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

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**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 carbo-hydrate reach 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**


**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 (Andronics, 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 a 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 absicised 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...
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 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-ellipse 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 ellipse (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, fully coloured (Khalal) to soft brown (Rutab) and finally hard raisin (Tamra) (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 Gueudre 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 Gueuldre 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 Gueuldre & 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, epipcarp and small seeds, is not ingested but spat out as a pellet (Banack, 1998; Nakamoto et al., 2007; Ratcliffe, 1932). De Gueuldre and De Vree (1984) suggest that ‘the extremely flattened bolus is pushed out of the mouth laterally by an exaggerated lateral movement
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 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
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 Guedre 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. DISPERAL 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 gastro-intestinal 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 x 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, presumable 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.

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