

Herb endozoochory by cockatoos: Is ‘foliage the fruit’?

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Abstract Establishing whether herb seed endozoochory is accidental or has evolved independently or in combination with other dispersal mechanisms may be valuable in the study of plant–animal interactions, but it remains unexplored for birds. We tested whether an Australian cockatoo, the galah (*Eolophus roseicapilla*), swallows entire seeds when feeding on other tissues without subsequent seed digestion, thus enhancing seed dispersal (the ‘foliage is the fruit’ hypothesis). Our preliminary sampling provides strong evidence supporting that this seed predator also acts as a legitimate endozoochorous disperser. A large proportion of droppings contained numerous seeds of six herb species of three plant families, surviving gut passage to be dispersed as viable propagules. The wide range in the number of seeds found in combinations with up to five species in particular droppings suggests both simultaneous and sequential passive ingestion without seed digestion and/or focused seed predation and digestion. As expected for inadvertent ingestion and inefficient digestion, our findings suggest that seed number and richness of dispersed plants are associated traits in this particular mutualistic interaction. This relationship can have important implications in community-wide processes, favouring herbs whose seeds are disseminated in a viable state over those predated or negatively affected by gut transit.

Key words: Australia, *Eolophus roseicapilla*, grasslands, herbaceous plants, internal dispersal.

INTRODUCTION

The use of a variety of seed dispersal mechanisms may increase the effectiveness of recruiting seedlings. It is widely accepted that seeds of fleshy-fruited plants and large seeds of dry-fruited plants are largely dispersed by animals, while smaller seeds without flesh are often assumed to be dispersed by a variety of abiotic and biotic vectors (Nathan *et al.* 2008). Even when particular plant species evolve a specific dispersal syndrome, alternative nonstandard dispersal modes acting sequentially, simultaneously or accidentally can play an important but often unclear role in the ecology and evolution of plants (Nathan *et al.* 2008).

Seeds of weeds, sedges, pasture grasses and other small-seeded herbaceous plants (hereafter herbs) have not been generally associated with a specific kind of dispersal, but with a suite of methods based on their morphology, including wind (anemochory), explosive dehiscence (ballochory), fur and feather attaching through specialised appendages (epizoochory), internal dispersal (endozoochory) or by a combination of these methods in complex two-phase processes, that

is diplochory. These seeds represent valuable food resources for multiple organisms acting as dispersal vectors, ranging in size from ants to large ungulates. Among vertebrates, large herbivores are common endozoochorous dispersers as a result of passive foliage browsing, which inspired the ‘foliage is the fruit’ hypothesis (Janzen 1984). This hypothesis proposes that foliage acts as the attractant for seed dispersal selecting for traits enhancing ingestion and gut passage of viable seeds. Foliage browsing can lead to indiscriminate seed ingestion allowing the simultaneous dispersal of several herb species, which can have implications on pasture communities (Janzen 1984; Pakeman *et al.*, 2002).

The environmental factors and selective pressures behind the effectiveness of herb seed dispersal by animals other than ants and ungulates have received comparatively little attention. Regarding mutualistic herb–bird interactions, the available information is limited to the role of ducks and ratites as legitimate dispersers (Calviño-Cancela *et al.* 2006; Soons *et al.* 2016). Recently, granivorous birds considered only as seed predators have been highlighted as legitimate dispersers (Orłowski *et al.* 2016). Despite its relevance to the study of plant–animal interactions, whether endozoochory can be accidental or has

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evolved independently or in combination with other dispersal mechanisms remains unexplored in birds. Even if seeds are the main foraging target, a proportion of them could survive gut passage depending on generally unknown factors (Soons *et al.* 2016). Despite its potential to be applied to species that focus on seeds and other herb tissues as alternative or simultaneously food, the ‘foliage is the fruit’ hypothesis has been only tested in ungulates.

In this study, we tested this hypothesis by considering a medium-sized cockatoo, the galah (*Eolophus roseicapilla*), as a potential seed disperser of its food herbs. Galah is assumed to be only a plant antagonist, although whether seeds are ingested intact and dispersed as a consequence of granivory or foliage grazing has been, to our knowledge, never evaluated. The ‘foliage is the fruit’ hypothesis predicts that (i) numerous seeds should survive gut passage and be excreted as viable propagules after being inadvertently ingested while consuming other edible tissues of herbaceous plants. Instead, if seeds rather than other tissues are the main feeding target, a few intact seeds are expected to be found in a small proportion of droppings, but large quantities of seed fragments and semi-digested unviable seeds would be common. Indiscriminate foliage grazing implies the passive ingestion of seeds from multiple herb species composing pastures, or that of seeds in the vicinity of the target plants, rather than focused predation on particular herb species. Therefore, we predict that (ii) the number of seeds dispersed should be less in droppings with the presence of single rather than multiple herb species.

METHODS

The galah (Fig. 1) is a widespread species that forages on the ground in grasslands, agricultural crops and open eucalypt forests. Habitat clearing, agriculture, livestock management and urbanisation have favoured this cockatoo (Cameron 2007).

Galah surveys were conducted by slowly driving 1010 km along unpaved and secondary roads during 11–26 March 2017 in Queensland, Australia, to record the foraging behaviour, substrate and food exploited.

Whole fresh droppings were collected at sunrise beneath trees used as communal roosts by a monospecific flock of about one hundred galahs in Artemis Station, southern Cape York Peninsula. All droppings found ($n = 34$) in a single morning were collected in paper bags, dried with an air heater and stored at room temperature until arrival at the laboratory. Seeds were measured, photographed and identified based on size and external features following Erickson *et al.* (2016). Seed viability was determined with the tetrazolium test for all seeds retrieved in particular droppings, or for a maximum of 25 seeds of each species and dropping.

RESULTS

We recorded 61 foraging flocks totalling 704 galahs. Most individuals (99.7%) were on the ground feeding on herbs in pastures; only two individuals were observed consuming bark of *Eucalyptus* sp. The mean \pm SD size of the foraging flocks was 13.6 ± 42.5 ($n = 61$, range = 1–150).

About 60% of droppings (20 of 34) contained intact seeds, but fragments of predated or semi-digested seeds were not found. Overall, 726 intact seeds of six herb species with tiny seeds (two of them identified to the genus level) of three families were found in 20 droppings (Table 1).

Half of the droppings with seeds contained a single herb species, mostly *Rumex* sp., while the remaining droppings showed seeds of 2–5 species (Table 1). Most seeds (about 90%) were found in droppings with several herb species (Table 1). The mean \pm SD number of plant species per dropping with seeds was 2.1 ± 1.4 ($n = 20$). The number of seeds per dropping differed between herb species (Kruskal–Wallis test, $H = 11.73$, $P = 0.039$, d.f. = 5, $n = 20$), being

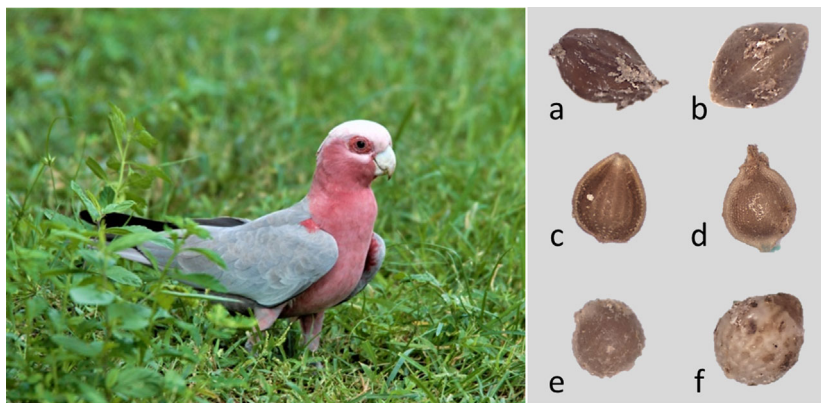


Fig. 1. Galah feeding on pastures (left panel). Seeds of each species retrieved from droppings (right panel). a: *Rumex* sp., b: *Setaria surgens*, c: *Fimbristylis dichotoma*, d: *Fimbristylis cf. acicularis*, e: *Fimbristylis* sp., f: *Scleria laxa*.

Table 1. Number and percentage of galah droppings with intact seeds of each herb species and combination of species

Herb species (code) (seed size, mm)	Droppings ($n = 34$)		Seeds ($n = 726$)	
	#	%	#	%
Polygonaceae				
<i>Rumex</i> sp. (a) (1.22 × 0.82, $n = 21$)	18	52.9	624	86.0
Poaceae				
<i>Setaria surgens</i> (b) (1.80 × 1.16, $n = 20$)	7	20.6	69	9.5
Cyperaceae				
<i>Fimbristylis dichotoma</i> (c) (1.04 × 0.81, $n = 8$)	6	17.6	12	1.7
<i>Fimbristylis cf. acicularis</i> (d) (1.12 × 1.01, $n = 4$)	5	14.7	10	1.4
<i>Fimbristylis</i> sp. (e) (1.16 × 1.06, $n = 7$)	5	14.7	8	1.1
<i>Scleria laxa</i> (f) (1.93 × 1.15, $n = 3$)	1	2.9	3	0.4
Species composition	Droppings with seeds ($n = 20$)		Seeds ($n = 726$)	
	#	%	#	%
a	10	50.0	72	9.9
d	1	5.0	3	0.4
c + e	1	5.0	2 (1 + 1)	0.3
a + b + c	2	10.0	380 (323 + 55 + 2) [†]	52.3
a + c + d	1	5.0	40 (37 + 2 + 1)	5.5
a + b + e	1	5.0	12 (10 + 1 + 1)	1.7
a + b + f	1	5.0	187 (176 + 8 + 3)	25.8
a + b + d + e	1	5.0	8 (2 + 2 + 3 + 1)	1.1
a + b + c + d + e	2	10.0	22 (4 + 3 + 7 + 3 + 5) [†]	3.0

[†]Data in brackets correspond to the sum of seeds of each herb species found in both droppings. Seed size (mean length × width) was indicated for each species. n = sample size.

highest for *Rumex* sp. and lowest for *Fimbristylis* sp. (Fig. 2a). Droppings with seeds of a single herb species ($n = 11$) showed a lower number of seeds compared to those with seeds of several species ($n = 9$) (Mann–Whitney U test, $z = 2.28$, $P = 0.023$, Fig. 2b). All seeds identified to species correspond to native herbs, while those identified only at the genus level can correspond to native or introduced herbs.

Most droppings with seeds contained viable seeds (14 of 19 droppings, 73.7%; seeds of *Fimbristylis acicularis* from a single dropping were used for identification and not analysed for viability). The proportion of droppings with viable seeds was 77.8% for *Rumex* sp. (14 of 18 droppings) and 42.9% for *Setaria surgens* (3 of 7 droppings). 40.3% of *Rumex* sp. ($n = 186$) and 20.0% of *S. surgens* seeds ($n = 40$) were viable. No viable seeds of the remaining herb species were found, although the numbers of analysed seeds were much less due to their lower frequency in droppings (*Fimbristylis dichotoma*: $n = 10$ seeds from six droppings; *F. acicularis*: $n = 7$ seeds

from four droppings; *Fimbristylis* sp.: $n = 6$ seeds from five droppings; *Scleria laxa*: $n = 3$ seeds from one dropping).

DISCUSSION

Generalist herb exploitation has been highlighted to explain damage by galah on natural pastures and agricultural crops. No information on mutualistic interactions between galah and its food plants has been previously reported, except for the consumption of invertebrates (Cameron 2007) potentially parasitising these plants. Our sampling provides strong evidence supporting that this seed predator also acts as an internal seed disperser. Cockatoo-mediated dispersal of tiny herb seeds thus adds to the growing evidence on the role of mutualism–antagonism continuums driving the interactions between psittacines and their food plants (Blanco *et al.* 2015; Tella *et al.* 2016; Montesinos-Navarro *et al.* 2017).

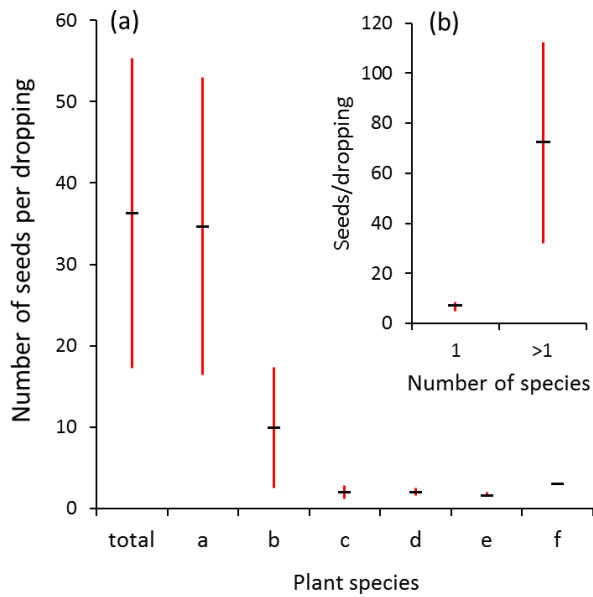


Fig. 2. Number (mean \pm SE) of herb seeds per galah dropping according to (a) plant species (species codes as in Table 1) and (b) number of plant species present in individual droppings, considering those with a single or multiple (2–5) species. a: *Rumex* sp., b: *Setaria surgens*, c: *Fimbristylis dichotoma*, d: *Fimbristylis cf acicularis*, e: *Fimbristylis* sp., f: *Scleria laxa*.

We found that a large proportion of droppings contained numerous viable seeds. Strikingly, we found no seed fragments or semi-digested seeds in the droppings, which implies that seeds are not the main feeding target of galah during the study period and/or that its gut is not efficient at digesting seeds of particular herbs. In agreement with the hypothesis tested, galah can inadvertently swallow entire seeds without subsequent digestion, thus enhancing seed dispersal. These seeds may be actively searched for, but only a proportion of them would be intensively chewed to promote efficient digestion, thus limiting seed dispersal. Given the wide range in the number of seeds of several species found in particular droppings (1–355), a combination of both possibilities (i.e. passive browsing without seed digestion and/or focused seed predation and digestion) is likely. Indeed, a proportion of seeds can survive unharmed because complete digestion does not work continuously as a by-product of gut morphology and physiology, as well as due to other factors such as activity, stress and food features (Kleyheeg *et al.* 2015). The observed proportion of viable seeds of the two most abundant herbs retrieved, and the lack of viability in the remaining species can also be influenced by gut transit conditions, reduced sample size and methodological limitations for assessing seed viability (Cope land & McDonald 1995). Whatever the mechanisms behind, the high number of viable seeds dispersed suggests selection for seed traits (e.g. tiny size)

enhancing ingestion and survival from gut passage, as expected from the ‘foliage is the fruit’ hypothesis (Janzen 1984). Further research is required to evaluate the complete suite of plants dispersed among those consumed by galah and other grazing cockatoos and parrots.

An indiscriminate foliage grazing predicts the passive ingestion of seeds from multiple herb species (Janzen 1984). Despite the limited number of droppings collected in our ‘snapshot’ sampling, combinations of seeds of up to five species were found in particular droppings. Most samples showed a variable proportion of viable seeds, and those of the two most frequently dispersed species showed a relatively high viability rate. As expected from inadvertent ingestion and inefficient digestion, the number of seeds dispersed was lower in droppings with the presence of single compared to multiple species. Regardless of whether galah fed passively on multiple herbs or focused on particular species, our findings indicate that seed number and richness of dispersed plants are associated traits in this mutualistic interaction. This can have important implications in community-wide processes, favouring herbs disseminated in a viable state over those predated or negatively affected by gut transit (Janzen 1984; Pakeman *et al.* 2002).

There is a growing body of information on external seed dispersal by psittacines (Tella *et al.* 2015, 2019; Baños-Villalba *et al.* 2017; Blanco *et al.* 2018). Long overlooked based on assumptions that their strong beaks and gizzards destroyed and digested consumed seeds; parrot endozoochory has been documented mostly involving fleshy-fruited plants (Young *et al.* 2012), although dispersal of dry-seeded herbs by the Monk parakeet (*Myiopsitta monachus*), a species frequently foraging on pastures, has also been cited (Blanco *et al.* 2016). Because galah is an open-country specialist, the probability that seeds are dispersed in a favourable habitat for establishment (directed dispersal) could be relevant as compared to non-directed abiotic vectors, often considered the ‘standard’ for many herbs (Nathan *et al.* 2008). The mean size of foraging flocks recorded was lower than the total number of galahs using the sampled roost. This suggests that the seeds retrieved were from individuals foraging in smaller flocks during daylight and concentrating in the roost to pass the night. Moreover, galah foraging routines involve frequent daily and seasonal movements (Cameron 2007) likely contributing to widespread dispersal, including long-distance flights potentially connecting patches of suitable habitat. Therefore, the potentially relevant ecological contribution of galah to the structure, functioning and conservation of Australian grasslands is worthy of further attention, given its huge abundance and expanding range. Similarly to the pervasive ecological impact of herbivores defecating large

quantities of tiny seeds (Janzen 1984; Pakeman *et al.* 2002), galah endozoochory could exert an overlooked influence on community dynamics of native grasslands in the absence of native terrestrial ungulates in Australia. As reported for domestic livestock, the galah exploitation of exotic herbs (Cameron 2007) could contribute to disseminating these plants, with implications in the ecology and conservation of grasslands and threatened granivorous birds (Garnett *et al.* 2010). Given its interest in the understanding of grasslands structure, diversity and functioning, efforts are encouraged to refine the ‘foliage is the fruit’ hypothesis within the framework of ecological and evolutionary plant–bird interactions.

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AUTHOR CONTRIBUTIONS

Conceptualization-lead, formal analysis-equal, investigation-lead, methodology-lead, supervision-lead, writing-original draft-lead: G.H. Formal analysis-lead, methodology-lead, writing-review & editing-supporting: C.B., D.C., Á.L.K. Conceptualization-lead, funding acquisition-lead, investigation-lead, supervision-lead, writing-review & editing-supporting: F.H. Conceptualization-lead, formal analysis-equal, funding acquisition-lead, investigation-lead, methodology-equal, project administration-lead, resources-lead, supervision-lead, writing-review & editing-supporting: J.T.

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