

Rites of Passage: Germination of Vertebrate Dispersed, Regurgitated or Defecated *Phoenix canariensis* Seeds

DIRK HR SPENNEMANN¹ AND MELISSA PIKE²

¹Institute for Land, Water and Society; Charles Sturt University; PO Box 789; Albury NSW 2640 (dspennemann@csu.edu.au) (corresponding author); ²School of Environmental Sciences, Charles Sturt University; PO Box 789; Albury NSW 2640.

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Canary Island Date Palms are widely planted as ornamental plants in private and public spaces. As both prolific and long-duration seeders, their drupes provide food for a range of volant and terrestrial vertebrates. This study experimentally examined the germination of vertebrate digested seeds. Whereas seeds in Flying-fox spat did not yield a higher germination rate than undigested controls, seeds that had passed through the gastro-intestinal tract and were deposited in scats, or those that were ingested and regurgitated from the crop, have a significantly better probability of germinating. This establishes Pied Currawongs as effective short-range dispersers and canid frugivores, such as the Red Fox, as major medium- and long-distance vectors of ornamental palms.

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INTRODUCTION

The seeds of many plants are dispersed via the gastro-intestinal tract of volant and terrestrial vertebrates (Corlett 1998; Corlett 2017; Fedriani and Delibes 2009; Levey, Silva and Galetti 2002; Tsuji, Morimoto and Matsubayashi 2009). Palms are no different in that regard (Zona and Henderson 1989). In addition, studies have shown that some plants benefit from ingestion as mastication and digestive action, as well as immersion in gastric and intestinal fluids, scarifies the seed coat aiding germination (Colon and Campos-Arceiz 2013; Reid and Armesto 2011; Rodriguez-Perez, Riera and Traveset 2005; Traveset 1998).

While a number of volant and terrestrial species are documented as vectors of Canary Island Date Palms (*Phoenix canariensis*) and their congeners (Spennemann 2018f; Zona and Henderson 1989), and thus contribute to the plants' invasiveness, there is a lack of experimental studies that assesses the germination potential of vertebrate dispersed seeds compared with naturally abscised seeds.

A study into the spread of horticulturally-planted Canary Island Date Palms into an agricultural landscape in south-eastern Australia yielded a number of vertebrate dispersed seeds extracted from scats and regurgitates, which allowed for an experimental examination of the issue.

BACKGROUND

Phoenix canariensis

Phoenix canariensis H.Wildpret ex Chabaud (Arecaceae) is a dioecious anemophilous plant that is solely propagated by seed (Barrow 1998), with pollination occurring at distances in excess of 390m (Saro, Robledo-Arnuncio, González-Pérez and Sosa 2014). Canary Island Date Palm readily and reliably sets fruit and seeds freely, annually producing between 5,000 and 30,000 obovoid drupes ('dates') (Djouab, Benamara, Gougam, Amellal and Hidous 2016; Saro et al. 2014), which are a fleshy fruit with a small, single seed and small amount of fibrous pericarp. The drupes range from 15-30mm in length, 12-17mm in

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thickness and 2–5g in mass (Djouab et al. 2016), of which the seed contributes between 0.9–1.5g. The drupes, which occur in hanging clusters, vary widely in their physical properties (shape, length, diameter, mass, colour) between individual palms. When ripe, they attain a dark orange to red colour.

The Canary Island Date Palm reaches reproductive maturity and first flowers after six to seven years (in some locales between 8 to 10 years) (Borzi 1912), which is the first time that a plant's gender can be determined. In the southern hemisphere *P. canariensis* drupes ripen between March and June (northern hemisphere: November and February), with fruit available to birds until late November (pers. obs.) (Núñez 1997:82). Immediately following ripening, the germination rate of *P. canariensis* is very high (~93%) (Noto and Romano 1987). The seed, which requires temperatures between 25°C and 35°C to germinate (Chatty and Tissaoui 1999; Pimenta, da Luz, Pivetta, de Castro and Pizetta 2010) shows its first two-leave shoots at about one year of age (Borzi 1912; Noto and Romano 1987).

Unless affected by disease or pests, the plant can live for 200–300 years (Beech 2017). In its natural distribution, *P. canariensis* is endemic to the Canary Islands (Lipnitz and Kretschmar 1994; Sosa, Naranjo, Márquez, Gil and Saro 2016). It was quickly and widely dispersed during the second half of the nineteenth century as a horticultural feature plant and street tree (Spennemann 2018a; Spennemann 2019b; Zona 2008). Today it is distributed globally in all warm temperate regions (Spennemann 2018b).

As the plants seed freely and their fruits ('drupes') are consumed by a number of vectors, *P. canariensis* has become a weed species that is known to colonise and invade natural areas. In various Australian states. *P. canariensis* it is widely referred to as a 'nuisance plant' (Ku-ring-gai Council 2007:20), 'a garden escape taking up much time to control' (Gye and Thomas 2007), a 'species with huge potential as an invasive weed' (Anonymous 2016) or is even listed 'among the ten worst environmental weeds' (Landcare Echuca 2013). Richardson et al. noted it as a weed plant that "has started to establish along waterways across the regions (NSW, Vic, SA, WA)" (Richardson, Richardson and Shepherd 2006:13f; Richardson, Richardson and Shepherd 2011:19f). In the Australasian setting, *P. canariensis* have been formally regarded as naturalised in New South Wales (Hosking, Conn, Lepschi and Barker 2007), South Australia (Brodie and Reynolds 2012), south-eastern Queensland (Biosecurity Queensland 2018), Victoria (Conn and Walsh 1993), and Western Australia (Lohr and Keighery 2016:32), as well as Norfolk Island

(Biosecurity Queensland 2018) and New Zealand (Esler 1987).

Vectors

The primary, long-distance dispersal agent for *P. canariensis* are people, in particular when planting specimens of the palm species as ornamentals (Spennemann 2018a; Spennemann 2018c; Zona 2008). Globally, a range of volant and terrestrial vertebrate vectors are responsible for the dispersal of *P. canariensis* (Spennemann 2019c). Given the size of the seed (8.8–12.2 mm diameter) (Spennemann 2019d), in the Australian context fruit bats (such as *Pteropus poliocephalus*) are possible (Augee and Parry-Jones 1991; Parry-Jones and Augee 1991), but less common dispersers (Spennemann 2018d). The gape size of birds determines their ability to swallow and disperse seeds (Lord 2004; Rey and Gutierrez 1996; Wheelwright 1985). In the Australian context dispersers these are primarily Blackbirds (*Turdus merula*) dispersing to the closest cover (pers. obs.) and Pied Currawong (*Strepera graculina*) predominantly dispersing to the closest perch (Bass 1995). A major consumer of abscised drupes are canids such as the Red Fox (*Vulpes vulpes*), which can transport seeds in their gastro-intestinal tract over greater distances (Debussche and Isenmann 1989; Szuman and Skrzydlewski 1962). The defecation occurs gradually. Field trials suggest that the Red Fox defecates five times in a 24-hour period (Ryszkowski et al. cited after Sequeira 1980). Their behaviour of territorial scent marking results in defecation on or near the same spots, leading to accumulation of scats (Spennemann 2018e) and thus an increased potential for germination.

Germination Studies

A plethora of papers exist that comment on the germination of palm seeds in general (Baskin and Baskin 2014; Broschat and Donselman 1989; Chatty and Tissaoui 1999; Donselman 1982; Gátin 1906; Marcus and Banks 1999; Meerow and Broschat 2017; Mifsud 1996; Pritchard, Wood, Hodges and Vautier 2004; Robinson 2009), as well as on the germination on the congener of *P. canariensis*, the commercially grown date palm *P. dactylifera* (Azad, Rahman and Matin 2011; Singh and Bhargava 2009; Sumianah, Makki and Rumney 1984). Only two studies refer specifically to *P. canariensis* (El-Tarawy, Menesy and Nofal 1989; Pimenta et al. 2010).

There is only a limited number of papers on the germination of vertebrate-ingested palm seed, all relating to seed consumed by coyotes (*Canis latrans*) and raccoons (*Procyon lotor*). Studies of the germination



Figure 1. Excreta of the Red Fox (Glenalvon palm n° 7). Sample APV6.



Figure 2. Pellet of undigested material regurgitated by a Pied Currawong (Lieschke palm n° 16). Sample APS24.

of *Washingtonia filifera* seeds ingested by coyotes and racoons provided no or only limited guidance on an appropriate, and replicable methodology (Bullock 1980; Cornett 1985; Cypher and Cypher 1999; Silverstein 2005). Silverstein's (2005) paper is the only study that examined the germination of *Phoenix* spp. seeds after ingestion by vertebrates.

He obtained *Phoenix* spp. (and *Washingtonia*) seeds from coyote scats and planted them in a seed starter potting soil in compartmentalized plastic growing trays which were placed in various outdoor and indoor locations. Some of the seeds were pre-treated by washing them for 30 seconds in a 5% bleach solution. Silverstein found that 46.7% of the *Phoenix* seeds (n=60) germinated with a mean of 95 days to germination, whereas *W. filifera* had a germination rate of 75.8% (mean of 71 days) (Silverstein 2005).

MATERIALS AND METHODS

The origin of the samples

The *P. canariensis* seeds used for the experiment were extracted from fox scats (Figure 1), Currawong regurgitates (Figure 2) and flying fox spats collected at the Lutheran Church as well as the property 'Glenalvon' at Alma Park, NSW (Spennemann 2018e). As controls, abscised clean seeds as well as abscised seeds with adhering flesh were collected under palm 15 at 'Glenalvon,' Alma Park. The Alma Park location has been used for a number of studies relating to *P. canariensis*.

Design

The basic methodology used for the experiments reported here followed that of Pimenta et al. (2010). It comprised a regime of 16 hours of simulated daylight and 8 hours of darkness and with environmental temperatures fluctuating between 20°C during the 'night' and 30°C during the 'day.'

The experiment was set up in a climate controlled, window-less laboratory room of 2.6 x 2.8 m. Light was provided by three AquaOne® EcoGlo90 LED lights,

Table 1. Percentage of seeds germinating at Alma Park: Natural soil conditions experiment

Type	Location	2 weeks	3 weeks	4 weeks	5 weeks	n
Currawong	Church	67.52	79.62	80.25	80.25	157
Flying-fox	Glenalvon	50.00	50.00	50.00	50.00	12
Fox	Glenalvon	78.57	88.10	88.10	88.10	84
Abscised seed (2017 season)	Glenalvon	12.00	32.00	48.00	52.00	25
Abscised seed (2018 season)	Glenalvon	38.46	53.85	57.69	57.69	26

each set up centrally above a plastic container. These lights primarily emit at the 430–490 nm spectrum (blue light) and 420–780nm spectrum (white light, peaks at 460nm and 540–620nm). A stable ambient temperature was achieved by the room-specific air-conditioning system, which was manually adjusted twice a day. The temperature was set at the start of the simulated ‘day’ to 30°C (17:00–9:00) and left cool at the end of the ‘day’ with the ‘night’ (9:00–17:00) set at a stable 20°C. Given the small air space, both the drop and rise of ambient temperature were rapid. Actual room temperatures were logged with a TinyTag Plus 2 TGP-4500 temperature and humidity logger.

The results were analysed in MS Excel and compared with the Chi-squared test with n-1 correction (Campbell 2007; MedCalc Software 2018; Richardson 2011).

Natural soil conditions experiment (A)

To replicate natural germination conditions to the extent possible, the samples were housed in three transparent plastic tubs with lids (34 l, 390 x 790 x 155mm), each filled with 13.33 l of evenly mixed planting substrate comprised of 50% peat moss and 50% Perlite. The surface was levelled and divided into a 3 x 6 grid using wooden skewers. Each cell was populated with nine seeds (3 x 3 pattern). The seeds had been cleaned of adhering material (if any) and measured prior to the experiment (see above). No fungicides were applied in order to simulate natural conditions. The seeds were pressed into substrate, level with the surface, and with their operculum pointing upwards. The surface was then moistened with 1.35 l of standard tap water sprayed with a pressurised mist sprayer evenly across the surface of the tub. The lids were then replaced for the first 48hrs, after which they were removed. This experiment was carried out between 14 June and 27 July 2018. The total number of seeds pertinent to this paper are set out in Table 1.

Soaked seeds experiment (B)

Numerous advice pages on palm seed germination recommend to place seeds between a peatmoss and vermiculite mixture placed in sealed plastic bags or merely between moist paper tissues in sealed plastic bags which are then placed in a warm space (Marcus and Banks 1999; Spanner 2018). The latter method was employed in order to test the germination success of this seasons seeds compared to last season’s seeds and to assess the effect of soaking on larger samples. In addition to these primary samples, a number of seeds regurgitated by Currawongs were added.

One half of the samples was pre-treated by soaking the seeds in tap water for 24hrs, while the other half remained untreated. As before, no fungicides were applied in order to simulate natural conditions. The bags were opened after two weeks to assess the rate of germination. All germinated seeds were removed, the bags remoistened and resealed for another week. This process was repeated twice after which the experiment was terminated. The experiment was carried out between 21 June and 20 July 2018. The total number of seeds pertinent to this paper are set out in Table 3.

Recording of germination

In all experiments, the emergence of the cotyledonary petiole (often mistakenly called the radicle) from the operculum was taken as successful germination (Pimenta et al. 2010).

RESULTS

The percentage of animal dispersed seed germination reached its maximum after three weeks, whereas non-ingested seeds continued to germinate in the weeks after that (Table 1; 2). The highest rate of germination was observed for *P. canariensis* seed in fox scats (88.1%) followed by Currawongs (80.3%) and the controls. The germination rate of seeds

Table 2. Percentage of seeds germinating: Soaked seeds experiment

Treatment	Type	Location	2 weeks	3 weeks	4 weeks	5 weeks	n	
not	Currawong	Alma Park Church	72.7	72.7	72.7	./.	66	$\chi^2= 46.941$; $p < 0.0001$
soaked	Abscised seed	Alma Park Glenalvon	16.5	19.3	20.2	./.	109	
	rodent eaten	Alma Park D14	0.0	0.0	0.0	./.	18	
soaked	Currawong	Alma Park Church	71.2	72.7	72.7	./.	66	$\chi^2= 16.275$; $p = 0.0001$
	Abscised seed	Alma Park Glenalvon	38.3	41.1	41.1	./.	107	

**Figure 3. *Phoenix canariensis* seed gnawed by a small rodent (D14).**

recovered from Flying-fox spats was 50%, while, not surprisingly, none of the rodent-bitten seeds (Figure 3) germinated.

The natural soil conditions experiment found that the observed germination rate for seeds in fox scats and Currawong regurgitates was significantly better than that for and the undigested abscised control seeds (Table 2). There was, however, no statistical difference between the germination rate of seeds in Flying-fox spats and undigested abscised controls (Table 3).

DISCUSSION

While vertebrates are prime dispersers of palm seeds, their effectiveness varies. The comparatively low level of germination success of seeds in Flying-fox spats can be interpreted as the result of a complete lack of scarification. The mastication action of the animal will either tear the pericarp off the seed, leaving striations (Figure 4) or will chew the whole drupe, separating the pericarp from the seed in the oral cavity (Spennemann 2018d). The seed itself is not subjected to any further physical impact, but is pushed to the front of the mouth and ejected with masticated epicarp platelets and squeezed-out endocarp fibres. The observation that the germination rate among Flying-fox dispersed seeds is less than that of the controls could be explained by the fact that the controls lying on the ground had been exposed to some modicum of photo-chemical erosion. As the majority of spit-outs occur at the source tree, Flying-foxes provide very little dispersal benefits.

Even though only a small percentage of volant vectors ingest drupes, birds are by far the most significant in terms of pure quantities of seeds dispersed (in litt.). The size of the seeds that can be dispersed is regulated by the bird's gape size, whereas the overall size of the bird and its crop determines the quantity of seed that can be consumed and thus dispersed. The majority of birds, such as Currawongs, tend to fly to the closest perch to digest their food. There the seeds

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Table 3. Differences between the germination rates of vertebrate dispersed seed and controls (naturally abscised seed), Natural soil conditions experiment

	Fox	Currawong	Flying Fox	abscised seeds	
				2017 season	2018 season
Fox	—	$\chi^2=2.378$; $p=0.1230$	$\chi^2=10.862$; $p=0.0010$	$\chi^2=15.445$; $p=0.0001$	$\chi^2= 11.780$; $p=0.0006$
Currawong	—	—	$\chi^2=6.351$; $p=0.0117$	$\chi^2=9.485$; $p=0.0021$	$\chi^2=6.384$; $p=0.0115$

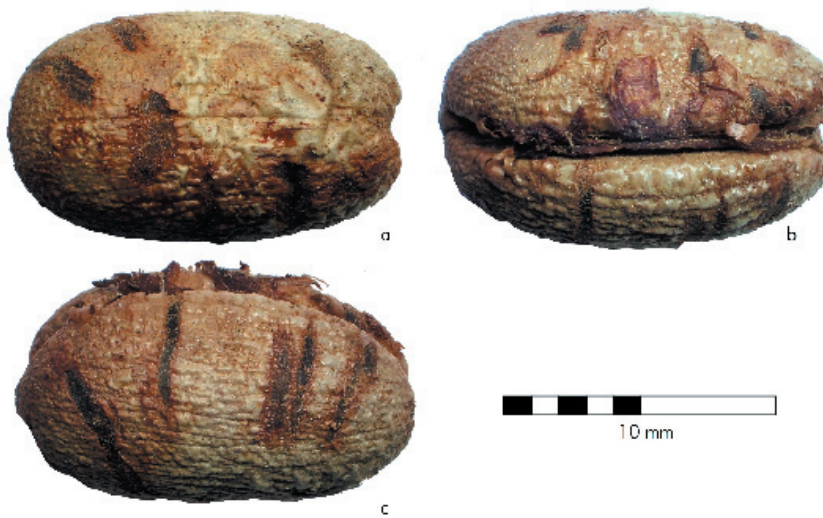


Figure 4. *P. canariensis* seed chewed by a Flying-fox.

are regurgitated after less than 20 minutes (Bass 1995). Even though large quantities of seeds accumulate under these perches, their residence time in the bird’s gizzard is only very short. Albeit short, the residence time, coupled with the abrading action in the gizzard is sufficient to significantly increase the germination potential compared to naturally abscised seed. Thus the main benefit of Currawongs as vectors rests in the albeit short-distance spatial dispersal of seeds, the quantity of seeds deposited at given locations and the improved germination potential. The net benefit to the palm is less an increase in spatial distribution, but an intensification of its coverage. Dispersal over greater distances occurs only when Currawongs return to their night roosts (Bass 1995).

These findings cannot be extrapolated for smaller birds, such as Blackbirds (*Turdus merula*), Starlings (*Sturnus vulgaris*) and Common Myna (*Sturnus [Acridotheres] tristis*), all of which are known dispersers (Spennemann 2019c), but which have both a smaller gizzard and shorter residence times for ingested fruit.

Canids are major dispersers of fruit including palm drupes (Graae, Pagh and Bruun 2004; Rico-Guzmán, Terrones, Cantó and Bonet 2012; Schmelitschek, French and Parry-Jones 2009; Spennemann and Allen 2000). In most instances the consumption of fruit and subsequent defecation of seed improves a seed’s chances or germination success (Traba, Sagrario, Herranz and Clamagirand 2006; Varela and Bucher 2006), even though exceptions are on record (Morales-Paredes, Valdivia

and Sade 2015). The findings of this study of enhanced germination capacity conform with the majority of observations.

While vertebrate-dispersed seeds have a greater chance of germination, there are a number of *factors* post-dispersal that affect germination success, namely infestation by insects, predation by rodents and environmental factors. Seeds that successfully germinate while lying on the ground are on occasion lifted above the surface by their emergent radicles (Spennemann, Kent and Cook 2018:9), thus exposing the radicle to consumption by small rodents as well as to desiccation during warm weather events. It is not uncommon to find dry seed with open opercula under palms (pers. obs.). *P. canariensis* seeds under the source palms have a high chance of being predated by rodents (Figure 3), or becoming infested by date stone beetles (*Coccotrypes dactyliperda*) (Spennemann 2019a) which reduces a seed’s ability to germinate and successfully develop into a small seedling. Seeds dispersed in canid faeces, however, tend to be avoided

by these beetles (Spennemann in press) and thus have a greater chance of establishment. Furthermore, as the germinating seeds are embedded in the matrix of the scats, they are less likely to be raised by the emerging radicle, and thus further protected from predation.

IMPLICATIONS

In the Australian setting, the findings of this study establish the Red Fox as the main long-distance seed vector for Canary Island Date Palm seeds, not only in terms of dispersal distance and dispersal intensity due to repeated defecation at the same location in consequence of territorial scent marking (Gese and Ruff 1997; Macdonald 1979), but also in terms of dispersal success due to the high germination success and low level of post-depositional predation by seed boring beetles. Significantly, Red Foxes are also instrumental in the establishment of Canary Island Date Palms in spaces lacking perch trees, such as in (ungrazed) grassland and scrublands (see example in Spennemann 2018g). Only in areas where the Red Fox is less common, such as in inner urban areas (White, Gubiani, Smallman, Snell and Morton 2006), does dispersal by volant vectors appear to gain greater significance. Among these, Pied Currawong are an effective major vector due to their revisitation of preferred perches.

It would be beneficial to examine the germination potential of Canary Island Date Palm seeds regurgitated by smaller vectors, such as Blackbirds, Starlings and Common Myna. Given the difficulty of identifying and obtaining sufficient quantities of seeds regurgitated by these species, captive feeding experiments may be required.

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