



The contribution of the Canary Island date palm (*Phoenix canariensis*) to the winter diet of frugivores in novel ecosystems

¹Institute 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^{1*}

ABSTRACT

With the increasing expansion in urban areas, many species have adapted to utilising horticulturally used plants as alternate or augmentary food sources, in particular, during winter – when native foods are largely absent. Ornamental palms, particularly Canary Island Date Palms, fruit continuously during most of the year and thus provide a stable food supply. Based on observational, metric and bio-chemical data, this paper examines the role Canary Island Date Palms can and do play in the nutrition of frugivorous animals, in particular, for birds. It demonstrates that with its nearly year-round provisioning of drupes, the palm plays a major role as a 'staple' and backup food source for several species.

KEYWORDS

Frugivory; novel ecosystems; urban landscapes, nutritional analysis

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INTRODUCTION

Across the globe, the later periods of the Anthropocene have seen a rapid expansion of urban as well as production landscapes at the expense of 'natural' (i.e., largely unmodified) environments, which are reduced in size and increasingly fragmented (e.g., Atasoy, 2018; Canedoli et al., 2018; Gbanie et al., 2018; Liu et al., 2019). In these heavily modified landscapes, novel ecosystems have developed, which are populated by a pastiche of native and exotic animals feeding on native and exotic food sources (Adams et al., 2005; Hobbs et al., 2013; Miller & Bestelmeyer, 2016).

The diversity of ornamental plants is dependent on the age of the urban development and the horticultural fashions prevalent at the time of establishment. Whereas the older urban landscapes tend to have established gardens with established ecosystems dominated by large remnant trees and established horticulturally planted trees in street and garden plantings, the recent urban sprawl increasingly converts exotic

cleared production landscapes into suburbia, dominated by architectural monotony, small parcellation and a horticulturally largely treeless monoculture of lawns and low scrub (e.g., Boling, 1990; Laws, 1995; Hall, 2010; Brunner & Cozens, 2013; Giner et al., 2013). Despite concerted research (e.g., Burghardt et al., 2009; Lerman & Warren, 2011) and policy moves to the contrary (e.g., Müller et al., 2013; Hartin et al., 2014), by and large, native plants have been replaced by exotics (e.g., Yee, 1990; Hernández et al., 2014) with implications on avifauna biodiversity (e.g., Clergeau et al., 2006; van Heezik & Adams, 2016).

These new urban landscapes with their entirely novel environment provide for new ecological resources (i.e., shelter, nesting site and food) and are rapidly filled with commensal, commonly invasive animal species (G. C. Smith & Carlile, 1993; Williams et al., 2006; A. C. M. Smith & Munro, 2010; Shazali et al., 2016; Pike et al., 2017; Spennemann & Watson, 2017). Additionally, resources provided by the novel environment are

utilised by species that arrive from surrounding areas to forage on fruit-bearing plants and human refuse in urban spaces and return to their external roots at night (Bass, 1996; Guix, 2007; Washburn et al., 2013; Jankowiak et al., 2016; Santana & Armstrong, 2017). Often, over a short period of time, the latter species are becoming habituated and adapt to or exploit the new opportunities (Kark et al., 2007; Carrete & Tella, 2011; Blumstein, 2014; Johnson & Munshi-South, 2017; Howell & Clements, 2019).

In an ecosystem of reduced biodiversity, the number of plant-animal interactions are reduced as well. In urban environments, all horticultural plantings are governed by the needs to satisfy the anthropocentric amenity values of utility, to ameliorate the thermal stress, both through the provision of shade and through cooling provided by evapotranspiration (Shashua-Bar et al., 2012; Brown et al., 2015; Lee et al., 2016), and of visual satisfaction (size, shape, colour, scent of plants). It is in particular the latter ornamental plants that provide a diversity of flowers, nectar, fruit and seeds that are consumed by commensal or habituated species. While there are numerous studies that examine the plant-animal interactions in urban environments (e.g., G. C. Smith & Carlile, 1993; Shazali et al., 2016), studies on the nutritional value of such diets and their implications are rare (e.g., Møller et al., 2010; Spennemann & Watson, 2017; Townsend et al., 2019). There is even less work conducted that looks at the nutritional values and seasonal availability of food sources in relation to the consumer species.

Ornamental plants are subject to fashion trends. Whereas flowers (bulbs or creepers) and shrubs are readily replaced as fashion changes, trees tend to be retained. One of these previously fashionable and now persistent types of plants are palms. Palms are ubiquitous ornamental plants in many urban and sub-urban landscapes in warm temperate to tropical climates. Often planted during the palm craze of the late nineteenth and early twentieth century, the palms evoked a sense of the exotic (Watts, 2000; Hodel, 2009; Piana et al., 2019) and, on a public level, also to demonstrate colonial connections and aspirations (Casid, 2015; Griggs, 2015). They also conjured up a sense of status reflective of a life of leisure and luxury along the French and Italian Riviera (Campodonico et al., 2015; Spennemann, 2018a). Because of its hardiness as well as its lush ornamental crown, the Canary Island Date palm was particularly popular, and thus, is widespread.

This paper will review what is known about fruiting patterns and nutritional value of the drupes of Canary Island Date Palms and, drawing on observational, metric and chemical-analytical data collected in Australia, it will discuss the role of these palms in present and emerging urban eco-systems.

1. BACKGROUND

There is an increasing body of literature that examines the aspects of frugivory among avian as well as terrestrial vertebrates and the associated dispersal of seeds in urban landscapes (G. C. Smith & Carlile, 1993; Wood, 1998; Williams et al., 2006; A.

C. M. Smith & Munro, 2010; Washburn et al., 2013; Shazali et al., 2016; Santana & Armstrong, 2017; Spennemann & Watson, 2017). Such landscapes are commonly comprised of urban and sub-urban gardens, street plantings and urban parks as well as patches of remnant bushland. This hybrid environment provides for new ecological niches, where dispersal opportunities have developed for a range of fruiting ornamental plants to invade surrounding bushland and patches of remnant vegetation. This dispersal is facilitated, in particular, by vectors that exhibit a high level of connective potential between ecological landscapes (urban, suburban, agricultural, etc.) (unpubl. ms.)

While many species are commensal and resident all year round, others are more seasonal. Some bird species, such as the Pied Currawong (*Strepera graculina*) flock into towns during winter (Anonymous, 1934; Platypus, 1939; Binns, 1940; Readshaw, 1968b, 1968a; Bass, 1995) to feed on fruits and seeds of ornamental plants, commonly exotics. Some work has been carried out on the winter diet of urban and sub-urban birds, noting that both native species, such as Lilly Pilly (*Acmena smithii*), and exotics, such as various privet species (*Ligustrum* spp.) play a role (Bass, 1995; Wood, 1998). The majority of prior research has focussed on berries and small drupes, which can be fed on and dispersed by numerous vectors.

Exotic plants are often seen as alternate or augmentary food sources, in particular, during winter when native foods are largely absent (Greenberg & Walter, 2010). Studies noted that exotic plants often provide higher returns in selective nutrients than endemic species and are thus favoured by frugivores (Seychelles: Kueffer et al., 2009; Thabette et al., 2015). Yet, some studies have shown that exotic fruit may have less nutritional value in anti-oxidants and trace minerals (Oguchi et al., 2017).

2. THE CANARY ISLANDS DATE PALM

The Canary Island Date Palm (*Phoenix canariensis* Wildpret 1882 ex Chabaud 1882) (Arecaceae) (Rivera et al., 2013) is a dioecious plant that is solely propagated by seed (Barrow, 1998). The seed germinates after 85–110 days and the plant shows its first two-leave shoots at about one year of age. It reaches reproductive maturity and first flowers after six to seven years. The palm seeds freely, annually producing between 5,000 to in excess of 30,000 obovoid dates. These dates, which have a limited fibrous flesh content, measure 15–20 mm in length and 12–15 mm in diameter. In its natural setting, *P. canariensis* will grow to about 18–20 m in height, with a stem usually of 0.6 to 0.8 m, but up to 1.2 m diameter. The crown has a diameter of 10–12 m, made up of in excess of 200 arching, pinnate fronds of 5–6 m (max 7 m) length. Unless affected by disease or pests, the plant can live for 200–300 years (Beech, 2017). A specimen in excess of 400 years was known (Bois, 1918, p. 43). Fully mature palms can weigh up to 10 tons in mass.

Distributed by the horticultural industry since the mid 1860s (Spennemann, 2019), and planted out in the open air from the 1890s until the present, the Canary Island date

palm has become a common landscaping element (Zona, 2008; Spennemann, 2018b). They have been employed as feature trees in private and public gardens as well as in the form of street trees lining avenues and boulevards. Compared to other hardy ornamental palm species, such as the Californian Fan Palm (*Washingtonia filifera* L. Linden) and the Mexican Fan Palm (*W. robusta* H. Wendl.), *P. canariensis* has seen the most rapid and widespread uptake and today is distributed globally in warm temperate zones (Spennemann, 2018c). The ease with which mature palm specimens can be transplanted makes them eminently suitable for 'instant' gardens. Suburban landscaping saw a resurgence in the interest in palms during the 1990s and early 2000s, so much so that some 3,500 mature Canary Island Date Palms were acquired in the Southern Riverina of Australia and transplanted to Melbourne and its suburbs (Booth, 2019). This trend was not confined to Australia, but also played out *inter alia* in Turkey (Sayan, 2001) and Spain. For example, during 2007 alone, over 600,000 palms were sold for landscaping during the millennial housing boom in Spain (Hernández et al., 2014).

Setting aside the consumption of young shoots and flowers, Canary Island Date Palm produce an abundance of drupes, which provide a food source for a range of species. While some of the vectors of the plant have been discussed in more detail such as Flying-Foxes (Spennemann, 2018d), Crows (Nogales et al., 1999), Currawongs (Spennemann, 2018e) and lizards (Nogales et al., 2015), little work has been carried out on the contribution that the Canary Island date palm might make to the diet of frugivores in novel ecosystems.

Traditional, as well as commercial date palm production in the Middle East and North Africa distinguishes four distinct stages of ripening of the drupe, from immature green (Arabic: *Khimri*) and mature, full coloured (*Khalal*) to soft brown (*Rutab*) and finally raisin (*Tamr*) (Ahmed et al., 1995; Baliga et al., 2011). Studies that discuss the nutritional values of *Phoenix canariensis* are rare, with the majority of work not directly relevant to the contribution of *Phoenix canariensis* to the diet of frugivores. Two papers focus on the chemical composition of the seeds (Nehdi et al., 2010; Nehdi et al., 2011), which is irrelevant for frugivorous birds. An Algerian study, looking at the potential uses of Canary Island Date Palm drupes (or their parts) as food additives, compared the phenolics and anti-oxidant qualities of *Phoenix canariensis* with those of the domesticated date palm (*Phoenix dactylifera*) and found that the total phenolics were several orders of magnitude larger among the Canary Island Date Palms (Djouab et al., 2016).

Canary Island Date Palms drupes are non-toxic but have an unpleasant, astringent taste that makes them unpalatable for human consumption (Djouab et al., 2016). A study by Amorós et al. (2014) assessed the sugar content of several *Phoenix* species as well as the content of a number of acids that contribute to the perception of sour and acrid tastes. The majority of *Phoenix* species examined in that paper are of no concern here, as they were not used in ornamental plantings and thus do not play a role in novel ecosystems. The values

for the *Khalal* and *Rutab* stages of *Phoenix canariensis* analysed by Amorós et al. (2014) have been reproduced in Table 1. Noteworthy is the dramatic increase in sugars between the two stages.

As commercially grown date palms (*Phoenix dactylifera*) form a staple in many countries in the Middle East as well as North and Central Africa (see the various country studied in Al-Khayri et al., 2015), it is not surprising that there is a large body of literature that exists on the chemical composition and nutritional values of various varieties (Marshall, 2003; e.g. Al-Farsi & Lee, 2008; Amorós et al., 2009; El-Sohaimy & Hafez, 2010; Sadiq et al., 2013; Juhaimi et al., 2014; Fatima, 2016). Even though the Canary Island Date Palm freely hybridises with its congener *P. dactylifera*, dates have been horticulturally grown as food crops for millennia, with concomitant systematic selection for various qualities (appearance, sugar content, texture, etc.). While the numeric values of these studies are therefore not directly applicable, several underlying trends for the various stages of ripening have informative value for the understanding of the nutritional value of Canary Island Date Palms.

The total carbohydrate, fructose and glucose content varies between *P. dactylifera* varieties and ripening stages. The fruit attains its maximum weight and size at the end of the *Khalal* stage. As fruits continue to ripen, the fructose and glucose content continues to rise with increasing sun hours. A study of twelve date varieties by Ahmed et al. (1995) showed on average, a 57.5% increase between the *Khalal* and *Rutab* stages, which ranged from 38% to 75%, depending on the variety. At the *Rutab* stage, the apex starts ripening and the texture of the fruit becomes soft, losing moisture (and thus, weight) and the drupe starts turning brown or black in colour. There is little in-

Table 1. Nutrient data from *Phoenix canariensis* drupes (values per 100 g fresh weight) (Amorós et al., 2014)

	Khalal	Rutab
Glucose	4.07 ± 0.20	13.56 ± 0.00
Fructose	5.27 ± 0.21	15.84 ± 0.01
Sucrose	0.06 ± 0.04	0.13 ± 0.00
Total sugars	9.4 ± 0.18	29.53 ± 0.01
Maturity index	44.19	136.67
Malic acid	0.64 ± 0.00	1.11 ± 0.07
Citric acid	0.82 ± 0.23	0.72 ± 0.00
Succinic acid	0.61 ± 0.02	1.79 ± 0.69
Ascorbic acid	0.05 ± 0.009	0.05 ± 0.001
Trolox equivalent antioxidant capacity	1077.25 ± 43.57	360.21 ± 12.63
Total phenols	179.87 ± 3.41	85.31 ± 7.64
Number of drupes	15	15

Table 2. Measurements of mid-season *Phoenix canariensis* drupes at Forrest Hill, Albury, and Alma Park, NSW

Location	Sample	Length (mm)	Thickness (mm)	Drupe Weight (g)	Pulp Weight (g)	% pulp by weight	n
Albury	Khalal Stage (Orange)	21.16 ± 1.29 (18.23–25.4)	14.01 ± 0.59 (12.73–15.37)	2.57 ± 0.25 (2.1–3.15)	1.38 ± 0.16 (1.04–1.87)	53.78 ± 3.22 (46.88–61.11)	100
	Rutab Stage (Brown)	19.85 ± 1.56 (17.9–25.4)	12.89 ± 0.72 (11.85–14.76)	2.11 ± 0.41 (1.64–3.16)	1.02 ± 0.24 (0.71–1.62)	47.93 ± 3.59 (39.66–54.27)	26
Alma Park	Khalal Stage (Orange)	19.99 ± 1.12 (18.39–22.33)	12.81 ± 0.31 (12.18–13.43)	2.18 ± 0.14 (1.97–2.51)	0.82 ± 0.09 (0.68–1.07)	66.89 ± 4.46 (56.48–72.0)	25
	Rutab Stage (Brown)	19.99 ± 0.92 (17.84–21.57)	12.76 ± 0.39 (12.11–13.73)	1.78 ± 0.25 (1.36–2.08)	0.59 ± 0.11 (0.41–0.84)	37.52 ± 3.12 (33.98–47.56)	25

crease in sugar content between the *Rutab* and *Tamr* stage, but the moisture loss is significant (Ahmed et al., 1995; Amira et al., 2011; El Arem et al., 2012; Martín-Sánchez et al., 2014).

3. METHODOLOGY

As the drupes of Canary Island Date Palms ripen in the same pattern as drupes from commercially grown date palms, this paper will adopt the Arabic terminology for the classification of ripening stages (see above).

Numerous Canary Island Date Palms have been planted throughout Albury (NSW, Australia). The palms can be found in the botanic gardens, as formal plantings of street trees, as feature plants in numerous private gardens in a suburban setting and as self-seeded plants that were tolerated and now have attained substantial height. One of these is a well-irrigated female palm, located in a well-established inner suburb (coordinates -36.074175, 146.907128). The palm has 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. According to the current owner of the property, the palm grew as a self-seeded plant and was first noticed, then about 40 cm tall, at the time of purchase in 1968.

Visitation of the palm by various birds, predominantly Pied Currawong (*Strepera graculina*) was observed during mornings and evenings at irregular intervals between March 2018 and February 2019 and frequently documented photographically (Spennemann, 2018e).¹ Grey-headed Flying-Foxes (*Pteropus poliocephalus*) were observed directly and frequently photographically (Spennemann, 2018f), as well as via spat-outs at various palms in Albury.

Two samples of fresh mid-season drupes of two ripening stages (Khalal and Rutab, see below) were harvested straight off the palm by cutting off infructescences. The sam-

¹ The specific palm is located on the route of the author's daily commute to work, as well as on the route of walks for recreational purposes (dog walks, etc.). This allowed for intermittent observation almost every morning and evening, with specific visits for prolonged periods of observation.

Table 3. Seasonal variations in the average pulp weight (g) of *Phoenix canariensis* drupes at Forrest Hill, Albury

Season	Khalal Stage	Rutab Stage
mid-season (June)	1.38 ± 0.16	1.02 ± 0.24
late-season (October)*	0.51	0.47

* adjusted weight loss due to peeling technique (see text)

ples were measured with digital callipers (maximum length and maximum diameter) and weighed with a digital scale. A comparative sample of fresh drupes of two ripening stages (Khalal and Rutab) was harvested straight off a palm at a rural property at Alma Park (NSW) (coordinates -35.583571, 146.78456). For efficiency, seeds were peeled using a paring knife, which meant that a small amount of epicarp, in particular at the ends, remained on the seed (10–15%) and was discarded. The analysis was limited to measurements and assessment of pulp weight.

A second set of (late season) samples was harvested off the Albury specimen. 344 drupes of the Khalal stage and 227 drupes of the Rutab stage were de-pitted, with the pulp submitted for standard Nutrition Information Panel Analysis as well as a determination of vitamins and a various trace metals and minerals. All analyses were carried out by the Analytical Services laboratory of the Australian Export Grains Innovation Centre (Sydney) (Table 4).

4. RESULTS

The observations showed that Grey-headed Flying-Foxes fed on the palm from March to mid-October, while Pied Currawongs did so between early March and late December 2018. By the end of December, all drupes had been removed. At the same time, there was an abundance of drupes of the *Khimri* stage, indicating another large crop for the following season. In addition, feeding was observed on palms in Albury by Starlings (*Sturnus vulgaris*), Red Wattlebirds (*Anthochaera carunculata*) and Blackbirds (*Turdus merula*) and inferred for the Pacific (Eastern) Koel (*Eudynamis orientalis*). Australian Raven (*Corvus*

coronoides), which have been observed feeding on *P. canariensis* in a rural setting, are also seasonally present in Albury.

The collection of fresh samples for the analysis of pulp content (see Table 2) allowed the author to estimate the number of drupes on the tree judging by the number of drupes per infructescence, the number of infructescences per bunch and the number of fruit bunches on the palm. The Albury palm would have borne about 30,000–35,000 drupes during the

Table 4. Nutrient data from late-season *Phoenix canariensis* drupes at Albury (values per 100 g dry weight)

	Khalal (Orange)	Rutab (Brown)
Drupes sampled	344	227
Sample weight	156 g	94 g
Avg pulp weight/drupe	453 mg	414 mg
Avg pulp weight/drupe adjusted	511 mg	466 mg
Energy	605 kJ	755 kJ
Carbohydrate (by diff.)	11.7 g	14.3 g
Sugars	11.3 g	13.3 g
Total Dietary Fibre	37.0 g	46.8 g
Protein (N x 6.25)	4.6 g	5.7 g
Moisture	40.2 g	25.5 g
Ash	5.6 g	6.6 g
Fat (Hydrolysis)	0.9 g	1.1 g
Saturated	0.2 g	0.3 g
Trans	< 0.1 g	< 0.1 g
Mono-unsaturated	0.2 g	0.2 g
Poly-unsaturated	0.5 g	0.5 g
Sodium	6 mg	9 mg

2018 fruiting season. The smaller palm at Alma Park would have borne between 15,000 and 20,000 drupes.

The measurements of both Khalal and Rutab stage drupes from Albury and Alma Park are set out in Table 2. The drupes show a high variability in drupe proportions and drupe volume. No statistically significant correlation among the Khalal stage drupes from Albury could be observed for the following parameter combinations: drupe length and seed length; drupe length and flesh weight and drupe diameter and flesh weight; seed size and flesh weight; or drupe weight and flesh weight. The same applies to the drupes harvested at Alma Park.

Significant differences, however, were observed between the ripening stages. Differences in all measurements (length, thickness, weight), as well as the percentage of fruit pulp, between the samples of (mid-season) drupes of the Khalal and the Rutab stage collected at Albury (Table 1) were all highly significant (t-test, $p < 0.0001$). For the Alma Park samples, only the differences in weight and percentage of fruit pulp were highly significant ($p < 0.0001$).

In view of the peeling technique (see methodology), the pulp weight of the late season drupes was adjusted by a factor of 0.125 (Table 4). The differences in the average pulp weight between mid-season and late season drupes of the same palm were significant ($p < 0.001$) (Table 3). The results of the nutrient analysis are put on record in Table 4–Table 6.

5. DISCUSSION

To understand the significance of *Phoenix canariensis* in the diet of frugivores in urban environments, we need to consider the aspects of seasonality, nutritional reward of palm drupes, and the variability in the drupes.

5.1. Seasonality

The vast majority of plants fruit during summer and autumn (MacFarlane, 2012, p. 73). Few fruit sources, however, are available during the middle of winter and early spring (July to

Table 5. Vitamins and vitamin-precursors present in late-season *Phoenix canariensis* drupes at Albury (values per 100 g dry weight)

	Khalal (Orange)	Rutab (Brown)	Role in bird health
α -Carotene	80.0 μ g	70.0 μ g	deficiency causes reduced growth, lowered resistance to disease, eye lesions, muscular incoordination, lowered egg production and blood spots in eggs (DSM, 2011b)
β -Carotene	2,200.0 μ g	1,400.0 μ g	
Vitamin B3 (Niacin)	2.3 mg	2.3 mg	aids in metabolism and growth, with deficiencies causing ill development of feathers and skin lesions (DSM, 2011a)
Vitamin B6 (Pyridoxine)	0.08 mg	0.06 mg	aids in metabolism and growth, with deficiencies causing ill development of feathers and also lead to nervous disorders (DSM, 2011c)
Vitamin B12 (Cobalamin)	0.0253 μ g	0.0393 μ g	aids in the formation of red blood cells, and feather production (DSM, 2011d)
Vitamin D3 (Cholecalciferol)	< 0.5 μ g	< 0.5 μ g	used in intestines to absorb calcium and facilitates bone mineralisation as well as egg shell quality (El-Maksoud, 2010), as well as beak strength (DSM, 2011e)
Vitamin E (α -tocopherol)	12.0 mg	6.2 mg	acts as an antioxidant and helps to alleviate the costs of reproduction (Badás et al., 2015; Parolini et al., 2017)

Table 6. Minerals and metals present in late-season *Phoenix canariensis* drupes at Albury (values per 100 g dry weight)

	Khalal (Orange)	Rutab (Brown)
Aluminium	1.2 mg	1.6 mg
Antimony	< 0.001 mg	< 0.001 mg
Arsenic	< 0.005 mg	< 0.005 mg
Cadmium	0.001 mg	0.001 mg
Calcium	145 mg	182 mg
Copper	0.6 mg	0.6 mg
Iron	2.3 mg	2.8 mg
Lead	0.004 mg	0.006 mg
Magnesium	155.0 mg	188.0 mg
Manganese	0.8 mg	1.0 mg
Mercury	< 0.001 mg	< 0.001 mg
Phosphorus	116 mg	130 mg
Potassium	4,420 mg	4,550 mg
Selenium	< 0.005 mg	< 0.005 mg
Tin	0.003 mg	0.002 mg
Zinc	1.0 mg	1.2 mg

October in the Southern Hemisphere, December to April in the Northern Hemisphere) (Table 7).

Some plants, such as the Chilean Peppercorn (*Schinus molle*) can produce fruits all year-round if conditions are favourable, while others have a much more confined season. Some species of figs (*Ficus macrophylla* and *Ficus rubiginosa*) have complimentary fruiting seasons, allowing frugivores to potentially move from one to the other. The fruiting seasons, as represented in Table 7, primarily collate data from NSW and Victoria. Given the geographic latitudinal spread, there is some variation between the onset and end of the fruiting seasons, which in the case of some species, may be as much as six to eight weeks.

Other palms common in urban areas, such as *Washingtonia robusta*, produce a large quantity of small drupes, but given their short fruiting season, they are quickly exhausted as a large number of smaller birds (with smaller gape sizes) can feed on them. Once a *Washingtonia* has ripened, the palm is stripped of all fruit in less than a week (pers. obs.).

Only one species consistently bears fruit throughout the winter period, from autumn to early spring: the Canary Island date palm (Table 7). The ripening season of Canary Island date palms depends on regional and micro climatic conditions. For example, at the Gordon Fruit-bat colony (Sydney, coordinates -33.75228, 151.1618), *P. canariensis* plant matter was found in *P. poliocephalus* spat-outs during February, March,

May, August, and December (Parry-Jones & Augee, 2001), whereas in Albury, some 1.8° latitude further south, Canary Island date palms fruited between late February and late December. Even within Albury, two-week variations in fruiting times could be observed, depending on the elevation of the plant's location (pers. obs.).

With its nearly year-round provisioning of drupes, the Canary Island date palm plays a major role as a 'staple' and backup food source for several species. At least in the Australian setting, some species, such as Pied Currawong, tended to be seasonal vectors, favouring urban habitat and its resources of fruits and seeds of ornamental plants (commonly exotics) solely during winter (Anonymous, 1934; Platypus, 1939; Readshaw, 1968b, 1968a). Today, the species seems to be present in many urban areas nearly all year round (Woodall, 2004) and appears to have adapted to breeding in anthropogenic structures (Fulton, 2018). At least in the Albury example, where they once were entirely seasonal (Readshaw, 1968b, 1968a), the now appear to draw on these drupes as part of their daily diet (pers. obs.).

6. NUTRITIONAL REWARD OF PALM DRUPES

The observation of the presence and feeding on a Canary Island date palm by birds in Albury found that Pied Currawong stopped feeding on the drupes only once the crop had been exhausted, whereas Grey-headed Flying-Foxes stopped feeding on the palm some two months earlier. The rationale for this difference rests in the way the two species consume fruit. While Pied Currawong swallow whole drupes and process them in their gizzard, eventually regurgitating the rough and indigestible matter (seeds, epicarp, fibrous parts of pericarps) in the form of pellets (Spennemann, 2018e), flying-foxes bite off fruit flesh and masticate it into a bolus, squeezing out and swallowing the fruit juices, and eventually spitting out the epicarp and fibrous parts of pericarps (Spennemann, 2018d). The late season drupes of the Rutab and Tamr stage are clearly too dry to be efficiently processed by Flying-Foxes.

Very ripe *P. canariensis* drupes (of the Rutab stage) offer a higher reward in terms of protein, energy and sugars (Table 4), but a lesser return on vitamins, with the exception of vitamin B12 (Table 5). The concentration of minerals is higher among drupes of the Rutab stage, but this is likely to be a direct factor of the lower moisture content. As there are few studies that examine the nutritional characteristics of fruit that are not fit or used for human consumption, it is impossible at this time to accurately correlate the nutritional value of *Phoenix canariensis* with other fruit and berry sources in the absence of analytical data.

6.1. Variability in the drupes

The Australian examples of *Phoenix canariensis* show a size and weight loss between the Khalal and Rutab stages with a commensurate decrease in the proportion of pulp weight to seed weight (Table 2). This weight loss is not replicated among

Table 7. Seasonality of some food sources available to urban frugivores in the Australian setting. Relative fruit availability shown by the number of large and small tick marks.

Common name	Scientific name	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Exotics													
Hackberry	<i>Celtis sinensis</i>	XX						xx	XX	x	x	x	x
Camphor Laurel	<i>Cinnamomum camphora</i>			xx	xx	XX	XX	xx					
Washington Hawthorn	<i>Crataegus phaenopyrum</i>				XX	XXX							
Kaffir Plum	<i>Harpephyllum caffrum</i>		xx	xx	xx	xx	XX	XX	XX	XX	xx		
Small-leaved Privet	<i>Ligustrum sinense</i>					XX	XX	XX					
Large-leaved Privet	<i>Ligustrum lucidum</i>		xx	XX	XX	XXX	XXX	XX	xx				
Can Isl Date Palm	<i>Phoenix canariensis</i>		xx	XXX	XXX	XXX	XXX	XXX	XXX	XXX	XXX	XXX	xx
Peppercorn	<i>Schinus molle</i>	x	XXX	XXX	XXX	XXX	x	x	x	x	x	x	x
MickyMouse Plant	<i>Ochna serrulata</i>	XX	xx	xx						xx	xx	XX	XX
Olive	<i>Olea europaea</i>			XX	XXX	XXX	XX	xx	x				
Chinese Pistachio	<i>Pistacia chinensis</i>				X	X	X	X	X				
Rum Cherry	<i>Prunus serotina</i>	x	XX	x									
Japanese Cherry	<i>Prunus serrulata</i>	xx	xx									xx	xx
Firethorns	<i>Pyracantha sp</i>				XXX	XXX	XXX	XXX	XXX				
Wax tree	<i>Rhus succedanea</i>					XX	XX	XX					
Rice paper plant	<i>Tetrapanax papyrifer</i>						x	XX	x				
Umbrella tree	<i>Schefflera actinophylla</i>	XX	XX	x								xx	XX
Mexican Fan Palm	<i>Washingtonia robusta</i>			XX	XX								
Natives													
Lilly Pilly	<i>Acmena smithii</i>							XX	XX				
Bangalow Palm	<i>Archontophoenix cunningghamiana</i>						xx	XX	XX	XX	XX	xx	
Moreton Bay Fig	<i>Ficus macrophylla</i>	XXX	XXX	XXX	xx	xx	xx						XX
Port Jackson Fig	<i>Ficus rubiginosa</i>	xx	xx	XX	XXX	XXX	XXX	XXX	xx				
Cabbage Tree	<i>Livistonia Australis</i>	xx					xx	XX	XXX	XXX	XXX	XXX	XXX

Sources: Howard and Minnich (1989); Innis (1989); Green (1993); Bass (1995); Wood (1998); Spennemann and Allen (2000); Mkize et al. (2008); Reid and Armesto (2011); Mo and Waterhouse (2015); Wotton and McAlpine (2015)

the published samples from Spain, where both size and weight seem to increase (Amorós et al., 2014). This discrepancy is possible due to the small size of the Spanish sample.

A key observation is the high level of variability of drupe sizes and their associated seed size and pulp content of the same palm, not only between successive years, but also, as data in Table 3 show, within a given year. In addition, there is a great variation in drupe and seed sizes between individual palms, even those planted at the same time at the same location (unpubl. data). The cause of the variation, both between

and within palms, is the fact that *P. canariensis* are wind pollinated. Consequently, different infructescences on a palm, which flower at slightly different times, may be fertilised by pollen from different male trees, leading to variation in drupe size and pulp content. Moreover, *P. canariensis* freely hybridises with other *Phoenix* species. During the late nineteenth century, free-land production of palm seed for sale to the horticultural industry was carried out on a commercial scale in the south of France (Spennemann, 2019). There is evidence that some hybridisation through male pollen occurred early on with other

Phoenix species propagated in nurseries as well as private and public gardens close to the seed farms (André, 1888). This seed and plant stock was then exported to various countries (Zona, 2008; Spennemann, 2019), where it formed the basis for in-country propagation.

There is every reason to assume that some of the seed stock originally imported to Australia from the South of France during the late nineteenth and early twentieth century (Spennemann, 2018b) represented a mixture of (a possible small number of) hybrids as well as pure plants. Other planting stock in circulation were pure plants derived from seed imported directly from Tenerife (Canary Islands). The extent to which this genetic 'cocktail' influences the nutritional values of the drupes is unclear at present. In consequence, however, a caveat needs to be issued here: the nutritional values reproduced in Table 4–Table 6 have indicative value only and should not be taken as universal.

7. IMPLICATIONS AND FUTURE DIRECTIONS

While the data presented in this paper show that the availability of Canary Island Date Palm drupes as a food source for frugivores for most of the year is beyond dispute, there is a dearth of knowledge on the relative value this food plays in the nutrition of numerous bird species. A number of lines of future enquiry are indicated.

Further studies of exotic and native vectors are needed, especially stratified studies that examine the diet of vectors

that inhabit the various ecological niches along the landscape gradient urban↔sub-urban↔peri-urban↔agricultural | remnant bushland. There is also a need to more systematically study the provisioning services of Canary Island date palm in diverse ecosystems such as southern Europe, southern China, and the southern states of the USA, and to assess whether species have become reliant on the provisioning of drupes as a 'staple' and backup food source.

In order to place the nutritional value of palms into the context of other fruiting plant species, food preference studies among captive birds are desirable, which examine the energy and mineral balance of different vectors with mixed sets of diets.

Finally, additional analyses are needed that diachronically track changes to the nutritional values on the same palm plant, including the diachronic variability within infructescences, between different infructescences on the same and different bunches (to examine the effects of different pollen sources and seasonal flowering), and between individual palms planted at the same location (to exclude parameters of sun hours ground moisture and ground fertility).

Acknowledgments

Dr. Hayfa Salman (Analytical Services Laboratory, Australian Export Grains Innovation Centre, Sydney) supervised the analysis of the nutritional composition.

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