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Consumption of Canary Island Date Palm *Phoenix canariensis* drupes by Pied Currawongs *Strepera graculina*

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Abstract. In Australia, Canary Island Date Palms *Phoenix canariensis* are ubiquitous, widely planted as ornamental trees in private gardens and along streets and seaside promenades. Seeding freely, a single female palm can produce up to 30,000 fleshy drupes annually. Pied Currawongs *Strepera graculina*, which can swallow several drupes whole in a single feeding event, present as a major vector in the plant's dispersal. Based on observations of feeding behaviour as well as an examination of resulting regurgitated pellets, this paper discusses critical factors that influence the performance of Pied Currawongs as a vector of palms. Pied Currawongs exhibit drupe selection preferences, which seem related to a drupe's ripeness and nutritional value, and a feeding behaviour that consists of short bouts of consumption, followed by longer periods of digestion at nearby perches. As increased ripening of the fruit correlates with an increased maturation of the seed, resulting in a higher germination rate, and as repeated use of nearby perches increases the density of regurgitated seeds, such behaviour has implications on the effectiveness of Pied Currawongs as dispersers of Canary Island Date Palms.

Introduction

Canary Island Date Palms *Phoenix canariensis* (Arecaceae) now have a global distribution throughout warm temperate zones (Spennemann 2018a). Introduced to Australia in the late 1870s, they were planted from the 1890s onwards as feature trees in private and public gardens, as well as street trees lining avenues and boulevards. Today, they have become a common landscaping element in Australia favoured by those wishing to give their area an exotic feel (Spennemann 2018b).

The Canary Island Date Palm is a monoecious plant propagated solely by seed (Barrow 1998), reaches reproductive maturity after 6–7 years, and grows to ~18–20 m in height. The crown is made up of >100 arching, pinnate fronds 5–6 m long. The plant can live for 200–300 years (Beech 2017), and seeds freely, annually producing 5000–30,000 obovoid drupes (dates, the size of a large olive) with limited fibrous flesh content: Virtue *et al.* 2008). It is readily dispersed by a range of volant and terrestrial vertebrate vectors (Spennemann 2019b). It is regarded as naturalised (i.e. an exotic plant established so that it lives wild, with multiple generations reproducing successfully) in Australian states of New South Wales (Hosking *et al.* 2007), South Australia (Brodie & Reynolds 2012), Victoria (Conn & Walsh 1993) and Western Australia (Keighery 2010; Lohr & Keighery 2016), as well as Norfolk Island (de Lange *et al.* 2005) and New Zealand (Esler 1987).

Vertebrate species known to feed on Canary Island Date Palm drupes, and thus to act as putative vectors responsible for seed dispersal, include Australian native species Grey-headed Flying-Fox *Pteropus poliocephalus*, Silver Gull *Larus novaehollandiae*, Blue-faced Honeyeater *Entomyzon cyanotis*, Australian Raven *Corvus coronoides* and Pied Currawong *Strepera graculina*, and introduced species Red Fox *Vulpes vulpes*, Common Starling *Sturnus vulgaris*, Common Myna *Acridotheres tristis* and Common Blackbird *Turdus merula* (Spennemann 2019b and references therein). In New Zealand, large frugivorous pigeons, such as the New Zealand Pigeon *Hemiphaga novaeseelandiae*, feed on palm drupes, indicating that other large fruit-pigeons, such as the White-headed Pigeon *Columba leucomela* and Topknot Pigeon *Lopholaimus antarcticus*, could also be potential vectors (Spennemann 2019b). The majority of records of feeding are based on secondary evidence such as ejecta (regurgitated pellets and spat outs), scats and seed concentrations under roosts. Actual observational data on the vectors that feed on Canary Island Date Palm drupes and disperse their seeds have not been recorded.

Observations were conducted to examine the potential for the Pied Currawong to act as a dispersal vector of Canary Island Date Palm seeds in Australia. This species is an omnivorous, medium-sized, robust bird distributed across the eastern seaboard of Australia (Barrett *et al.* 2003; Higgins *et al.* 2006; ALA 2018) and is seasonally sedentary within a home-range of 12–14 ha (Wood 2001; Higgins *et al.* 2006). It feeds on a wide range of native and exotic fruit, particularly during the non-breeding season, as well as insects, reptiles and other birds (Cooper & Cooper 1981; Mulvaney 1986; Barker & Vestjens 1989; Bass 1989, 1990, 1995, 1996; Buchanan 1989; Lenz 1990; Loyn & French 1991; Allison 1993; Lepschi 1993, 1997; McLean 1997; Wood 1998, 2000, 2001; Rose 1999; Bayly & Blumstein 2001; Menkhorst & Morley 2017). As an altitudinal migrant, it tends to flock to inland urban areas during the winter months, feeding on a broad diet, including a range of exotic plants (Binns 1940; Readshaw 1968a,b; Bass 1995), some of which produce drupes with large seeds, such as European Olives *Olea europaea* (Spennemann & Allen 1998, 2000). In recent years, it has become increasingly residential in urban and peri-urban areas (e.g. Lenz 1990, 2019; Loyn & Menkhorst 2011; Fulton 2018). Bass (1989) noted that feeding movements of Pied Currawongs were more extensive (up to 5 km) during winter, but most observed seed-dispersal movements are <50 m (Green 1993; McLean 1997).

Earlier observations of Pied Currawongs feeding on Canary Island Date Palm drupes have been limited to observations of seeds in regurgitated pellets and casual observations. Buchanan (1989) recorded *Phoenix* spp. seeds in regurgitated pellets at a roost near Thornleigh, 19 km north-west of Sydney, NSW. A YouTube videoclip showed Currawongs feeding on date drupes in the Lachlan Valley near Forbes, NSW (zuditaka 2013), and newspaper articles noted Currawongs repeatedly visiting palms in downtown Cobram, Victoria (Binns 1940) and feeding on palms at Duntroon, Canberra, ACT (Boden 1991).

If Pied Currawongs are a major consumer of the drupes of this Palm, they may function as a major vector bridging the urban with the peri-urban space. This paper describes direct observations of Pied Currawongs selecting and consuming drupes as well as the nature and appearance of regurgitated pellets containing palm seeds. An analysis of seed scatters under perch-trees allowed an examination of the spatial feeding pattern between source trees and digestion perches.

Methods

Study areas

Observations were gathered at two sites in southern New South Wales: the regional centre of Albury on the Murray River and the small rural location of Alma Park in the southern Riverina. The latter was the location of an ongoing study into the distribution of self-seeded palms in an agricultural landscape, and the Albury observations were opportunistic.

Albury

Canary Island Date Palms have been planted throughout Albury, in the botanic gardens, as formal plantings of street trees and commonly as feature plants in private gardens in a suburban setting. Most observations occurred at a well-irrigated female palm, located on private property in suburban Albury (–36.074175, 146.907128), that had a total height of 9.2 m, a minimum trunk height of 4.4 m, a trunk girth (at 1.3 m above the ground) of 2.6 m, and crown ~8 m in diameter. According to the current owner, the palm grew as a self-seeded plant and was first noticed, when about 40 cm tall, at the time of purchase of the property in 1968 (M. Andronicos pers. comm. 2018). On a nearby property is a male palm 10.6 m in height (Figure 1, tree N) that may be the pollen source.

Alma Park

Alma Park is a rural community, 55 km north-west of Albury, comprised of dispersed farms without a suburban area. During the late 1940s, two groups of palms were planted in front of the Lutheran Church (–35.60452, 146.791506) and church hall (–35.604518, 146.791507). Each group is comprised of three female and one male palm planted in a square 7m × 7m. The second location is a palm-lined section of a driveway leading to the farm property 'Glenalvon', ~2.2 km north-west of the Alma Park church (–35.583548, 146.78454).

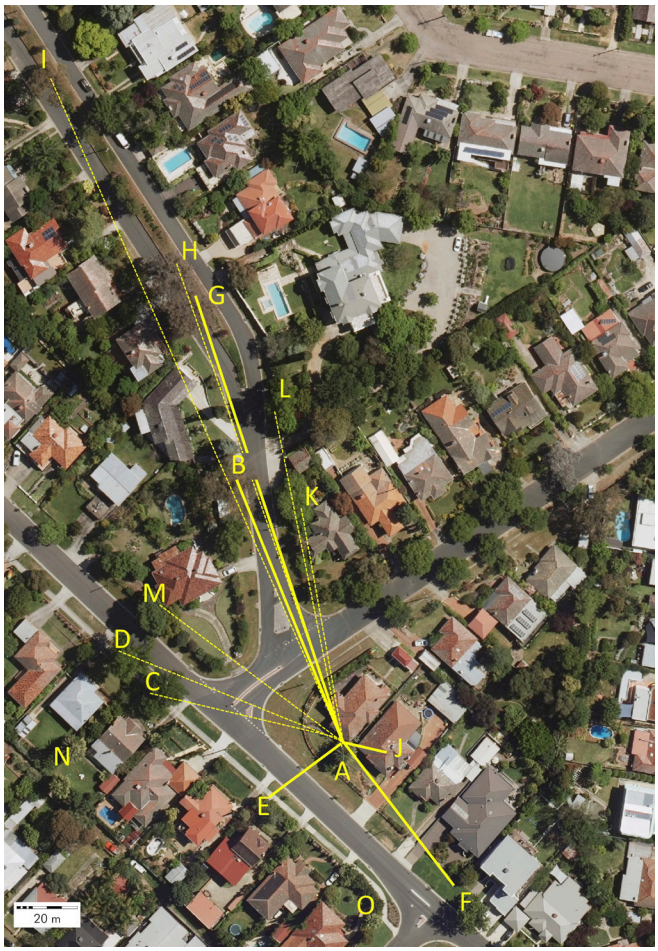

Figure 1. Relationship of the Canary Island Date Palm source palm (A) to the confirmed perches of Pied Currawongs (B–J), possible perches (K–L) and additional palms (M–O), Albury, NSW. Solid lines show sightings of actual flights, dashed lines show flight inferred from regurgitates. A: Source palm (height 9.2 m); B: Yellow Box *Eucalyptus melliodora* (height 24.5 m, distance 95 m); C: Green Ash *Fraxinus pennsylvanica* (height 13 m, distance 60 m); D: Red Canadian Maple *Acer rubrum* (height 17 m, distance 75 m); E: Silver Birch *Betula pendula* (height 11 m, distance 30 m); F: Green Ash (height 14 m, distance 65 m); G: Yellow Box (height 27 m, distance 160 m); H: Yellow Box (height 21.4 m, distance 180 m); I: Yellow Box (height 20.4 m, distance 275 m); J: roof (height 4.6 m, distance 15 m); K: Green Ash (height 17 m, distance 80 m); L: Red Canadian Maple (height 15.3 m, distance 116 m); M:2 trees—Lilly Pilly *Acmena smithii* (height 12 m) to south-east, Green Ash (height 15 m) to northwest, distance to centre 74 m; N: Canary Island Date Palm (height 10.6 m) and (<2 m away) Mexican Fan Palm *Washingtonia robusta* (height 21 m); O: Mexican Fan Palm (height 11.4 m). Aerial image, November 2017, courtesy Albury City Mapping Portal.

Observation methods and sample collection

Albury

Visitation of the palm and the ground below the palm by Pied Currawongs was observed during mornings and evenings at irregular intervals (several times per week) between March 2018 and March 2019. These observations were augmented by five specific visits (between 21 April and 27 May 2018) to allow prolonged periods of observation

(20–30 minutes each). The ground beneath all trees within 200 m of the palm was repeatedly (at least once per week) searched for regurgitated currawong pellets and palm seeds (Figure 1), all of which were collected. All seeds had apparently originated from the palm under investigation as there were no other fruiting female palms within 500 m. A male palm, the probable source of most of the pollen, was located 86 m to the west (Figure 1, tree N).

Alma Park

The Alma Park church site was visited on ten occasions between December 2017 and April 2019 while mapping self-seeded Canary Island Date Palms as part of an associated study. Opportunistic observations of the presence and behaviour of Pied Currawongs were made during these visits.

Size of drupes

To ascertain whether the drupes ingested by Pied Currawongs at Albury and Alma Park differed in size from the drupe population of the palms at the respective locations, the seeds under the perch-trees in Albury were collected during May–September 2018 and in Alma Park during June 2018. For comparison, samples of fresh drupes at the two ripening stages [*Khalal* (orange) and *Rutab* (brown)] were harvested directly from the palms, measured (maximum length and maximum diameter) with digital callipers, and weighed with a digital scale. Differences in dimensions and weight were compared using standard *t*-tests to compare means.

Terminology

Traditional as well as commercial Common Date Palm *Phoenix dactylifera* 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 hard raisin (*Tamr*) (Ahmed *et al.* 1995; Baliga *et al.* 2011). As this classification of ripening stages can be inferred for Canary Island Date Palms, this paper will use the same terminology.

Results

Pied Currawongs were present during most observation periods. At Albury, up to four at a time were observed feeding in the canopy and among drupes. During the fruiting period, the ground underneath the palm was littered with complete drupes, incomplete drupes, seeds, and seeds with part of the epicarp ('skin') attached (Figure 2). By mid December 2018, that palm had been stripped of all drupes. The next season's drupes ripened in late February, with the first observation of Currawongs feeding on drupes being on 2 March 2019.

Perches used for voiding (as confirmed by the presence of dropped seeds; Figure 2) were limited to street trees in the line of sight of the crown of the palm. Tall trees in landscaped gardens, but not in direct line of sight (see Figure 1), were apparently not used as perches as no dropped seeds could be found under them.

Figure 2. Accumulation of Canary Island Date Palm seeds under a perch (Alma Park church hall, NSW). Variation in the coloration of the seeds indicates multiple seasons of deposition, including a very fresh one (Sample APS4, top left). Photo: Dirk H.R. Spennemann

Observations of drupe selection and consumption

Two patterns of feeding were observed for Pied Currawongs feeding on Canary Island Date Palm drupes. The majority involved birds standing on the drupe clusters and eventually picking off individual drupes, which were swallowed whole while still standing on the drupe cluster. Predominantly, birds tended to pick off a drupe, holding it in its thickest part and at right angles to the beak (Figure 3). On fewer occasions, birds detached drupes at the panicle with the beak. Typically, when detaching the drupes, especially using the latter technique, numerous drupes were abscised and fell to the ground. The birds swallowed between one and five drupes during each feeding event. For the second pattern, Currawongs were observed perching on nearby trees or powerlines, before descending to the garden lawn next to the palm to pick fallen drupes from the ground. On several occasions, it was noted that a drupe was dropped when it was flicked about in order to rotate and eventually align it with the long axis of the bird's beak for swallowing (see Figure 4 for successful realignment of a drupe by a bird on the ground).

During single feeding events, individual birds were very specific, consistently displaying preferences for exclusively either lighter or darker drupes, be they on the tree or the ground. Three examples can exemplify this. One individual, preferring darker drupes of the *Rutab* stage, appeared to scan for predators before repeatedly sticking its head deep (up to one-third of its body length) into the drupe cluster to extract a drupe; this was repeated several times during the feeding event. The individual shown in Figure 3 consistently picked orange (*Khalal*) drupes from the top of the cluster. Another individual repeatedly 'tested' darker and lighter drupes with its beak, moving from one panicle stalk to another until finally picking off and swallowing only lighter-coloured drupes (Figure 4). None of the birds feeding on

Figure 3. Pied Currawong feeding on an orange Canary Island Date Palm drupe (top: 21 April 2018, bottom: 20 May 2018). Photos: Dirk H.R. Spennemann

Figure 5. Almost intact Canary Island Date Palm drupe regurgitated by a Pied Currawong, found under perch-tree, opposite 735 Fellowes Crescent, Albury, NSW, 21 July 2018. Note the compression and incipient shredding of the epicarp. Photo: Dirk H.R. Spennemann

Figure 4. Pied Currawong handling and swallowing an orange Canary Island Date Palm drupe, 21 April 2018. The total duration of the image sequence (a–f) was 12 seconds. Photos: Dirk H.R. Spennemann

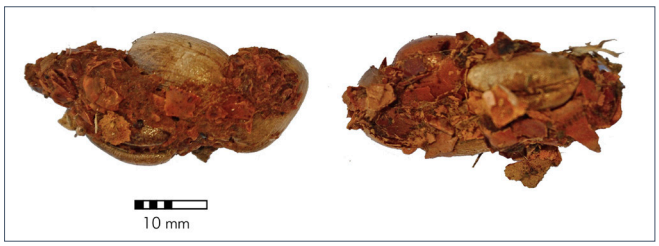

Figure 6. Pellets of undigested material regurgitated by a Pied Currawong, Alma Park church, NSW. Sample APS1 (left) and APS2 (right). Photo: Dirk H.R. Spennemann

drupes on the palm were observed to then directly alight to the ground to feed.

Palm seeds in regurgitated pellets

The regurgitated pellets of the Pied Currawong are a mixture of large sections of epicarp, some bits of pericarp and the seed of the palm drupes (Figures 5–6). Those containing palms seeds are moister and more uncompressed (unlike Flying-Fox ejecta: Spennemann 2018c) and tend to break up on impact with the ground (Figure 7), unless their fall is buffered by grass and leaf-matter.

In Albury, twelve perches, with concomitant evidence of regurgitated seeds below (Figure 1) were located. Currawongs were observed flying from the source palm to some of these. The closest perches were the eaves of residences immediately adjacent to the palm. Any seeds that were regurgitated on the eaves either fell into the gutter (and thus were inaccessible) or on the ground, where they indiscriminately commingled with seeds of varied origin (autogenously abscised, bird-dropped and regurgitated), making them unsuitable for analysis. Many palm seeds were encountered under two tall Yellow Box *Eucalyptus melliodora* trees located 95 m and 160 m upslope of the source palm (Figure 1, trees B and G). The seed scatter

Figure 7. Pellet of undigested material regurgitated by a Pied Currawong, Alma Park church hall, NSW. Sample APS4 *in situ*. Photo: Dirk H.R. Spennemann

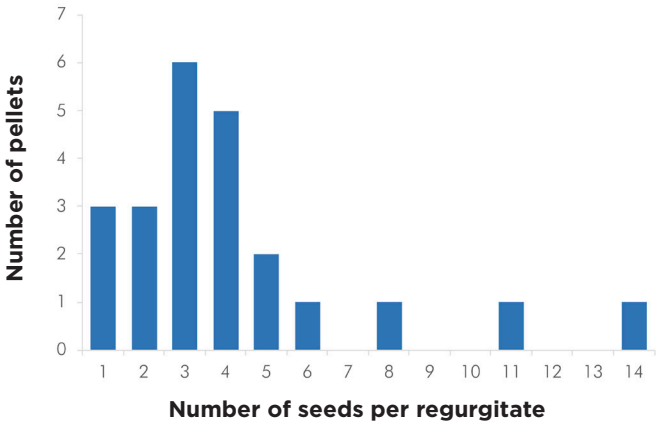

Figure 8. Frequency distribution of Canary Island Date Palm seeds in Pied Currawong pellets recovered at Alma Park, NSW (*n* = 23).

under each tree was confined to a segment to the south-south-east, indicating that Currawongs used branches closest to, and in line of sight of, the source tree. The third major perch was an 11-m-tall Silver Birch *Betula pendula* on the opposite side of the road from the source palm (Figure 1, tree E). A few additional seeds were encountered under other nearby perches, again mostly underneath branches closest to the source palm.

At Alma Park, an individual Pied Currawong was noted flying from a palm to the closest perch option at the north-western corner of the church hall, where it was observed to sit and eventually regurgitate before it flew to surrounding trees. Immediate inspection of the ground showed a high concentration of palm seeds from multiple regurgitation events (Figure 2). In addition, a few fresh pellets of undigested material regurgitated by Currawongs were also found under the eaves of the north-western corner, but not under any of the other eaves. Additional fragmented pellets were encountered under the palms. The majority of pellets had disintegrated on impact, making it difficult, in all but two cases, to assign seeds to specific pellets (Figure 7).

Size of drupes

At Albury and Alma Park, there were consistent differences between drupes of the *Khalal* and *Rutab* stages (Table 1): *Rutab* drupes tended to be smaller and lighter.

The differences in measurements, as well as the percentage of fruit pulp, between the mid-season drupes at the *Khalal* and the *Rutab* stage of samples collected at Albury (Table 1) were all significant (*t*-Test, $P < 0.001$). At Alma Park, only the differences in weight and percentage of fruit pulp were significant ($P < 0.001$).

At Albury, there was no significant difference between a grab sample of seeds (*n* = 190) collected underneath the source palm and seeds deposited by Currawongs under the perch-trees (*n* = 69) (Table 2). The seeds extracted from *Khalal* drupes were significantly ($P < 0.001$) larger and heavier than those encountered under the perch-trees and seeds collected underneath the source palm (Table 2). Seeds extracted from *Rutab* drupes, however, were significantly shorter ($P = 0.005$) and thinner ($P < 0.001$) but heavier ($P = 0.036$) than those deposited by Currawongs.

Table 1. Measurements of Canary Island Date Palm drupes at two different stages of ripening collected at Forrest Hill, Albury, and Alma Park, NSW: mean ± standard deviation (range in parentheses); *n* = number in sample.

Location	*Ripening stage*	*Length (mm)*	*Thickness (mm)*	*Weight (g)*	*Pulp (g)*	*% Pulp by weight*	*n*
Albury	*Khalal* (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 (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
Glenalvon Palm no. 15, Alma Park	*Khalal* (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 (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

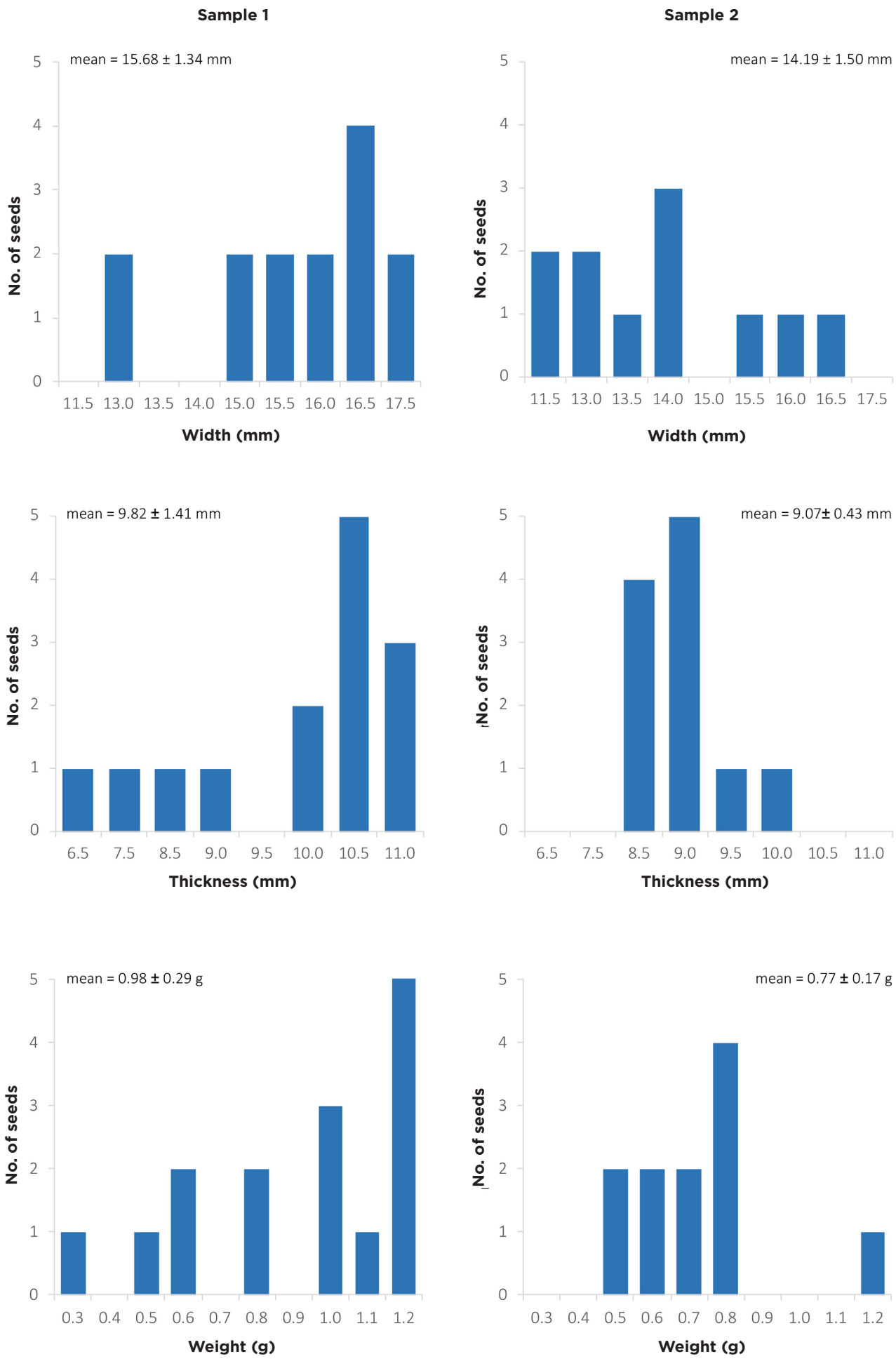

Figure 9. Size (length, width and weight) distribution (and means) of Canary Island Date Palm seeds in two Pied Currawong pellets recovered at Alma Park, NSW.

Table 2. Measurements of Canary Island Date Palm seeds from drupes harvested at two different stages of ripening and from beneath Pied Currawong perch-trees and the source palm, Forrest Hill, Albury, NSW: mean ± standard deviation (range in parentheses); *n* = number in sample.

Sample	*Length (mm)*	*Width (mm)*	*Thickness (mm)*	*Weight (g)*	*n*
Harvested drupes					
Khalal (orange)	16.60 ± 0.77 (14.77–18.99)	10.79 ± 0.46 (9.67–12.2)	9.29 ± 0.50 (8.02–10.56)	1.19 ± 0.14 (0.88–1.5)	100
Rutab (brown)	15.33 ± 1.08 (13.39–18.23)	9.68 ± 0.64 (8.79–11.09)	8.62 ± 0.60 (7.77–9.73)	1.09 ± 0.18 (0.82–1.54)	26
Collected seeds					
Underneath perhes	15.99 ± 0.94 (13.35–18.91)	9.80 ± 0.66 (8.17–11.38)	8.74 ± 0.68 (7.07–10.12)	1.02 ± 0.17 (0.7–1.5)	69
Underneath source palm	15.86 ± 0.78 (13.00–17.50)	9.81 ± 0.53 (8.50–11.30)	8.73 ± 0.55 (7.60–10.10)	Not measured	190

In total, 23 samples of discrete regurgitated pellets were collected at Alma Park. Of these, 52% contained ≤3 date seeds, and 13% had ≥6 seeds (Figure 8). One sample contained 14 seeds that had broken up before collection (for images see Spennemann 2018d). This matches observations by Buchanan (1989), who noted an average number of three and a maximum of 10 seeds per pellet. Of significance in the Alma Park case is the variation in seed size within a pellet: seeds ranged from small (13.11 × 7.37 × 6.26 mm) to large (17.48 × 10.91 × 9.58 mm, see Figure 3). A second pellet containing 11 seeds showed greater variation in size (11.12 × 8.42 × 7.08–16.58 × 10.04 × 9.24 mm) (see Figure 9).

Discussion

This study set out to examine the consumption of Canary Island Date Palm drupes by Pied Currawongs, as possible dispersers of the palm. The critical factors that influence the performance of the species as a vector are drupe selection (which is coupled with a drupe's state of ripeness and nutritional value) and feeding behaviour (which consists of short bouts of consumption, followed by longer periods of digestion at nearby perches). The latter has implications on the effectiveness of a seed disperser (*sensu* Schupp *et al.* 2010).

The normal pattern of fruit consumption by Pied Currawongs is to ingest several drupes/fruits at the source plant and then to fly to a perch (nearby tree, building, telegraph pole, powerline), where they process the food (Bass 1995). The feeding on drupes in the palms or on the ground observed at Albury was of short duration (<5 minutes per event, despite an abundance of available drupes), as in observations elsewhere (e.g. Green 1993). It is likely that this is governed by the size of the Currawong's crop. Once at the perch, it takes 5–15 minutes for a Currawong to process the fruit in the crop (pers. obs. at perch E; see also Moran *et al.* 2004) before it flies off to feed again. As Canary Island Date Palm drupes are far too large to be passed through the bird's intestine, the Currawong regurgitates the rough and indigestible matter (seeds, epicarps, fibrous parts of pericarps) in the form of pellets, after which feeding can resume (see also Bass 1995).

Table 3. Measurements of Canary Island Date Palm seeds from drupes harvested at two different stages of ripening and from regurgitated Pied Currawong pellets, Alma Park, NSW: mean ± standard deviation (range in parentheses); *n* = number in sample.

Sample	*Length (mm)*	*Width (mm)*	*Thickness (mm)*	*Weight (g)*	*n*
Harvested drupes					
Glenalvon palm no. 15 Khalal (orange)	18.13 ± 0.47 (17.48–19.15)	10.30 ± 1.90 (1.27–11.17)	9.69 ± 0.29 (8.94–10.18)	1.36 ± 0.11 (1.18–1.57)	25
Glenalvon palm no. 15 *Rutab* (brown)	16.60 ± 2.21 (10.38–18.87)	10.12 ± 0.70 (8.99–11.2)	9.12 ± 0.59 (8.28–9.99)	1.19 ± 0.20 (0.91–1.44)	25
Seeds collected from regurgitates					
Alma Park church	14.33 ± 1.28 (11.26–16.58)	9.29 ± 0.96 (6.56–10.78)	8.20 ± 0.90 (6.16–9.8)	0.80 ± 0.19 (0.4–1.2)	35
Alma Park church hall	14.57 ± 1.50 (10.52–17.49)	8.14 ± 1.06 (5.33–10.26)	9.26 ± 1.13 (6.53–11.04)	0.82 ± 0.27 (0.3–1.4)	77
Glenalvon driveway	15.10 ± 1.36 (12.24–17.53)	8.92 ± 1.02 (7.4–10.52)	8.02 ± 0.98 (6.41–9.55)	0.79 ± 0.28 (0.3–1.3)	38

Fruit consumed

Canary Island Date Palm drupes are oblong fruit, with the length ~1.5 times the diameter (Table 1). As Pied Currawongs have a gape size of 20.1 ± 0.4 mm (Moran *et al.* 2004), they can readily swallow drupes of 12–15 mm diameter. However, as some drupes are longer than this gape size and thus cannot be swallowed sideways, Currawongs tend to flick the drupes into the air and align them in the beak (see e.g. Figure 4). A comparison of seeds contained in single regurgitated pellets showed a great variation in size (length, width) and weight. Since sizes of the drupes and of their seeds are broadly correlated, the individual bird(s) that dropped the pellets did not appear to exercise size preferences when selecting drupes for consumption (Figure 9).

Observations of feeding behaviour show that Pied Currawongs exhibit clear preferences for either orange (*Khalal*) or brown (*Rutab*) drupes (at least during single feeding events). The reason behind the selective consumption of these drupes may rest in differences in nutritional value. Nutritional reward in the pulp content differs significantly between the *Khalal* and the *Rutab* stage (Table 1). The sugar content of the drupes rises with increasing sun hours throughout the ripening stages in the commercially significant Common Date Palm, a congener with which the Canary Island Date Palm freely hybridises (Ahmed *et al.* 1995; Amira *et al.* 2011; El Arem *et al.* 2012; Martín-Sánchez *et al.* 2014). The same holds true for the Canary Island Date Palm. Amorós *et al.* (2014) assessed the content of sugar and of several acids that determine the extent of sour and acrid tastes when the flesh is consumed in several *Phoenix* species. Albeit based on a small sample, they noted a dramatic increase in total sugars from 9.4 ± 0.18 g/100 g fresh weight at the *Khalal* stage to 29.53 ± 0.01 g/100 g at the *Rutab* stage in the Canary Island Date Palm. Drupes harvested from the Albury palm in the present study showed more moderate increases in sugars (*Khalal*: 11.3 g/100g, *Rutab*: 13.3 g; a 17.7% increase), with a concomitant increase in energy (605 kJ/100 g vs 755 kJ/100 g; a 28.8% increase), but a decrease in moisture (40.2% vs 25.5%; a 36.6% decrease) (see Spennemann 2019a).

Selection of drupes at Khalal *and* Rutab *stages*

The rationale behind the selective consumption of orange vs brown drupes may rest in differences in the drupes' water and sugar content and the corresponding alcohol-mediated kairomones, which have been documented as attractants for Date Stone Beetles *Coccotrypes dactyliperda* predating seeds of Common Date Palms and Canary Island Date Palms (Meisner *et al.* 1985; El-Barbary *et al.* 2002). Ethanol concentration in fruit, which positively correlate with fruit sugars, increases with the fruit ripening process (Dudley 2004) and is thus higher in *Rutab* stage drupes compared with those of the *Khalal* stage. Ethanol concentration has been demonstrated as an olfactory cue for primates (Dudley 2004) and fruit-bats (Sánchez *et al.* 2006). The ability of frugivores to detect even small variations in sugar content (Levey 1987; Schaefer *et al.* 2008), fatty acids (Bairlein 2002), lipids (Schaefer *et al.* 2003) and protein/nitrogen content (Bosque & Calchi 2003) has been documented for several species, which suggests that alcohol-mediated kairomones may play a role in making a choice among like foods. There has been little research on how differences in fruit stage influence passerines (Mazeh *et al.* 2008), and future research into olfactory cues for fruit and drupe selection is warranted.

Intriguingly, although the sugar content of orange drupes (*Khalal* stage) is less than that of brown drupes (*Rutab* stage), it is orange drupes that are preferred in most instances (Spennemann 2019a). This is not accidental—repeatedly, individual Currawongs were observed testing the softness of the drupes with the beak before eventually picking off an orange drupe and swallowing it. Grey-headed Flying-foxes exhibited a similar preference (based on the colour of the ejecta), feeding almost solely on orange drupes (Spennemann 2018d,e). The avoidance of drupes of the *Rutab* stage could be because of the olfactory cues. Bats, for example, avoid a higher concentration of methanol which emanates from very ripe fruit (Sánchez *et al.* 2006). The rationale behind the selective consumption of the orange vs brown drupes is not clear. The epicarp of the drupes is softer at the *Rutab* stage and the pericarp readily detaches from the seed, so processing of a soft-fleshed drupe in the crop/gizzard would probably be more efficient. Yet, even though the sugar content is proportionally higher at the *Rutab* stage, the drupes are drier, which may influence digestion. Given that little is published about the anatomy and food processing of the gizzard of Pied Currawongs, this is an avenue of future investigation.

Dispersal distances

The availability of suitable perches in the vicinity of the seed source determines the distance of local dispersal (<1 km) and thus the minimal dispersal distance. If perches are few and more distant, such as in cleared and managed agricultural landscapes, then dispersal will likely be further. The density of seed deposition at a given spot is also linked to the density of perches. In areas with few perch options, multiple individuals will repeatedly use the same perch, resulting in more high concentrations of seeds underneath these perches (Figure 2). This contrasts with dispersal in dense, yet scattered, urban situations with a greater density of perches and thus a greater choice of perch use (see model discussion in Spennemann 2019b). There are two conceptually different dispersal distances: dispersal within feeding sessions (i.e. short-distance dispersal to the closest perch) and dispersal between feeding session [i.e. long(er)-distance dispersal to nests or overnight roosts].

McLean (1997) noted that a majority of Pied Currawongs flew short distances (~10–30 m) to a perch, where they perched and processed their meal. Green (1993), in subtropical rainforests in northern New South Wales, noted that the majority (51%) of perches were between 20 and 50 m away from the source tree, with another 22% at distances >50 m. Shorter distances were less favoured (Green 1993). In Albury, 58% perches were between 60 and 95 m away, with minimum distances of 15 m and maximum distances of 275 m (Figure 1). Based on the number of Canary Island Date Palm seeds collected under perch-trees, the distance between perch and seed source

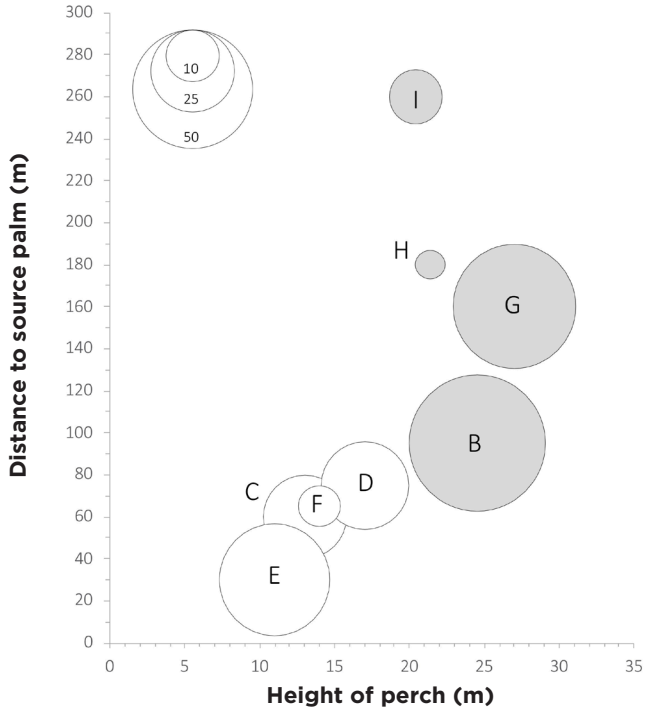

Figure 10. Bubble-plot showing the relationship between the number of regurgitated seeds found and the height of and distance to the perch-tree. Eucalypts are shaded grey. All perches were in line of sight from the source palm. For location and identification of perch-trees see Figure 1.

may be less significant than the height and nature of the perch, with tall eucalypts preferred (Figure 10). All perches with regurgitated palm seeds were in the line of sight of the crown of the source palm (Figure 1).

A study of the Pied Currawong in the New England region, NSW, showed that Pied Currawongs fed in rural townships, but then flew to their overnight roosts, usually <5 km distant but could be 10–15 km away (Bass 1995). There, they regurgitated the final meal, thereby contributing to medium-range seed dispersal (Bass *et al.* 2006). Similar observations were made in Cobram, Victoria, where Pied Currawongs fed at street plantings of Canary Island Date Palms and then flew a distance of 1–2 km to overnight roosts in the Murray River floodplain, where they regurgitated seeds (Binns 1940).

Frugivorous birds need to retain fruits for a sufficient length of time to assimilate nutrients yet be able to discard the indigestible seed as swiftly as possible to make room for more digestible fruit pulp (Sorensen 1984). Thus, drupes with large seeds are commonly processed rapidly by regurgitation (Levey 1986). As Pied Currawongs have a short gastrointestinal transit time of 15–20 minutes (Moran *et al.* 2004), the bulk of regurgitated pellets will be dropped at perches close to food sources (Bass 1990), and only the remains of the final meal should be dispersed further afield either at the night roost or at a perch along the way. Thus, the primary dispersal capacity of this species is limited to short distances with the resultant seed dropped at select perch locations. In terms of effectiveness as a seed disperser (*sensu* Schupp *et al.* 2010), the Currawong primarily facilitates an intensification of the presence of Canary Island Date Palms, rather than a range expansion or colonisation (*sensu* Spennemann 2020). Over time, however, expansion creep will occur.

In addition, the processing of the ingested drupe in the gizzard leads to a chemical and physical scarification of the seed. Experimental studies of the germination rate of seeds dispersed by Pied Currawongs have shown a statistically significantly higher germination rate among seeds dispersed by Currawongs compared with undigested autogenously abscised seeds (Spennemann & Pike 2019).

Implications for further research

Planted as ornamentals, Canary Island Date Palms are primarily distributed in urban and suburban areas and thus rely on vectors for dispersal beyond the urban space. The effective dispersal success of plant species is governed not only by the biomechanical aspects of the vectors (gape size, number of seeds ingested, flight distances) and the biochemical influences of seed viability (gastrointestinal treatment), but also by the connective potential of a vector species to inhabit multiple ecological niches and thereby disperse seeds across multiple ecological landscapes (e.g. urban↔suburban↔peri-urban/production↔remnant vegetation) (Spennemann 2019b). Pied Currawongs are a prime example of this kind of vector as they cover all four ecological landscape types (Higgins *et al.* 2006).

Significantly, the connective potential of some vectors is increasing, as some species increasingly adapt to features of the urban built environment and thus increase in population density. The Pied Currawong is a good example, as it has been noted as not only feeding in urban spaces, but also nesting in urban trees (Lenz 1990), structures (Lenz 2019) and even underground carparks (Fulton 2018).

Although data are available for the seasonal movement of Pied Currawong populations (Readshaw 1968a; Bass 1989; Griffioen & Clarke 2002; Menkhorst & Morley 2017) as well as some general data on movement from roosts to food sources (Bass 1995; Bass *et al.* 2006), reliable data on the movement of individuals are lacking. In particular, data that shed light on the movement between roosts and food sources as well as patterns (if any) of movements between different food sources are lacking. For example, the question remains to be answered on the relative importance of Canary Island Date Palms in the fruit diet of the Pied Currawong: in areas where the palms are common (such as the study area in Albury), are they a staple food that is augmented by other sources, or do the palms merely augment other components of the diet? Therefore, it would be desirable to furnish some Currawongs nesting and/or feeding in urban areas with GPS trackers to assess diurnal and seasonal movement patterns.

In this study, it was noted that individual Pied Currawongs expressed preferences on the state of ripening of the Canary Island Date Palm drupes. As increased ripening of the fruit from the *Khalal* to the *Rutab* stage correlates with an increased maturation of the seed, which results in a higher germination rate (Pimenta *et al.* 2010), such food preferences have implications on the effectiveness of Pied Currawongs as dispersers of Canary Island Date Palms.

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