



Observations on the consumption and dispersal of *Phoenix canariensis* drupes by the Grey-headed flying-fox (*Pteropus poliocephalus*)

Institute for Land, Water and Society, Charles Sturt University, PO Box 789, Albury NSW 2640, Australia
Corresponding author, E-mail: dspennemann@csu.edu.au

Dirk HR Spennemann

ABSTRACT

Aided by their transplantability as adult plants, *Phoenix canariensis* and *Washingtonia robusta* palms have a long history as ornamental feature trees in urban settings. With their plentiful production of carbohydrate rich drupes, palms have become a major food source for the grey-headed flying-fox (*Pteropus poliocephalus*) during late autumn and early winter. This paper reviews the consumption of *Phoenix canariensis* and *Washingtonia robusta* drupes based on the field observations and a morphological and metric analysis of spat-out remains ('ejecta'). Based on a review of the mastication mechanics of fruit consumption, the paper demonstrates that *P. poliocephalus* can be ruled out as a disperser of the invasive *Phoenix canariensis*, but must be considered for the dispersal of *Washingtonia robusta*.

KEYWORDS

Grey-headed flying-fox, *Pteropus poliocephalus*, diet, frugivory, *Phoenix canariensis*, *Washingtonia robusta*, dispersal of exotic palms

 © 2018 Dirk HR Spennemann

This is an open access article distributed under the Creative Commons Attribution-NonCommercial-NoDerivs license

INTRODUCTION

Introduced to the European nursery trade in the 1860s, and to Australia in the 1870s and 1880s, the Canary date palm (*Phoenix canariensis*) has developed into a major ornamental tree species, widely planted in private and public gardens, as well as a street tree common to many Australian communities with a temperate climate (Spennemann, in press, subm.-a; Zona, 2008).

Phoenix canariensis is a dioecious, wind pollinated palm that is solely propagated by seed (Barrow, 1998). It seeds freely, annually producing between 10,000 and 30,000 obovoid drupes ('dates'), which are a fleshy fruit with a single seed and small amount of fibrous pericarp. The fruits are non-toxic but have an unpleasant taste which renders them fit only for animal consumption. The drupes range from 15–30 mm in length, 12–17 mm in thickness and 4–6 g in mass (Djouab et al., 2016; Spennemann, 2018b), of which the seed contributes 2–2.5 g. As its fruits are dispersed by a range of volant and terrestrial

vertebrate vectors (Spennemann, subm.-c), *Phoenix canariensis* has a relatively high dispersal potential (Virtue et al., 2008) and has thus been identified as a noxious plant in many areas (e.g., Biosecurity Queensland, 2018; Campbelltown City Council, 2015; Shire of Manjimup, 2008), but has not been formally declared as a noxious weed by any of the Australia's states. In the Australasian setting, *Phoenix canariensis* have been regarded as naturalised in New South Wales (Hosking et al., 2007), South Australia (Brodie & Reynolds, 2012), Victoria (Conn & Walsh, 1993), and Western Australia (Lohr & Keighery, 2016, p. 32), as well as New Zealand (Esler, 1987).

Recent research has begun to compile and analyse the nature, role and range of volant and terrestrial dispersal vectors for *Phoenix canariensis* and allied ornamental palm species (Spennemann, 2018a, 2018d, 2018e, subm.-b, subm.-c) and to document the actual range of dispersal from single seed sources (Spennemann & Pike, in prep.).

One of the reputed dispersal vectors noted for Australia is the grey-headed flying-fox (*Pteropus poliocephalus*) (Nelson, 1989), which has a distribution across the eastern seaboard of Australia (Department of the Environment and Energy, 2017; Eby et al., 1999; Roberts et al., 2012). The bat, which feeds on a wide range of flowers and fruits, both in bushland and in suburban and urban settings (McDonald-Madden et al., 2005; Williams et al., 2006), is known to feed on the fruit of various palm species, among them on *Phoenix canariensis*. Dietary studies of grey-headed flying-foxes have shown them to be feeding on *Phoenix canariensis* in the Gordon colony in Sydney, NSW (Augee & Parry-Jones, 1991; Parry-Jones & Augee, 1991, 2001); at Matcham near Gosford, NSW (Augee & Parry-Jones, 1991), Albury, NSW (this paper) and at Burrumbuttock, NSW (Messaro, 2018). In addition, grey-headed flying-foxes have been reported as roosting in *P. canariensis* palms in a locality in the south of Sydney (Eco Logical Australia, 2014, p. 56) as well as at Murrurundi in northern NSW (Hunter Councils Environment Division, 2017, p. 14).

The dispersal potential of a given vector is commonly circumscribed by the seed shadows they generate from the source trees (Tsoar et al., 2011). These seed shadows include seeds dropped while feeding on the source tree, those dropped at feeding perches, those defecated/regurgitated at other feeding locations or at the roosts, and those that were dropped or defecated mid-flight. These shadows are defined by the individual feeding behaviour and the time it takes to digest food and excrete the waste (the gastro-intestinal transit time). Tsoar et al. (2010) examined the feeding behaviour of *Rousettus aegyptiacus* and documented the seed rain around source, as well as perch trees, noting the average diameters of 10 m. Some seeds were dropped as far as 500 m from the source tree. Much larger seed shadows of up to 5,000 m have been reported for *Pteropus rufus* (Oleksy et al., 2017). The question arises as to the size of the seed shadow for *Phoenix canariensis*.

As will be discussed below, when eating, the bats bite pieces off of their food, and then chew it vigorously, spitting out portions that are not swallowed in the form of ejecta pellets. While there is frequent reference to such ejecta pellets (Nakamoto et al., 2007), there appears to be no documentation of the appearance and composition of the masticated material that is not ingested but spat out as ejecta. A sole exception is Barbara Triggs' (2004, p. 241) compilation of animal scats, which contains an image of several ejecta that does not provide much detail.

While the fact that *Pteropus poliocephalus* are feeding on *Phoenix canariensis* drupes has been documented, the effects of this consumption on the seeds, and the viability of the grey-headed flying-fox as a seed vector has never been formally examined. This paper will discuss the consumption of *Phoenix canariensis* drupes based on field observations, an examination of dropped drupes, and a morphological and metric analysis of spat-out remains ('ejecta') and will place these observations into the context and the fruit consumption behaviour and mastication mechanics of *Pteropus poliocephalus*.

1. METHODS

Numerous *Phoenix canariensis* have been planted throughout Albury (NSW), in the botanic gardens, as street trees, and in private gardens in a suburban setting. One of these is located at n° 708 Forrest Hill Avenue (coordinates -36.074175, 146.907128). While the palm is seemingly associated with a Spanish Mission style-influenced residence of the inter-war period (Figure 1), it apparently grew as a self-seeded plant and was first noticed, then about 0.4 m tall, about 50 years ago (Andronicos, 2018). At the time of the documentation in April 2018, the female palm had a total height of 9.2 m, with a minimal trunk height of 4.4 m, a trunk girth (at 1.3 m) of 2.6 m and crown of approximately 8 m diameter.

Every night, hundreds of grey-headed flying-foxes are moving into central Albury to feed. A census in February 2018 counted 2,500 grey-headed flying-fox roosting in a camp located at Padman Park in the floodplain of the Murray River (-36.085, 146.8975) (DEWLP Hume, 2017; Roots, 2018), approximately 1.5 km to the south-southwest of the study site.

During March and April 2018, *Pteropus poliocephalus* frequented the drupe clusters of the *Phoenix canariensis* palm on most nights, as observed by the owners of n° 704 Forrest Hill Avenue, as well as by the author in mid-April 2018. The ground underneath the palm was littered with complete drupes, incomplete drupes, seeds, and seeds with part of the epicarp ('skin') attached, as well as clumps of spat-out epicarp (in the literature sometimes referred to as 'bolus,' and herein henceforth as 'ejecta pellets'). These have been collected, with the majority photographically documented in a data source document (Spennemann, 2018b).

2. OBSERVED PATTERNS OF DRUPE CONSUMPTION

The feeding activity of the grey-headed flying-fox dislodges some drupes from the panicle stalk, causing them to drop, which results in a number of complete drupes found on the ground. While it has been noted elsewhere that rodents predate *Phoenix canariensis* drupes both on trees and on ground (Walters, 2006), inspection of the fallen drupes showed none with fresh chew marks. Some of the fallen drupes showed evidence of ants removing the carbohydrate-rich pericarp and leaving behind a shell of epicarp and a clean seed (see Spennemann, 2018b).

The bulk of debris underneath the canopy was comprised primarily of clean, fully defleshed seeds, and a smaller proportion (ca 10%) of seeds with minor amounts of pericarp remaining (Figure 3) with a similar proportion of abscised complete drupes. Comparatively rare were partially eaten drupes (Figure 2), which were presumably dropped, accidentally or intentionally, by the flying-foxes during the feeding process. One of the recovered drupes exhibited bite marks that seemed to have been inflicted while the drupe was still ripening as the scars are calloused over (Figure 2, Figure 4).

In addition to the drupes and seeds, a number of ejecta were recovered and recorded. As the ejecta are merely



Figure 1. The *Phoenix canariensis* at 708 Forrest Hill Avenue, Albury, NSW



Figure 2. *Phoenix canariensis* seed with large amounts of pericarp remaining, but some epicarp removed



Figure 3. *Phoenix canariensis* seed with small amounts of pericarp adhering

comprised of fibre and epicarp platelets, they lacked a binder, and thus were compact but fragile, in particular the thin dental surfaces (Figure 5). When the pellets were ejected, they fell between 5 to 7 m onto a clipped lawn, which buffered their impact. When collected in the early morning, they were dried

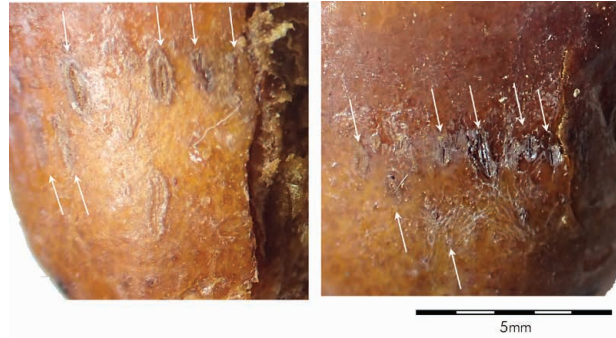


Figure 4. Detail of Figure 2, note the teeth marks

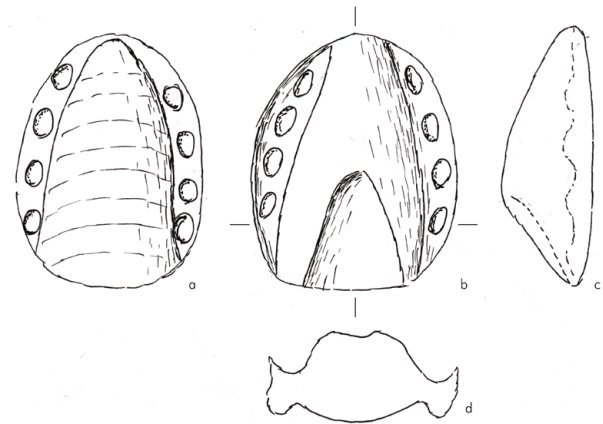


Figure 5. Schematic of a spat-out mastication pellet a–maxillary surface, b– mandibular surface, c–longitudinal cross-section, d–transverse cross-section



Figure 6. Spat-out mastication debris (ejecta pellet) primarily comprised of pericarp fragments; a) showing the mandibular surface of the pellet; b) showing the maxillary surface of the pellet

pellets that could be recovered largely intact. Any rain, or lawn watering, however, rehydrated the pellets and broke them down to small fragments.

The ejecta recovered ranged from nearly complete units to fragments. A complete ejecta pellet (Figure 6) is comprised of a bulbous central part with an asymmetrically attached thinner area that exhibits a rim and a broad groove. The groove exhibits some pitting on both surfaces. The outline

shape of the ejecta is that of a semi-ellipsis with a flattened base. On one side, the ejecta has a smooth arched central surface (Figure 5a) that is bounded by the pitted groove and an ill-defined rim/edge. The opposite side is much more domed, but shows a central depression that deepens to the base of the ellipsis (Figure 5b). This too is bounded by the pitted groove and an ill-defined rim/edge.

Judging from the spat-out remains, *P. poliocephalus* feeding on *Phoenix canariensis* bites chunks of epi- and pericarp off the seed and then masticates these well until most epicarp fragments are reduced to 1 mm pieces or smaller. The largest epicarp pieces observed measured 2 x 3 mm. None of the pellets contained *P. canariensis* seed. The *P. canariensis* remains spat out by the bats seem to solely consist of stacked epicarp platelets, giving the ejecta pellets the appearance of pieces of 'wheat-bix' breakfast cereal. Figure 7 shows an ejecta pellet superimposed over the maxilla and mandible of a *P. poliocephalus* skull.

3. SELECTION OF DRUPES

Traditional, as well as commercial, date palm (*Phoenix dactylifera*) production distinguishes four distinct stages of ripening, from immature green (Arabic: Khimri) and mature, full coloured (Khalal) to soft brown (Rutab), and finally hard raisin (Tamr) (Ahmed et al., 1995). These stages can also be applied to *P. canariensis*. While the fruit attains its maximum weight and size at the end of the Khalal stage, the sugar content continues to increase (on average 57.5%) as the fruit further ripens to the Rutab stage. The colouring of the epicarp platelets in the bat ejecta pellets as observed at Albury, as well as at Alma Park (Spennemann, 2018c, in prep.), is bright orange, that is, that of the Khalal stage. There is no indication that fruit of the Rutab stage were consumed when both stages were available (in the Alma Park setting). It is possible that the preference for drupes at the Khalal stage is a function of the moisture content that is about 45% less when the drupe reaches the Rutab stage.

4. THE FEEDING AND MASTICATION PROCESS

There are only a few studies in the literature that discuss the process of food consumption or mastication among *Pteropus* sp. and the allied genera. Bite and chew marks left by fruit bats on fruit are rarely documented in the literature (McConkey & Drake, 2015). Dumont and O'Neal (2004) identified two postures of fruit handling (entire fruit in mouth of cheek vs. fruit held against chest) and four types of bites, depending on whether the bite is unilateral or bilateral, and the position of the fruit in the mouth, that is, centred over canine and incisor teeth (shallow) or centred over premolar and molar teeth (deep).

The relative hardness of fruit has been shown to be a major criterion for its attractiveness (Dumont, 1999; Dumont & O'Neal, 2004), with larger bats being able to utilise harder foods to a greater degree (Aguirre et al., 2003). De Gueldre

and De Vree (1984, 1990) examined the mechanics of chewing and the forces in the mastication process (see also Herrel et al., 2008). Not surprisingly, the mechanics of chewing changed with the ripeness (hardness) of the fruit consumed. The bites shifted from the molars (deep) to the front (shallow) as hardness decreased (see also Dumont & O'Neal, 2004). Dumont and Herrel (2003) looked at the effects of gape angle and bite point on the bite force and discussed the effects of unilateral and bilateral canine biting to penetrate the skin of fruit. Once bitten off, the fruit is well masticated.

Birt et al. (1997) examined the morphology of the tongue of six large Australian bat species. The tongue with its role of collecting and manipulating food within the mouth prior to swallowing, forms a major component of the megachiropteran digestive system. The *P. poliocephalus* tongue is broad and club-like, eminently suitable for compression at its tip and its root end.

While small fruit, such as the drupes of *Washingtonia robusta*, can be taken whole and then chewed (Spennemann, 2018e), larger fruits have to be handled. In this instance, fruit bats will bite or strip chunks of epi- and pericarp off larger seeds (Figure 2) and drop the stripped seed itself (Figure 3) (Nakamoto et al., 2007). The bitten off matter is then masticated to a bolus of smooth consistency. De Gueldre and De Vree (1984) noted that the bolus 'regularly shifted back and forth between sides during masticatory cycles' with posterior part of the tongue pressing the bolus against the palate. As far as it can be ascertained, the mastication process does not crush any seeds that may be present in the fruit mass. If the observations made at *Washingtonia robusta* pellets are any guide (see below), then any seeds that are present in the bolus are manipulated to the front of the mouth, away from the molars and pre-molars. Given the high concentration of clean seeds that were encountered underneath the *Washingtonia robusta*, scattered among the pellets (Figure 12), suggests that the majority of seeds are pushed to the frontal arc and spat out during mastication, while the bolus is still retained in the mouth. It can be surmised that the feeding habit of *Pteropus poliocephalus*, that is, masticating while hanging upside down, assists in the separation of seeds from the soft bolus and also prevents the accidental swallowing of larger seeds as only fruit juices are pushed towards the oesophagus.

During each chewing cycle, the bolus is pressed against the palate with the tongue, squeezing out some of the juices which are swallowed (Bonaccorso & Gush, 1987; De Gueldre & De Vree, 1984; Morrison, 1980; Richardson et al., 1987; Storch, 1968). In the process, small amounts of pulp, as well as very small seeds, can be ingested with the juice (and defecated in due course). In the final process, the bolus is firmly pressed against the palate with the tongue. The residual, a squeezed-out conglomerate of dry fruit pulp, epicarp and small seeds, is not ingested but spat out as a pellet (Banack, 1998; Nakamoto et al., 2007; Ratcliffe, 1932). De Gueldre and De Vree (1984) suggest that 'the extremely flattened bolus is pushed out of the mouth laterally by an exaggerated lateral movement

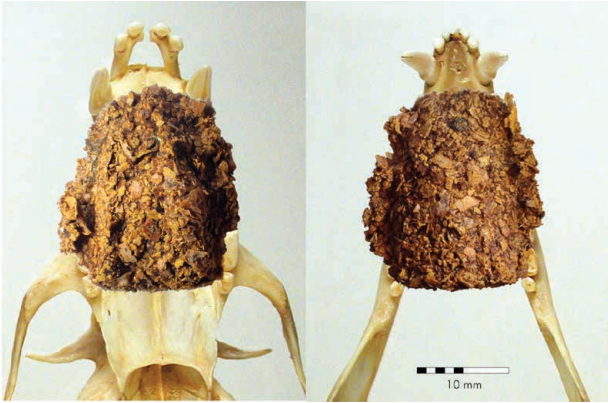


Figure 7. Ejecta pellet (Figure 6) superimposed on a skull a *Pteropus poliocephalus* (Base image of skull courtesy Museums Victoria [specimen n° C 17654])



Figure 10. Fragment of an ejecta pellet primarily comprised of *Washingtonia robusta* epicarp fragments with a complete seed

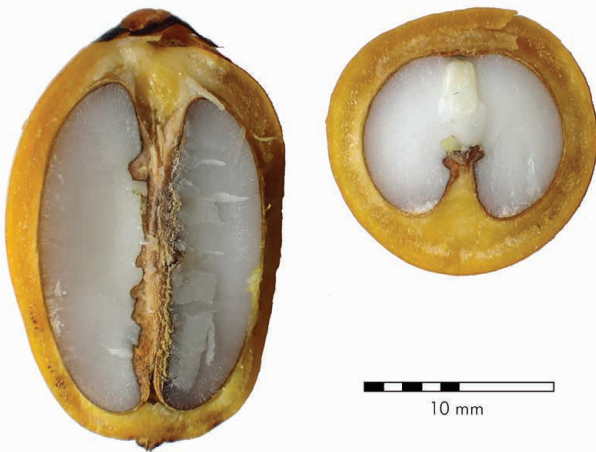


Figure 8. Longitudinal and transversal cross-section through a *Phoenix canariensis* drupe



Figure 11. *Phoenix canariensis* seed with *Pteropus poliocephalus* bite marks



Figure 9. Fragment of an ejecta pellet primarily comprised of *Phoenix canariensis* epicarp fragments with a complete seed (Alma Park)

of the tongue.' Each of the resulting pellets effectively represents one mouthful of fruit, the volume of which is determined by: i) the amount of juice versus fibre on the fruit, and ii) the size of the mouth cavity of the fruit bat species. There were no studies found that discuss the duration of the mastication prior to ejection of the pellet. The experimental study by De Gueldre and De Vree (1984) only considered comparatively soft and seedless foods (banana, apple and raisins). It can be assumed that the duration of mastication depends on both the hardness



Figure 12. Ground litter underneath the *Washingtonia robusta* at 701 Forrest Hill Avenue, Albury, NSW Note the heavy concentration of bare seeds and *Pteropus poliocephalus* spat-outs

and the consistency (fibrous-ness and juiciness) of the pericarp. In the case of high fibre, low pulp fruit such as those of *Phoenix canariensis*, we can assume a longer mastication time than, say, among other palm drupes such as those of *Washingtonia robusta*.

In total, 27 ejecta were measured in three dimensions: length (frontal to distal) 19.12 ± 2.70 mm (14.72–24.45); width (buccal to buccal) 20.84 ± 2.14 mm (16.62–24.64); and thickness 8.24 ± 1.31 mm (6.17–11.13). The most complete ejecta showed a proportion with a width of about 93% of the length (Spennemann, 2018b). The majority of the ejecta, however, were damaged, with the length (but not the width) curtailed. Some of the complete ejecta showed compression lines at right angles to the long axis. While they could correspond with the palate ridges, as asserted by De Gueldre and De Vree (1984), the alignment of epicarp platelets tends to suggest that the mastication process occurs in stages whereby the bolus is progressively compressed towards the frontal arc.

Unlike the agriculturally grown commercial date palm (*Phoenix dactylifera*), the Canary Island date palm (*Phoenix canariensis*) does not produce a very fleshy fruit (Figure 8). A sample of 100 ripe drupes showed an average non-seed component (epicarp and pericarp) of 53.8% (1.38 ± 0.16 g) (Spennemann, 2018b).

The 52 ejecta retrieved from underneath the *Washingtonia robusta* were smaller: length (frontal to distal): 14.67 ± 1.67 mm (12.33–20.00); width (buccal to buccal) 16.27 ± 1.62 mm (13.44–20.03); and thickness 6.52 ± 0.88 mm (4.67–8.69) (Spennemann, 2018e). The differences between the two samples are significant at $P > 0.00001$ for all the three dimensions. As each of the resulting pellets effectively represents one mouthful of fruit (see above), the reduced volume of the *Washingtonia robusta* ejecta suggests a much higher amount of juice versus fibre among the *Washingtonia* drupes compared to those of *Phoenix canariensis*.

The intestinal tract of *Pteropus* spp. is comparatively short (Richardson et al., 1987; Tedman & Hall, 1985) and designed to digest nectar, pollen, fruit juices and fruit pulp, but not hard matter such as seeds (Manley & Williams, 1979). Consequently, the gastro-intestinal transit time among *Pteropus poliocephalus* is comparatively short, ranging between 15 and 100 minutes (Tedman & Hall, 1982), with studies of captive specimens showing 18–32 minutes (Tedman & Hall, 1985). This is in the same range as the gastro-intestinal transit time among the slightly smaller *Pteropus rufus* (Oleksy et al., 2017). Even though the retention time is short, some accidentally swallowed, very small seeds may well have a slower passage time than pollen and fruit juices (Shilton et al., 1999).

5. DISPERSAL OF PHOENIX CANARIENSIS SEEDS

The vast majority of seed of fruits consumed by *Pteropus poliocephalus* will be deposited at the base of the food source. The spatial spread of the seed rain caused by *P. poliocephalus* can

be readily demonstrated in the case of a 21 m tall *Washingtonia robusta* standing isolated in a carpark with a bitumen surface (595 Stanley Street, coordinates -36.079039, 146.912351). An inner zone of 1.8 m radius around the trunk contains a high concentration of seeds (distances less than 3 cm) as well as numerous bat ejecta. An outer zone with a radius of 3.5 m contains a high concentration of seeds (distances 5–10 cm) but no ejecta, while the periphery, with a radius of 8–10 m shows a thin scatter of seeds (distances less 0.5 to 2 m) without ejecta. Given the hard surfaces, a certain amount of ‘bounce’ of the dropped seeds cannot be ruled out, which may account for the scatter at the periphery. Similarly, observations at a row of *Phoenix canariensis* at Alma Park (NSW) showed that the ejecta were limited to a zone of about 1.8 m diameter around the palm trunk, less than the overall reach of the crown (Spennemann, 2018c).

Studies of *Pteropus poliocephalus* faeces in the roosting areas/camps contain a large percentage of pollen grains but there is little evidence of bulk items such as seeds (Tedman & Hall, 1985), which suggests that the ingestion of seeds is an uncommon occurrence. While Dumont and Herrel (2003) measured the gape angles, there are no data on the actual gape (gullet) size of *P. poliocephalus*. The gastrointestinal tract of frugivorous bats is narrow, thus limiting the maximum seed size that can pass to about 5 mm in diameter (Corlett, 1998; Richards, 1990; van Leeuwen, 1935), even though longer, but not thicker, seeds can be ingested subject to ‘seed slipperiness’ (Bollen & Van Elsacker, 2002). During captive feeding studies, *P. poliocephalus* ingested seeds up to a maximum size of 4.2 mm (Eby, 1996).

Irrespective, the seeds of *Phoenix canariensis* are too thick to be ingested whole. The seeds extracted from the 100 ripe drupes (see above) had an average length of 16.60 ± 0.77 mm (range 14.77–18.99), an average width of 10.79 ± 0.46 mm (range 9.67–12.20), and an average thickness of 9.29 ± 0.50 mm (range 8.02–10.56) (Spennemann, 2018b). These dimensions rules out an accidental intestinal dispersal of *Phoenix canariensis* by *Pteropus poliocephalus*.

Given the process of mastication, ingestion of juices and ejection of dry matter, the bulk of food processing activity occurs at the feeding site. There is evidence, however, that the last mouthful of fruit may well remain in the mouth upon departure, to be processed later, with the dry bolus ejected either en route (Tsoar et al., 2010) or at the roost. Studies of *Pteropus* species frequently noted the presence of ejecta pellets under roost sites (Javid et al., 2017; Parry-Jones & Augee, 1991; Schmelitschek et al., 2009; Vendan & Kaleeswaran, 2011). In droppings (combined ejecta and faeces) on the ground underneath, the *Pteropus poliocephalus* colony at Matcham near Gosford, Parry-Jones and Augee (1991) even noted plant remains (but no seeds), which they attributed to *Phoenix canariensis*.

As studies of *Rousettus aegyptiacus* (Tsoar et al., 2010) as well as *Pteropus giganteus* attest (Gulraiz et al., 2016; Vendan & Kaleeswaran, 2011), mid- to long-range seed dispersal as part of the ‘last mouthful’ is certainly possible. This can

also be inferred for *Pteropus poliocephalus*, as twelve (22.2%) of the 52 measured ejecta underneath the *Washingtonia robusta*, contained a *Washingtonia* seed, with one of the ejecta containing two seeds (Spennemann, 2018e). The thirteen *Washingtonia robusta* seeds retrieved from the ejecta, measured 7.15 ± 0.81 mm (4.55–7.79) in length, 5.38 ± 0.45 mm (4.42–5.99) in width; and 4.48 ± 0.36 mm (3.63–4.87) in thickness (Spennemann, 2018e), and thus, were far smaller than the seeds of *Phoenix canariensis* seed (see above).

Self-seeded specimens of an unknown cultivar of the commercial-grown date palm (*Phoenix dactylifera*) have been noted underneath two roost sites of *Pteropus giganteus* in Southern India (Vendan & Kaleeswaran, 2011), suggesting that the seeds were carried to the roost as part of the final mouthful of food and ejected at the roost. Likewise, in northern Pakistan, complete seeds of an unknown cultivar of *Phoenix dactylifera*, were extracted from ejecta pellets of *P. giganteus*. Gulraiz et al. (2016) noted that these seeds measured on average 28.1×25.4 mm, but only had a mass of 0.06 g (i.e., were quite flat compared to the *Phoenix canariensis* seed).

As *Pteropus giganteus* is anatomically generally comparable with, but slightly smaller than *P. poliocephalus* (head length of 60.1 ± 2.7 mm compared to the 72.8 ± 2.8 mm *P. poliocephalus*) (Herrel et al., 2008), we can assume that *P. poliocephalus* too may be a disperser of large seed. Indeed, during an assessment of self-seeded palms and their parent trees in a managed agricultural landscape at Alma Park, NSW (Spennemann & Pike, in prep.), numerous *Pteropus poliocephalus* were noted under the seed trees (Spennemann, 2018c). A few of these contained a single *Phoenix canariensis* seed (e.g., Figure 9), usually located at the apex of the ejecta, i.e., close to the incisors.

6. IMPLICATIONS

Pteropus poliocephalus have been observed as feeding on ornamental palm species (*Phoenix canariensis* and *Washingtonia robusta*) in suburban settings. Unlike Pied Currawong (*Strepera graculina*), who can swallow multiple drupes whole (Spennemann, 2018a) and move them in their gut to perches and roosts (a maximum of ten is recorded in a regurgitate pellet, Buchanan, 1989), the dispersal capacity of *Pteropus poliocephalus* is limited to seeds that are contained in the last mouthful of food they were masticating, as well as the very small seeds that may have been accidentally ingested while swallowing fruit juices.

The size of the mouth cavity of *Pteropus poliocephalus* limits the size of the seed that can be manipulated during mastication. While *Washingtonia robusta* seeds have been documented in the ejecta, the seeds of *Phoenix canariensis* have not been found, presumably because they are far too large to be manipulated in the mouth. While it is theoretically possible for a *Pteropus poliocephalus* to carry a single drupe in its mouth in flight (and consume it at another perch or the roost), this behaviour has not been observed.

Consequently, *Pteropus poliocephalus* can be ruled out as dispersers of *Phoenix canariensis*, but need to be considered as dispersers of *Washingtonia robusta*. Even though *W. robusta* is much less successful as a colonising plant than *P. canariensis*, it has become naturalised in several parts of the world. In order to assess the actual dispersal success of ornamental palms, more studies are needed that focus on the seedling growth and established vegetation under and near *P. poliocephalus* roosts in urban and peri-urban areas.

References

- Aguirre LF, Herrel A, Van Damme R, Matthyssen E. The implications of food hardness for diet in bats. *Funct Ecol.* 2003;17(2):201-212. doi:10.1046/j.1365-2435.2003.00721.x.
- Ahmed I, Ahmed AWK, Robinson RK. Chemical composition of date varieties as influenced by the stage of ripening. *Food Chem.* 1995;54(3):305-309. doi:10.1016/0308-8146(95)00051-1.
- Andronicos, M. (2018, April 12). [Origin of the *Phoenix canariensis* at n° 708 Forrest Hill Avenue, Albury, NSW].
- Augee ML, Parry-Jones KA. The diet of Flying-foxes in the Sydney and Gosford areas of New South Wales, based on sighting reports 1986–1990. *Aust Zool.* 1991;27(3–4):49-54.
- Banack SA. Diet selection and resource use by flying foxes (genus *Pteropus*). *Ecology.* 1998;79(6):1949-1967. doi:10.2307/176701.
- Barrow SC. A Monograph of *Phoenix L.* (Palmae: Coryphoideae). *Kew Bull.* 1998;53(3):513-575. doi:10.2307/4110478.
- Biosecurity Queensland. (2018). *Phoenix canariensis* hort. ex Chabaud. Weeds of Australia Biosecurity Queensland Edition. Retrieved from https://keyserver.lucidcentral.org/weeds/data/media/Html/phoenix_canariensis.htm
- Birt P, Hall LS, Smith GC. Ecomorphology of the tongues of Australian megachiroptera (Chiroptera: Pteropodidae). *Aust J Zool.* 1997;45(4):369-384. doi:10.1071/ZO97005.
- Bollen A, Elsacker LV. Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce, SE Madagascar. *Acta Chiropt.* 2002;4(1):33-47. doi:10.3161/001.004.0105.
- Bonaccorso FJ, Gush TJ. Feeding behaviour and foraging strategies of active phyllostomid fruit bats: an experimental study. *J Anim Ecol.* 1987;56(3):907-920. doi:10.2307/4956.
- Brodie C, Reynolds T. (2012). Review of recent plant naturalisations in South Australia and initial screening for weed risk. Department for Environment and Natural Resources Technical Report 2012/02, n°. Adelaide
- Buchanan RA. Pied Currawongs (*Strepera graculina*): their diet and role in weed dispersal in suburban Sydney, New South Wales. *Proc Linn Soc N S W.* 1989;111(1–4):241-255.

- Campbelltown City Council. (2015). Garden Weeds & Bushland Invaders. n^o. Campbelltown, SA Conn, B., & Walsh, N. (1993). Areca-aceae. In N. Walsh & T. Entwistle (Eds.), *Flora of Victoria* (pp. 165–167). Inkata Press: Melbourne.
- Corlett RT. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biol Rev Camb Philos Soc.* 1998;73(4):413-448. doi:10.1017/S0006323198005234. Medline
- Greet DG, De Vree F. Movements of the mandibles and tongue during mastication and swallowing in *Pteropus giganteus* (Megachiroptera): A cineradiographical study. *J Morphol.* 1984;179(1):95-114. doi:10.1002/jmor.1051790109. Medline
- Gueldre G, Vree F. Biomechanics of the masticatory apparatus of *Pteropus giganteus* (Megachiroptera). *J Zool.* 1990;220(2):311-332. doi:10.1111/j.1469-7998.1990.tb04310.x.
- Department of the Environment and Energy. (2017). Species Profile and Threats Database. Species Profile and Threats Database. Retrieved from http://www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=186
- Hume DEWLP. (2017, Sep 6). Flying Foxes in the Hume Region [Facebook Post]. Retrieved from <https://www.facebook.com/DELWPHume/posts/1103797886419547>
- Djouab A, Benamara S, Gougam H, Amellal H, Hidous K. Physical and antioxidant properties of two Algerian date fruit species (*Phoenix dactylifera* L. and *Phoenix canariensis* L.). *Emir J Food Agric.* 2016;28(9):601-608. doi:10.9755/ejfa.2015-12-1056.
- Dumont ER. The effect of food hardness on feeding behaviour in frugivorous bats (Phyllostomidae): an experimental study. *J Zool.* 1999;248(2):219-229. doi:10.1111/j.1469-7998.1999.tb01198.x.
- Dumont ER, Herrel A. The effects of gape angle and bite point on bite force in bats. *J Exp Biol.* 2003;206(13):2117-2123. doi:10.1242/jeb.00375. Medline
- Dumont ER, O'Neal R. Food hardness and feeding behavior in Old World fruit bats (Pteropodidae). *J Mammal.* 2004;85(1):8-14. doi:10.1644/BOS-107.
- Eby, P. (1996). Interactions between the grey-headed flying fox *Pteropus poliocephalus* (Chiroptera: Pteropodidae) and its diet plants—seasonal movements and seed dispersal. (DPhil), University of New England, Armadale.
- Eby P, Richards G, Collins L, Parry-Jones K. 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. *Aust Zool.* 1999;31(1):240-253. doi:10.7882/AZ.1999.024.
- Eco Logical Australia. (2014). Kareela Flying Fox Camp Plan of Management – Final. Prepared for Sutherland Shire Council. n^o. Sutherland
- Esler AE, Astridge SJ. The naturalisation of plants in urban Auckland, New Zealand 2. Records of introduction and naturalisation. *N Z J Bot.* 1987;25(4):523-537. doi:10.1080/0028825X.1987.10410084.
- Gulraiz TL, Javid A, Mahmood-Ul-Hassan M, Hussain SM, Azmat H, Daud S. Role of Indian flying fox *Pteropus giganteus* Brünnich, 1782 (Chiroptera: Pteropodidae) as a seed disperser in urban areas of Lahore, Pakistan. *Turk J Zool.* 2016;40:417-422. doi:10.3906/zoo-1407-42.
- Herrel A, De Smet A, Aguirre LF, Aerts P. Morphological and mechanical determinants of bite force in bats: do muscles matter? *J Exp Biol.* 2008;211(1):86-91. doi:10.1242/jeb.012211. Medline
- Hosking JR, Conn BJ, Lepschi BJ, Barker CH. Plant species first recognised as naturalised for New South Wales in 2002 and 2003, with additional comments on species recognised as naturalised in 2000–2001. *Cunninghamia.* 2007;10(1):139-166.
- Hunter Councils Environment Division. (2017). Flying-Fox Camp Management Plan. Murrurundi Camp Management Plan. n^o. Thornton, NSW
- Javid A, Gulraiz TL, Ashraf M, et al. Proximate analysis of Indian flying fox's (*Pteropus giganteus*) natural food, with a note on its roost variations in urban areas of Lahore, Pakistan. *Turk J Zool.* 2017;41:714-721. doi:10.3906/zoo-1512-24.
- Lohr MT, Keighery GJ. The status and distribution of naturalised alien plants on the islands of the west coast of Western Australia. *Conserv Sci W Aust.* 2016;10(1):1-43.
- Manley DB, Williams LM. Structure of the Gastro-Intestinal Tract of the Flying Fox *Pteropus poliocephalus*. *J Anat.* 1979;128:649-650.
- McConkey, K. R., & Drake, D. R. (2015) Low redundancy in seed dispersal within an island frugivore community. *AoB PLANTS*, 7(plv088). doi: <https://doi.org/10.1093/aobpla/plv088>
- McDonald-Madden E, Schreiber ESG, Forsyth DM, Choquenot D, Clancy TF. Factors affecting Grey-headed Flying-fox (*Pteropus poliocephalus*: Pteropodidae) foraging in the Melbourne metropolitan area, Australia. *Austral Ecol.* 2005;30(5):600-608. doi:10.1111/j.1442-9993.2005.01492.x.
- Messaro, M. (2018, Feb 26). [Birds feeding in palms on my property at Burumbuttock].
- Morrison DW. Efficiency of food utilization by fruit bats. *Oecologia.* 1980;45(2):270-273. doi:10.1007/BF00346469. Medline
- Nakamoto A, Sakugawa K, Kinjo K, Izawa M. Feeding effects of Orii's flying-fox (*Pteropus dasymallus inopinatus*) on seed germination of subtropical trees on Okinawa-jima Island. *Tropics.* 2007;17(1):43-50. doi:10.3759/tropics.17.43.
- Nelson JE. (1989). 37. Pteropodidae. In D. W. Walton & B. J. Richardson (Eds.), *Fauna of Australia* (Vol. 1B Mammalia).
- Oleksy R, Giuggioli L, McKetterick TJ, Racey PA, Jones G. Flying foxes create extensive seed shadows and enhance germination success of pioneer plant species in deforested Madagascan landscapes. *PLoS One.* 2017;12(9):e0184023. doi:10.1371/journal.pone.0184023. Medline
- Parry-Jones K, Augée ML. Food Selection by Grey-headed Flying Foxes (*Pteropus poliocephalus*) Occupying a Summer Colony Site near Gosford, New South Wales. *Wildl Res.* 1991;18(1):111-124. doi:10.1071/WR9910111.
- Parry-Jones KA, Augée ML. Factors affecting the occupation of a colony site in Sydney, New South Wales by the Grey-headed Flying-fox *Pteropus poliocephalus* (Pteropodidae). *Austral Ecol.* 2001;26(1):47-55.
- Ratcliffe F. Notes on the fruit bats (*Pteropus* spp.) of Australia. *J Anim Ecol.* 1932;1(1):32-57. doi:10.2307/993.
- Richards GC. The spectacled flying-fox, *Pteropus conspicillatus* (Chiroptera: Pteropodidae), in North Queensland. 2. Diet, seed dispersal and feeding ecology. *Aust Mammal.* 1990;13:25-31.

- Richardson KC, Stuebing RB, Normah HK. Alimentary tract morphology and digesta transit of some Malaysian chiropterans. *Indo-Malayan Zoology*. 1987;4:399-412.
- Roberts BJ, Catterall CP, Eby P, Kanowski J. Long-distance and frequent movements of the flying-fox *Pteropus poliocephalus*: implications for management. *PLoS One*. 2012;7(8):e42532. doi:10.1371/journal.pone.0042532. Medline
- Roots, P. (2018, Apr 9). [Flying Fox colony near Albury].
- Schmelitschek E, French K, Parry-Jones K. Fruit availability and utilisation by grey-headed flying foxes (Pteropodidae: *Pteropus poliocephalus*) in a human-modified environment on the south coast of New South Wales, Australia. *Wildl Res*. 2009;36(7):592-600. doi:10.1071/WR08169.
- Shilton LA, Altringham JD, Compton SG, Whittaker RJ. Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proc Biol Sci*. 1999;266(1416):219-223. doi:10.1098/rspb.1999.0625.
- Shire of Manjimup. (2008). Shire of Manjimup Weed Strategy. n°. Manjimup
- Spennemann DHR. (2018a). *Phoenix canariensis* and *Washingtonia robusta* drupes consumed by the Pied Currawong (*Strepera graculina*). A photographic documentation. n°. Albury, NSW
- Spennemann DHR. (2018b). *Phoenix canariensis* drupes consumed by the Grey-headed flying-fox (*Pteropus poliocephalus*). A photographic documentation. n°. Albury, NSW
- Spennemann DHR. (2018c). *Phoenix canariensis* seed in scats and ejecta collected at Alma Park, and Walla Walla, NSW. A photographic documentation. n°. Albury, NSW
- Spennemann DHR. Review of the vertebrate-mediated dispersal of the Date Palm, *Phoenix dactylifera*. *Zool Middle East*. 2018d;64. doi: 10.1080/09397140.2018.1514785.
- Spennemann DHR. (2018e). *Washingtonia robusta* drupes consumed by the Grey-headed flying-fox (*Pteropus poliocephalus*). A photographic documentation. n°. Albury, NSW
- Spennemann DHR. Inter-specimen variability of drupes and seed among *Phoenix canariensis* palms in the Southern Riverina, Australia. *J Horticult Res*. (in prep.). projected journal.
- Spennemann DHR. Canary Date Palms (*Phoenix canariensis*) in Australia—introduction and early dispersal. *Palms*. In press. accepted.
- Spennemann DHR. (subm.-a) Canary Date Palms (*Phoenix canariensis*) as ornamental plants. The first thirty years of the horticultural trade. *Huntia*. (under review).
- Spennemann DHR. (subm.-b) Palms fanning out. A review of vertebrate vectors responsible for the dispersal of *Washingtonia filifera* and *W. robusta*. *Rodriguésia*. (under review).
- Spennemann DHR. (subm.-c) When Palms go AWOL. A review of vertebrate vectors responsible for the dispersal of the Canary Island date palm (*Phoenix canariensis*). *Plant Ecol Divers*. (under review).
- Spennemann DHR, Pike M. Feral *Phoenix Canariensis* in an agricultural landscape: nature and patterns of dispersal. *Aust J Bot*. (in prep.). projected journal.
- Storch G. (1968). Funktionsmorphologische Untersuchungen an der Kaumuskulatur und an korrelierten Schädelstrukturen der Chiropteren. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, n° 517. Stuttgart
- Tedman RA, Hall LS. The morphology of the gastrointestinal tract of the fruit bats *Pteropus alecto* and *P. poliocephalus* (Megachiroptera). *Bulletin of the Australian Mammal Society*. 1982;7:58.
- Tedman RA, Hall LS. The morphology of the gastrointestinal tract and food transit time in the fruit bats *Pteropus alecto* and *P. poliocephalus* (Megachiroptera). *Aust J Zool*. 1985;33(5):625-640. doi:10.1071/ZO9850625.
- Triggs B. (2004) Tracks, scats, and other traces: a field guide to Australian mammals (2nd ed.). Melbourne: Oxford University Press.
- Tsoar A, Shohami D, Nathan R. (2010). A Movement Ecology Approach to Study Seed Dispersal and Plant Invasion: An Overview and Application of Seed Dispersal by Fruit Bats Fifty Years of Invasion Ecology: The Legacy of Charles Elton (pp. 101 – 119).
- Tsoar A, Shohami D, Nathan R. (2011). A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats. In D. M. Richardson (Ed.), *Fifty Years of Invasion Ecology: The Legacy of Charles Elton* (pp. 101–119). New York: Wiley-Blackwell.
- van Leeuwen WMD. The dispersal of plants by fruit-eating bats. *Gardens' Bulletin. Straits Settlement*. 1935;9:58-63.
- Vendan SE, Kaleeswaran B. Plant dispersal by Indian flying fox *Pteropus giganteus* in Madurai region, India. *Elixier Bio Diversity*. 2011;30:1810-1813.
- Virtue JG, Spencer RD, Weiss JE, Reichard SE. Australia's Botanic Gardens weed risk assessment procedure. *Plant Prot Q*. 2008;23(4):166-178.
- Walters B. (2006). Preliminary investigation into the cause of crown damage in Canary Island Palm (*Phoenix canariensis*) at Catani Gardens, St. Kilda. n°. Melbourne
- Williams NSG, McDonnell MJ, Phelan GK, Keim LD, Van Der Ree R. Range expansion due to urbanization: Increased food resources attract Grey-headed Flying-foxes (*Pteropus poliocephalus*) to Melbourne. *Austral Ecol*. 2006;31(2):190-198. doi:10.1111/j.1442-9993.2006.01590.x.
- Zona S. The horticultural history of the Canary Island Date Palm (*Phoenix canariensis*). *Gard Hist*. 2008;36:301-308.