Mealworm dispensers as environmental enrichment for captive Rodrigues fruit bats (*Pteropus rodricensis*): *Animal Welfare*. (9) pp. 123-37
- Osunkoya, O. O. (1994) Postdispersal survivorship of north Queensland rain-forest seeds and fruits - effects of forest, habitat and species: *Australian Journal of Ecology*. (19) pp. 52-64
- Osunkoya, O. O., Ash, J. E., Graham, A. W., and Hopkins, M. S. (1993) Growth of tree seedlings in tropical rain-forests of north Queensland, Australia: *Journal of Tropical Ecology*. (9) pp. 1-18
- Palmer, C., Price, O., and Bach, C. (2000) Foraging ecology of the black flying fox (*Pteropus Alecto*) in the seasonal tropics of the Northern Territory, Australia: *Wildlife Research*. (27) pp. 169-78
- Palmer, C. and 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) pp. 823-38
- Parry-Jones, K. and Augee, M. L. (1991) Food selection by gray-headed flying foxes (*Pteropus poliocephalus*) occupying a summer colony site near Gosford, New-South-Wales: *Wildlife Research*. (18) pp. 111-24
- Parry-Jones, K. A. and Augee, M. L. (1992) Movements of gray-headed flying foxes (*Pteropus poliocephalus*) to and from a colony site on the central coast of New-South-Wales: *Wildlife Research*. (19) pp. 331-40

- Pettigrew, J. D. (1986) Flying Primates - Megabats have the advanced pathway from eye to mMidbrain: *Science*. (231) pp. 1304-6
- Pettigrew, J. D. (1991) Wings or brain? Convergent evolution in the origins of bats: *Syst. Zool.* (40) pp. 199-216
- Pettigrew, J. D., Jamieson, B. G. M., Robson, S. K., Hall, L. S., Mcanally, K. I., and Cooper, H. M. (1989) Phylogenetic relations between microbats, megabats and primates (Mammalia, Chiroptera and Primates): *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*. (325) pp. 489-559
- Pierson, E. D. and Rainey, W. E. (The biology of Flying-foxes of the genus *Pteropus*: A review: In D.E. Wilson and G.L. Graham *Pacific Island Flying-foxes: Proceedings of an international conservation conference*, Guam.
- Ratcliffe, F. N. (1931) The flying-fox (*Pteropus*) in Australia: *CSIR Bulletin No. 53*. (53)
- Ratcliffe, F. N. (1932) Notes on the fruit bats (*Pteropus* sp.): *Journal of Animal Ecology*. (1) pp. 33-57
- Richards, G. C. (2001) submission to review for Environment Australia;
- Richards, G. C. (1990a) The spectacled flying fox, *Pteropus conspicillatus*, (Chiroptera: Pteropodidae) in North Queensland 2. Diet, seed dispersal and feeding ecology.: *Australian Mammalogy*. (13) pp. 25-31
- Richards, G. C. (1990b) The spectacled flying fox, *Pteropus conspicillatus*, (Chiroptera: Pteropodidae) in North Queensland 1. Roost sites and distribution patterns.: *Australian Mammalogy*. (13) pp. 17-24
- Rigden, P., Page, J, and Chapman, J (2000). To net or not to net?: Flying fox control in orchards through netting. Unpublished report Queensland Horticulture Institute, Qld Dept. of Primary Industries.
- Shilton, L. A., Altringham, J. D., Compton, S. G., and Whittaker, R. J. (1998) Old world fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut: *Proceedings of the Royal Society of London*. (Series B 266) pp. 219-33.
- Sinclair, E. A., Webb, N. J., Marchant, A. D. and Tidemann, C. R. (1996) Genetic variation in the little red flying-fox, *Pteropus scapulatus* (Chiroptera: Pteropodidae): implications for management. *Biological Conservation* (76) pp. 45-50.
- Smith, J. D. and Madkour, G. (1980) Penial morphology and the question of chiropteran phylogeny: In Wilson, D. E. and Gardner, A. L. *Proceedings of the Fifth International Bat Research Conference* ,
- Sork, V. L. (1987) Effects of predation and light on seedling establishment in *Gustavia superba*.: *Ecology*. (68) pp. 1341-50
- Spencer, H (2001) submission to review for Environment Australia;
- Spencer, H. J., Palmer, C and Parry-Jones, K. (1991) Movements of fruit bats in eastern Australia, determined by using radio-tracking: *Australian Wildlife Research* (18) pp. 463-468
- Spencer, H. J., Flick, B. H., and Johnson, A. (1992) Infestation of a spectacled flying-fox (*Pteropus conspicillatus*) colony by paralysis tick (*Ixodes holocyclus*) in Far North

- Queensland, Australia: *Bat Research News*. (8) p. 61
- Start, A. N. and Marshall, A. G. (1976) Nectarivorous bats as pollinators of trees in West Malaysia: *Linn. Soc. Symp. Ser.* (2) pp. 141-50
- Tedman, R. A. and Hall, L. S. (1985) The morphology of the gastrointestinal tract and food transit time in the fruit bats *Pteropus alecto* and *P. poliocephalus* (Megachiroptera): *Australian Journal of Zoology*. (33) pp. 625-40
- Theimer, T. C. (2001) Seed scatterhoarding by white-tailed rats: Consequences for seedling recruitment by an Australian rain forest tree: *Journal of Tropical Ecology*. (17) pp. 177-89
- Thomas, D. W. (1982) The ecology of an African savanna fruit bat community: resource partitioning and role in seed dispersal : PHD Thesis, University of Aberdeen, Scotland.
- Tidemann, C. R. (1985) The status, habitat requirements and management of the two species of bat on Christmas Island (Indian Ocean). Report to the Australian National Parks and Wildlife Service. Zoology Department, Australian National University, Canberra.
- Tidemann, C. R. (1999) The biology and management of the Grey-headed Flying-fox, *Pteropus poliocephalus*.: *Acta Chiropterologica*. (1) pp. 151-64
- Tidemann, C. R., Kelson, S., and Jamieson, G. (1997) Flying-fox damage to orchard fruit in Australia - incidence, extent and economic impact: *Australian Biologist*. (10) pp. 177-84
- Tidemann, C. R. and Vardon, M. J. (1997) Pests, pestilence, pollen and protein: the need for community-based management of Flying-foxes in Australia.: *Australian Biologist*. (10) pp. 79-85
- Tidemann, C. R. and Vardon, M. J. (2001) The spectacled Flying-fox in Queensland: a review of available information:
- Tidemann, C. R., Vardon, M. J., Loughland, R. A., and Brocklehurst, P. J. (1999) Dry season camps of flying-foxes (*Pteropus Spp.*) in Kakadu World Heritage Area, north Australia: *Journal of Zoology*. (247) pp. 155-63
- Tracey J.G. & Webb L.J. (1975) Vegetation of the Humid Tropical Region of North Queensland. (15 maps at 1 : 100,000 scale + key.) CSIRO Aust. Long Pocket Labs: Indooroopilly, Qld.
- Turner, R. (1994) Management of Birds and Flying-foxes: an overview of present and future options: *In Bird and Bat control for Horticulture and Aquaculture, Seminar Proceedings*, Nambour, Queensland
- UNESCO (1972) Convention Concerning the Protection of the World Cultural and Natural Heritage; UNESCO, Paris
- UNESCO (1997) Operational Guidelines for the Implementation of the World Heritage Convention; UNESCO, Paris
- Utzurum, R. (1985) Fig fruit consumption and seed dispersal by frugivorous bats in the primary forest of Lake Balinsasayao, Negros Oriental, Phillipines: MSc thesis, Silliman University, Phillipines

- van der Pijl, L (1957) The dispersal of plants by Bats (Chiropterochory): *Acta Botanica*. (6) pp. 291-315
- Vardon, M. J, Brocklehurst, P. J., Woinarski, J. C. Z, Cunningham, R. B., Donnelly, C. F., and Tidemann, C. R. (2001) Seasonal habitat use by flying-foxes, *Pteropus alecto* and *P. scapulatus* (Megachiroptera), in monsoonal Australia: *Journal of Zoology, London*. (253) pp. 523-35
- Vardon, M. J, Simpson, B. K, Sherwell, D, and Tidemann, C. R (1997) Flying-foxes and tourists: a conservation dilemma in the Northern Territory: *Australian Zoologist*. (30) pp. 310-5
- Vardon, M. J. and Tidemann, C. R. (1998) Reproduction, growth and maturity in the black flying-fox, *Pteropus alecto* (Megachiroptera: Pteropodidae): *Australian Journal of Zoology*. (46) pp. 329-44
- Vardon, M. J. and 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) pp. 411-23
- Vazquez-Yanes, C. and Orozco-Segovia A. (1986) Dispersal of seeds by animals: effect on light controlled dormancy in *Cecropia obtusifolia*.: Dr W. Junk Publishers, Dordrecht
- Webb, N. J and Tidemann, C. R (1995) Hybridisation between black (*Pteropus alecto*) and grey-headed (*P. poliocephalus*) flying-foxes (Megachiroptera Pteropodidae): *Australian mammalogy*. (18) pp. 19-26
- Webb, N. J. and 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-Biological Sciences*. (263) pp. 497-502
- Wenny, D. G. (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal: *Evolutionary Ecology Research*. (3) pp. 51-74
- Wenny, D. G. and Levey, D. J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest: *Proceedings of the National Academy of Sciences of the United States of America*. (95) pp. 6204-7
- Werren, G. L. (2001) Contribution to review of scientific understandings of the spectacled Flying-fox in the context of the Wet Tropics World Heritage Area and its values. submission to review for Environment Australia.
- West, C. C. and Redshaw, M. E. (1987) Maternal behaviour in the Rodrigues fruit bat *Pteropus rodricensis*. *Dodo: Journal of the Jersey Wildlife Preservation Trust*. (24) pp. 68-81
- Westcott, D A and Bradford, M. (2000). The southern cassowary, *Casuarius casuarius*, and seed dispersal in Australia's tropical rainforests. Abstracts of the 3rd International symposium-workshop on frugivores and seed dispersal: biodiversity and conservation perspectives, p 281. Sao Pedro, Brazil
- Whittaker, R. J. and Jones, S. H. (1994) The Role of Frugivorous Bats and Birds in the Rebuilding of a Tropical Forest Ecosystem, Krakatau, Indonesia: *Journal of Biogeography*. (21) pp. 245-58
- Whybird, O. and Garnett, S. (no date) Report on the Census of Spectacled Flying-foxes

March 1999. Unpublished Report

Whybird, O. (no date) November 2000 Spectacled Flying-fox Survey. Unpublished Report.

Williamson, A. and Williamson, C. (1995) The story of 071-83111: *Newsletter Friends Far North Flying-foxes*. (3) pp. 4-5

Winter, J. W., Atherton, R. G., Bell, F. C. and Pahl, L. I. (1987) Rainforest clearing in North Queensland: *Proceedings of the Royal Society Queensland*. (98) pp. 41-57

9 APPENDIX A Experts consulted

Expert	Affiliation	General Expertise
Prof. B. Jackes	JCU	Pollination and plants of the Wet Tropics
Dr S Garnett	QPWS	Conservation management of endangered species, <i>P. conspicillatus</i>
Dr P Hitchcock	Old Cassowary Consulting	World Heritage
Dr C Kofron	QPWS	Conservation and management
Dr B Law	State Forests, NSW	Australian bats and Wet Tropics Megachiropterans
Dr L Martin	UQ	Pteropus reproduction and population biology.
Mr G Richards	Greg Richards and Associates.	Pteropus, <i>P. conspicillatus</i>
Dr H Spencer	Cape Tribulation Research Centre	Pteropus and the Wet Tropics
Dr C Tidemann	ANU	Pteropus
Dr G Werren	JCU	Conservation and World Heritage in the Wet Tropics
Dr M Vardon	ABS	Pteropus
Ms S. Clague	QPWS	Wet Tropics Bats

Experts emailed and/or phoned without successful contact and who did not therefore contribute

Mr Peter Valentine	JCU	Wet Tropics and World Heritage
Dr Les Hall	UQ	<i>Pteropus</i> expert
Dr Peggy Eby	UNE	<i>Pteropus</i> expert

Experts who provided verbal input

Ms O. Whybird	Consultant	Bat expert
Ms J. Maclean	Tolga Bat Hospital	Bat carer

10 APPENDIX B Natural criteria against which the Wet Tropics of Queensland was inscribed on the World Heritage List in 1988.

Examples of World Heritage values of the Wet Tropics of Queensland for which the property was inscribed on the World Heritage List in 1988.

Criterion (i) outstanding examples representing the major stages of the earth's evolutionary history.

The Wet Tropics of Queensland contains one of the most complete and diverse living records of the major stages in the evolution of land plants, from the very first land plants to higher plants (Gymnosperms and Angiosperms), as well as one of the most important living records of the history of marsupials and songbirds. The property provides exceptional examples representing eight of the major stages in the earth's evolutionary history including:

- Age of the Pteridophytes;
- Age of the Conifers and Cycads;
- Age of the Angiosperms;
- The final break-up of Gondwana;
- Biological evolution and radiation during 35 million years of isolation;
- The origin and radiation of the songbirds;
- The mixing of the continental biota of the Australian and Asian continental plates; and
- The extreme effects of the Pleistocene glacial periods on tropical rainforest vegetation.

The World Heritage values include:

- ancient plant taxa representing two main branches of the earliest land plants, the Psilotopsida and the Lycopsidea;
- 7 ancient families of true ferns, including Lycopodiaceae, Selaginellaceae, Ophioglossaceae, Marattiaceae, Osmundaceae, Schizaeaceae and Gleicheniaceae;
- taxa in the oldest and most primitive families of the largest group of pteridophytes, the Schizaeaceae and Gleicheniaceae;
- 31 of 36 families of pteridophytes (including 111 of 364 described genera);
- fern genera of East Gondwanan origins, including Coveniella, Lastreopsis, Polystichum, Pteridoblechnum, Steenisoblechnum, Oenotrichia, Leptopteris, Todea, Tmesipteris, Lycopodiella and Huperzia;
- the ancient, fern-like cycad *Bowenia spectabilis*;

- the cycad families Cycadaceae, Zamiaceae (including the genera *Cycas*, *Lepidozamia* and *Bowenia*);
- the rare assemblage of *Lepidozamia hopei*, *Podocarpus grayi* and *Agathis robusta* which includes the closest living counterparts of Jurassic-age fossils;
- species of the only two surviving araucarian genera *Araucaria* and *Agathis*;
- 3 endemic species of the podocarp genera *Prumnopitys* and *Podocarpus*;
- 12 primitive angiosperm families in the orders Magnoliales and Laurales (Annonaceae, Austrobaileyaceae, Eupomatiaceae, Himantandraceae, Myristicaceae, Winteraceae, Hernandiaceae, Gyrocarpaceae, Idiospermaceae, Lauraceae, Monimiaceae and Atherospermataceae);
- small, primitive, relict angiosperm families including Austrobaileyaceae, Idiospermaceae, Eupomatiaceae and Himantandraceae;
- plant taxa considered to occupy major nodal positions in the evolution of the angiosperms (including taxa in the orders Hamamelidales, Rosales, Euphorbiales, Dilleniales, Violales, Theales, Celastrales and Gentianales);
- relict taxa from Cretaceous angiosperm families (including Cunoniaceae, Proteaceae, Winteraceae, Myrtaceae, Monimiaceae, Rutaceae, Sapindaceae, Aquifoliaceae, Callitrichaceae, Chloranthaceae, Trimeniaceae, Epacridaceae, Olacaceae and Loranthaceae);
- 153 genera in 43 families of angiosperms believed to represent the longest continuous history associated with the Gondwanan landmass;
- frog species from the Gondwanan families Myobatrachidae and Hylidae (including primitive species from the genera *Mixophyes*, *Taudactylus*, *Litoria* and *Nyctimystes*);
- reptiles of Gondwanan origin including geckoes of the subfamily Diplodactylinae and legless lizards of the endemic family Pygopodidae;
- skinks of the *Sphenomorphus*, *Egernia* and *Eugongylus* groups, which are represented in the Oligo-Miocene fossil fauna of Riversleigh;
- rainforest birds of Gondwanan origins including the Southern Cassowary, the orange-footed scrubfowl (*Megapodius reinwardt*) and the Australian brush-turkey (*Alectura lathami*);
- primitive insect taxa that are relicts of the Gondwanan fauna;
- primitive genera of the Proteaceae including *Placospermum*, *Sphalmium* and *Carnarvonia*;
- 5 endemic species in the Myrtaceae group *Metrosideros*, which is the most primitive in the family and includes the genera, *Barongia*, *Ristantia*, *Sphaerantia* and the undescribed "*Stockwellia*";
- the East Gondwanan genus *Gymnostoma*, an ancestral form of the Casuarinaceae;
- species in the genera *Euodia* and *Medicosma* in the family Rutaceae;

- 9 species of dasyurids including one relict species, *Antechinus godmani*.
- mammalian genera related to those of Oligo-Miocene age at Riversleigh, including *Hypsiprymnodon*, *Cercatetus*, *Pseudochirops* and *Trichosurus*;
- the Musky Rat-kangaroo, *Hypsiprymnodon moschatus*, the most primitive of the kangaroos and the only living member of its group;
- 5 species of ringtail possums, including 4 rainforest-dependent species;
- passerine (Oscines) birds representing ancestral lineages of Australo-Papuan songbirds, (e.g. the bowerbirds and the scrubwrens, thornbills and gerygones);
- *Chowchilla*, *Orthonyx spaldingii*, a relict endemic species also found in late Oligocene deposits (~25 million years BP) at Riversleigh;
- areas where the extant rainforest flora and fossil pollen deposits provide a record of the mixing of long separated floras including old Gondwanan and Asian elements;
- plant genera considered to have been of Gondwanan or Laurasian descent and to have entered Australia following collision of the Australian and Asian plates (including: *Alangium*, *Allophylus*, *Althoffia*, *Alyxia*, *Anthocephalus*, *Barringtonia*, *Berrya*, *Bombax*, *Bulbophyllum*, *Calophyllum*, *Canthium*, *Celtis*, *Cordia*, *Epipogium*, *Garcinia*, *Gardenia*, *Leea*, *Lethedon*, *Melia*, *Oreodendron*, *Phaleria*, *Securinega* and *Trema*);
- taxa in the frog families *Microhylidae* and *Ranidae* which provide outstanding examples of the impact on the biota of the collision of the Australian and Asian plates;
- Bats and rodents (including *Hydromys*, *Pogonomys*, *Uromys* and *Melomys*) which are considered to have entered Australia since connections with the Asian Plate were established;
- fossil pollen records going back over 200, 000 years from Butcher's Creek, Lynch's Crater and Lake Euramoo; and
- Ancient taxa in the *Araucariaceae* (5 species), *Podocarpaceae* (7 species) and *Casuarinaceae* (1 species of *Gymnostoma*).

Criterion (ii) outstanding examples representing significant ongoing geological processes, biological evolution and man's interaction with his natural environment.

The Wet Tropics of Queensland provides outstanding examples of significant ongoing ecological processes and biological evolution including exceptionally high levels of species diversity and endemism reflecting long-isolated ancient biota of the Australian wet tropics.

The World Heritage values include:

- the high genetic diversity and endemism of the tropical rainforest ecosystems which constitute a major centre of evolution of rainforest flora;
- endemic rainforest plant taxa (including 43 genera and at least 500 species);
- plant and animal taxa exhibiting allopatric speciation (including the plant genera *Haplostichanthus*, *Pseuduvaria*, *Elaeocarpus*, *Ceratopetalum*, *Polyosma*, *Endiandra*, *Uromyrtus*, *Pilidiostigma*, *Buckinghamia*, *Orites*, *Stenocarpus*, *Sarcotoechia*, *Bubbia*, *Planchonella* and *Symplocos*);
- plant and animal taxa which occur as disjunct populations, such as those associated with altitudinal and geographic barriers to gene flow; and
- the diversity of flora and fauna, which includes:
- 3,000 species of vascular plants (representing 1164 genera in 210 families), 11 mammal species, 370 bird species, 53 frog species, 170 reptile species, and 78 species of freshwater fish (in 48 genera and 35 families), more than 200 species of butterflies, 6 species of crayfish, and 217 species of land snails, and stream invertebrates).

Criterion (iii) contain unique, rare or superlative natural phenomena, formations or features of exceptional natural beauty.

The Wet Tropics of Queensland has outstanding features of natural beauty and magnificent sweeping landscapes.

The World Heritage values include:

- the exceptional coastal scenery that combines tropical rainforest, white sandy beaches and fringing reefs just offshore;
- rugged mountain peaks and gorges;
- extensive vistas of undisturbed forest and valleys which descend rapidly in the lower reaches through spectacular waterfalls and cascades; and

- superb gorge scenery with swiftly flowing rivers and spectacular waterfalls (e.g. Wallaman Falls which has the longest single drop (278 metres) of any waterfall in Australia).

Criterion (iv) contain the most important and significant habitats where threatened species of plants and animals of outstanding universal value from the point of view of science and conservation still survive.

The Wet Tropics of Queensland provides important habitats for the in situ conservation of biological diversity, including the only habitat for numerous species of plants and animals of conservation significance which have outstanding universal value from the point of view of science and conservation.

The World Heritage values include:

- plant communities and animal habitats, recognised as being floristically and structurally the most diverse in Australia (including 13 major structural types and 27 broad communities types of rainforest fringed and dissected by a range of sclerophyll forest and woodland types, mangroves and swamp communities);
- plant taxa of conservation significance and their populations (which include more than 700 species of endemic plants representing 43 genera in 33 angiosperm, and 6 gymnosperm and fern families); and
- animal taxa of conservation significance and their populations.

(Department of the Arts, Sport, the Environment, Tourism and Territories December 1987.

11 APPENDIX C Summary of external reviewers comments

This report has been peer reviewed by two Australian and one international researcher from appropriate fields. The following summarizes the main points raised by the reviewers and outlines how these comments have been dealt with in the report.

All three reviewers agreed that our review was "exhaustive", "well organised" and fulfilled the requirements of the terms of reference. All were congratulatory of the authors and suggested that there were "no obvious omissions" or that they "would be surprised if any reviewer found any major areas of concern". All reviewers provided minor editorial comments or points for clarification on the text, which we have incorporated into the final version in most instances. In addition, each reviewer added comments on some aspects of the report that, in their minds, needed different or greater emphasis. Below, we outline how we have dealt with each of the reviewer's comments or why we chose not to.

One reviewer suggested that one of the most important roles of spectacled flying-foxes in seed dispersal was as an "edge spreader" and felt that we seemed to ignore this. In fact, we had mentioned this but had not emphasized it as a process on its own. We agree with the main thrust of the reviewer's comment and had already made changes to emphasize this role a little more before receiving his review. We re-examined our text to ensure that this component of the dispersal service was adequately covered. The reviewer also suggested that due to this "edge spreading" phenomenon, dispersal of large seeds by carrying them short distances may be relatively more important than the dispersal of small seeds through the gut. We agree that both types of dispersal are important. However, we disagreed with the reviewer's emphasis on the importance of "edge spreading" versus new patches establishing outside the forest, which may be a result of observations of the phenomenon in different areas. Much regrowth in disturbed areas in the Wet Tropics is in the form of new patches establishing well outside and disjunct from a rainforest boundary. In addition, the spread of rainforest into sclerophyll forest is sometimes in a patchy nature with moist or gully areas well away from a rainforest boundary establishing young rainforest well before any of the intervening sclerophyll

forest does. This suggests that both types of dispersal service are important for the spread of forests. Therefore, we did not change the emphasis on which service was more important.

A reviewer asked if "anyone" had examined the different germination rates resulting from seeds passing through the guts of different frugivores and whether this might not be an important component of the service provided by flying-foxes. We had considered this issue as part of our review but chose not to include anything on it for two main reasons. The first was that data on this subject in the Wet Tropics were restricted to cassowaries and our own incomplete work on a range of species. There was also no reasonable *a priori* reason to suspect that passage through the gut of a flying fox would necessarily create a different response in speed of germination or the proportion of seeds germinating to passage through the gut of any other frugivore. In combination this meant that anything said about this subject would be entirely speculative. Secondly, while much information on this subject is available from throughout the world, there is no indication that a disperser has a similar effect on all the species it consumes or that speeding of germination is necessarily more advantageous to the plant than slowing germination or not changing its rate at all. The likely outcome for a plant is that the wider the range of germination times it has the more likely that one or more of its seeds is in the right place at the right time for recruitment into the population.

One reviewer suggested that we "stress the ecotourism values of these bats a bit more" and go on to say, "for visitors from abroad, the opportunity to see flying foxes up close and personal is appealing". While we agree that this is probably the case it was difficult to add anything much to this section (3.9.2) on the basis that actual information on the frequency with which flying foxes were used in ecotourism products was not available to us. Our comments in this section were based on anecdotal evidence and our own casual observations.

Finally, one reviewer spoke about our tendency to be very conservative with drawing conclusions from limited data and that we emphasised the need for unequivocal information when science generally reduces uncertainty rather than provides unequivocal answers. We feel that the former point is true of our report and have specifically been

conservative in drawing conclusions as we felt that this was appropriate to the terms of reference. We were asked to assess the scientific value and limitations of knowledge on *P. conspicillatus*. However, we had intended to communicate "levels of certainty" associated with the data, rather than whether a statement was correct or incorrect. Because this reviewer had not clearly understood what we were trying to communicate we reviewed the relevant sections to ensure that our assessment of the data was clearly stated. We also altered a couple of statements that referred to management decisions needing to be based on "unequivocal information" as our true emphasis was that information needed to be appropriate and defensible.