

Avian–Shrub Interactions: Ingestion, Seed Recovery and Germination of Three Mediterranean Shrub Species Fed to Quail (*Coturnix coturnix*)¹

Juan Manuel Mancilla-Leytón^a, Pedro González-Redondo^b, and Ángel Martín Vicente^a

^aDepartamento de Biología Vegetal y Ecología, Universidad de Sevilla, Apdo. 1095, 41080 Sevilla, Spain

e-mail: jmancilla@us.es

^bDepartamento de Ciencias Agroforestales, Universidad de Sevilla, Ctra. de Utrera, km 1, 41013 Sevilla, Spain

Received October 29, 2014

Keywords: ornithochory, quail, seed germination, the Mediterranean

DOI: 10.1134/S1067413615040104

INTRODUCTION

Seed dispersal has been described as a ‘diffuse mutualism’ due to the fact that most, if not all, frugivores consume fruits of many different species of plants (Wheelwright and Orians, 1982; Jordano, 1995; Wessels and Schwabe, 2008; Pakeman and Small, 2009; D’Hont and Hoffmann, 2011). This has resulted in little coupling between the characteristics of fruits and their vertebrate dispersers (Jordano 1995; Pakeman and Small, 2009). However, seed dispersal is an important component of the plant colonization process (Harper, 1977) which may influence many key aspects of plant ecology and restoration management (survival, migration, recruitment, diversity, etc).

Plant–animal interactions, and in particular the processes of seed predation and dispersal, have strong spatial and temporal variation, affecting the patterns of plant regeneration and ecosystem dynamics. Seasonal production of fruits by species means a temporary abundance of resources, inducing a diet switch for many animals benefiting from these resources (Pérez-Ramos et al., 2007).

Birds can play an important role in the seed dispersal cycle through the active uptake of seeds and their subsequent internal transport (ornithochory) (Wang and Smith, 2002). The direct benefit obtained by the birds feeding on fruits is accompanied by a benefit for the plant—dispersal of progeny—and represents a classic example of mutualism. The seasonal diet switch of birds (from insectivory to frugivory) has strong ecological implications for plants, determining the genetic and population structure of (bird-dispersed) plant populations (e.g. see Jordano and Godoy, 2002). Thus, complex plant–animal interactions, including predation and dispersal, would determine the forest dynamics, these interactions being

vital for the maintenance of ecosystem functions (Pérez-Ramos et al., 2007). Just for native plants, passage through bird’s guts may increase, decrease, or not affect germination, depending on the species of bird and specie (Traveset, 1998).

Although a large number of scientific articles in the literature include ornithochory (e.g. see Traveset, 1998), studies of dispersion of the scrub by game birds, are rare. In recent years, hunting has reached a considerable importance in Mediterranean society, as Mediterranean ecosystems have very favorable geographical conditions for it. The economic importance of this activity has resulted in increased breeding for release of game birds, e.g. quail (*Coturnix coturnix*) and partridge (*Alectoris rufa*), in many farms (Dalmau, 1994; González-Redondo, 2004). The introduction of game species may cause changes in ecosystems: the studies, usually, take into account the effect of game bird on populations of predators (as food) or agriculture (crop damage) (Villanúa et al., 2007), but not usually take into account their role as seed disperser.

The objective of this study was to investigate whether quails (*Coturnix coturnix*) can potentially disperse the seeds of three common Mediterranean species in Doñana Natural Park: *Corema album* L., *Myrtus communis* L. and *Pistacia lentiscus* by quantifying the number of seeds that pass through the quail’s gut and germinate afterwards. We addressed the following questions: (i) how many seeds pass through the quail’s gut without damage?, (ii) What is the temporal pattern of seed defecation? and (iii) Does ingestion by quails enhance or depress seed germination?

MATERIAL AND METHODS

Fruit Collection and Characteristics

Fruits were collected in a rangeland located in Dunas del Asperillo (Doñana Natural Park) in SW

¹ The article is published in the original.

Spain (37°15 N, 6°31 W) where the three species were very common (Alvarez-Cansino et al. 2010). Ripe fruits of the three chosen species (*M. communis*, *P. lentiscus* and *C. album*) were randomly collected from 25 different plants of each species. The fruits collected from each species were mixed together and stored in the laboratory at room temperature in dry and darkness conditions until the beginning of the experiments.

The length was measured in a hundred fruits and a hundred seeds with a vernier caliper. In order to determine the number of seeds ingested by quails, the mean number of seeds per fruit was estimated by counting the seeds in 100 fruits of each species.

Seeds Retrieved After Gut Passage

Six female adult quails of similar size and age (100 g average weight and one year old) were fed seeds. They were individually housed at the Teaching and Experimental Farm of the Faculty of Agriculture, University of Seville. Quails were kept in individual metabolic pens with a collector system for faeces, where they were fed seeds. Fruits of each species were offered to each quail: 70 fruits of *M. communis*, 200 fruits of *P. lentiscus* and 67 fruits of *C. album* chosen at random from the pool of collected fruits. This represented around 200 seeds of each species to each quail. Afterwards, the animals were fed feed and had free access to water. All the dung produced by each quail were collected every 12 hours for two days (0–12, 12–24, 24–36, 36–48 h after ingestion) and dried at room temperature for 72 hours in a bell jar with silica gel to avoid seed fermentation and damage. All the dung recorded were crushed manually, counting the number of seeds retrieved.

Some of the seeds retrieved were partially broken, missing part of the cotyledons but with an intact embryo. Since the number of broken seeds was very low (*C. album* 0.01%, *M. communis* 0.03% and *P. lentiscus* 0.05%) they were not tested for germination. Only seeds with no evidence of apparent external damage, examined under a microscope, were used for the germination experiment.

Seed Germination After Gut Passage

The germination of seeds retrieved from quail's dung was compared to the germination of seeds that were not eaten. For each species, there were three treatments: (i) Control: seeds that were not eaten; (ii) 0–12 h: seeds retrieved between 0 and 12 h after ingestion; and (iii) 12–24 h: seeds retrieved between 12 and 24 h after ingestion. Very few seeds were retrieved after 24 h (only from *C. album*) and thus were not tested. The seeds of each species eaten by different quails, for the same treatment (0–12 h and 12–24 h), were mixed together for this experiment.

Seeds of all treatments were disinfected in a 1% sodium hypochlorite solution and then the seeds were placed on filter paper in a 5-cm Petri dish. Each Petri

dish contained 25 seeds, and there were 4 replicates per treatment. Three ml of distilled water were added to each dish. Dishes were wrapped with parafilm and placed in a germinator (ASL Aparatos Científicos M-92004, Madrid, Spain) for 60 days with a regime of 12 h of light (25°C, 35 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 400–700 nm) and 12 h of darkness (12°C). This temperature regime was chosen to represent the end of autumn temperatures in Mediterranean climate, when these species germinate. The dishes were inspected daily and seeds germinated were counted and removed. The water level was adjusted daily with distilled water. We considered that seeds had germinated after root emergence (1–2 mm).

Three parameters of germination were determined: final germination percentage, time of first germination and mean time to germination (MTG), calculated as: $\text{MTG} = \sum_i (n_i \times d_i) / N$, where n_i is the number of seeds germinated at day i , d_i the incubation period in days, and N is the total number of seeds that germinated in the treatment (Brenchley and Probert 1998).

The overall effect of quail passage on seed germination of each species was estimated by multiplying the mean percentage of seeds retrieved by their mean germination percentage.

Viability Test

The tetrazolium test was applied to three 20 seed samples collected from pellets and from seeds not eaten (control), to determine the viability of the embryo (MacKay 1972). Seeds were kept in water during 16 h at a constant 25°C temperature. Seeds were then submerged in a 1% aqueous solution of 2,3,5-triphenyl-tetrazolium chloride, pH 7, in darkness for 24 h at a constant temperature of 25°C. Then the seeds were dissected and the embryo was analysed with a magnifying glass (Bradbeer 1988).

Statistical Analysis

Differences in the total number of seeds retrieved from dung among treatments, total number of seeds germinated, time of first germination, mean time of germination, seed viability and number and size of seeds emerged from intact and crumbled dung collected at different dates were statistically evaluated with ANOVA. The data were tested for normality with Kolmogorov-Smirnov test. Tukey test was used for evaluating significant differences among treatments. SPSS 22.0 for Windows (SPSS, Inc., Chicago, IL, USA) was used in all statistical analysis.

RESULTS

Seeds Retrieved After Gut Passage

The number of seeds retrieved from quail's dung ranged from 30 to 54% with significant differences between species (Tukey test, F -value = 21.02 $p < 0.05$)

Table 1. Characteristics of control seeds and seeds retrieved from dung after ingestion by quail (Mean \pm standard error, $n = 100$). Different letters indicate significant differences (Tukey Test, $p < 0.05$)

Species		Length, mm	Volume, mm ³
<i>Corema album</i>	Control seed	2.58 \pm 0.03 a	7.23 \pm 0.15 a
	Seed retrieved 0–12 h	2.45 \pm 0.07 a	7.21 \pm 0.39 a
	Seed retrieved 12–24 h	2.56 \pm 0.03 a	7.01 \pm 0.13 a
<i>Myrtus communis</i>	Control seed	3.22 \pm 0.09 a	13.84 \pm 0.94 a
	Seed retrieved 0–12 h	3.82 \pm 0.11a	13.58 \pm 1.50 a
	Seed retrieved 12–24 h	–	–
<i>Pistacia lentiscus</i>	Control seed	4.54 \pm 0.21 a	34.77 \pm 2.71 a
	Seed retrieved 0–12 h	3.25 \pm 0.89 a	14.57 \pm 1.84 b
	Seed retrieved 12–24 h	3.39 \pm 1.16 a	13.31 \pm 0.56 b

Table 2. Percentage of germination, number of days to first germination, mean time-to-germination (MTG) and viability seeds, in control seeds and seeds retrieved from dung 0–12 and 12–24 h after ingestion by quail. Values are means \pm s.e ($n = 4$). Different letters indicate significant differences (Tukey Test, $p < 0.05$)

		Germination, %	1st Germination, d	MTG, d	Viability, %
<i>Corema album</i>	Control	4.0 \pm 1.2 a	39.3 \pm 2.8 a	46.9 \pm 3.8 a	51.1 \pm 8.7 a
	0–12 h	10.7 \pm 1.6 b	37.9 \pm 4.7 a	40.6 \pm 4.3 a	35.6 \pm 6.1 a
	12–24 h	8.0 \pm 1.8 b	35.5 \pm 9.3 a	41.9 \pm 6.7 a	37.5 \pm 13.5 a
<i>Myrtus communis</i>	Control	57.5 \pm 2.5	5.8 \pm 1.1	11.2 \pm 1.3	65.4 \pm 2.5 a
	0–12 h	–	–	–	0.6 \pm 0.5 b
	12–24 h	–	–	–	–
<i>Pistacia lentiscus</i>	Control	39.2 \pm 1.6	11.4 \pm 1.4	30.8 \pm 3.5	42.5 \pm 6.2 a
	0–12 h	–	–	–	0.2 \pm 0.1 b
	12–24 h	–	–	–	0.1 \pm 0.1 b

(Fig. 1). The highest percentages of seeds were found in *C. album* (53.47%), followed by *P. lentiscus* (37.61%) and *M. communis* (30%). In all the species, the majority of the seeds were retrieved between 0–12 hours after ingestion (*C. album* 40.77%, *P. lentiscus* 72.18% and *M. communis* 100% of the seeds retrieved), followed by 12–24 hours (*C. album* 33.29% and *P. lentiscus* 27.82% of the seeds retrieved). Only in *C. album*, a few seeds were retrieved after 24 hours (19.29% at 24–36 h and 6.65% at 36–48 h) (Fig. 1).

Seed Characteristics

The larger fruits were those of *C. album* (9.21 mm) and *M. communis* (7.66 mm), followed by *P. lentiscus* (4.38 mm). The number of seeds per fruit varied among species: *C. album* and *M. communis* (3 seeds/fruit) had more seeds per fruit than *P. lentiscus* (1 seed/fruit). The characteristics of control and retrieved seeds are listed in Table 1. *Corema album* and *M. communis* showed seeds smaller than *P. lentiscus*. In *C. album* and *M. communis*, we found no significant differences between seeds control and seeds retrieved for any of the biometric parameters analyzed. In the case of *P. lentiscus*, volume of seeds control was significantly greater than the volume of seeds recovered at 0–12 and 12–24 h ($F = 13.21$, $P < 0.05$) (Table 1).

Viability and Germination

The tetrazolium test showed significant differences between control seeds and seeds retrieved from quail's dung in all species (Table 2). In *C. album*, passage through the quail's gut not decreased the viability of seeds retrieved. In seeds retrieved of *P. lentiscus* the viability was significantly reduced by 99% ($F = 5.06$, $p < 0.05$) and in seeds retrieved of *M. communis* the viability was significantly reduced by 100% ($F = 45.62$, $p < 0.05$) (Table 2).

As expected, the passage through the quail's gut significantly decreased the retrieved seed germination in *M. communis* and *P. lentiscus* (Table 2). Only germinated seeds retrieved in *C. album*, which germinated significantly more than the no eaten seeds ($F = 6.33$, $p < 0.05$). So, the passage through the quail's gut had no effect on the speed of germination (time of first germination and mean time to germination, MTG) (Table 2).

When considering gut passage and germination together (global effect), gut passage notably depressed seed germination in *M. communis* and *P. lentiscus* (57.5 and 39.0% of control seeds compared to 0% of retrieved seeds, respectively), but not in *C. album*, where retrieved seeds germinated more (10.13%) than control seeds (4.0%).

DISCUSSION

Seeds of three Mediterranean plant species studied survived ingestion and gut passage by quails, so these could potentially be dispersed by quails. Seed size, seed shape, and hardseededness are important factors in seed recovery (Russi et al., 1992; Gardener et al., 1993; Pakeman et al., 2002; Pakeman and Small, 2009), i.e. the smaller, the harder, and the rounder a seed is, the higher the probability is that it will survive chewing. The number of seeds retrieved from quail's dung was high (30–54%), with significant differences between species. Smaller and harder seeds (*C. album*, 2.58 mm) were more retrieved than larger seeds (*M. communis*, 3.22 mm and *P. lentiscus*, 4.54 mm) (Table 1).

Food retention time within a digestive tract is not determined only by the intrinsic morphological and physiological traits of the particular animal. Seed retention time within the same frugivorous species can vary significantly depending on the fruit ingested, with high individual variability (Traveset, 1998; Pakeman and Small, 2009). The size and weight of a seed, usually, determines the speed at which it passes through the digestive tract of a bird, with large and heavy seeds being defecated more quickly than small and light seeds (Garber 1986; Levey and Grajal, 1991; Gardener et al., 1993; Pakeman and Small, 2009). This was reflected in our study, in the case of *M. communis* and *P. lentiscus*, because the major part of the seeds was retrieved between 0 and 12 h after ingestion (100 and 70%, respectively), while only in *C. album* a quarter of the seeds were retrieved after 24 hours (Fig. 1).

Seed coat thickness might perhaps be a more important factor determining whether germination patterns will be affected by seed ingestion. Germination may be enhanced by the softening of the seed coats during the digestive process (Baskin and Baskin 1998; Traveset and Verdú, 2002), but destruction and germination inhibition also occur (Traveset, 1998). Clergeau (1992) found that the effect of bird ingestion on germination was different for different species of birds and attributed this to differential abrasion of the seed coats by the birds' guts. Small seed size is also an important characteristic to survive ingestion and gut passage (Pakeman et al., 2002; Pakeman and Small 2009; D'Hont and Hoffmann 2011) due to the decrease of the abrasive effect of chewing (Fredrickson et al., 1997). This was detected in our experiment: larger seeds (*M. communis* and *P. lentiscus*) showed lower recovery rate and decreased viability of seeds than smaller and harder seeds (*C. album*), compared to seeds not ingested. This loss of viability may be due to damage to the embryo caused by digestion and the fermentation of the dung. The pH changes during digestion and the higher acidity of the faeces from quails may reduce the viability of *M. communis* and *P. lentiscus* seeds and inhibit the germination (Meyer and Witmer, 1998).

Frugivore seed dispersers have the capacity to modify the germination patterns of many plants by

varying the potential germinability of seeds, the rate of germination, or both (Traveset, 1998; Pakema and Small, 2009; D'Hont and Hoffmann, 2011). They can enhance germination by abrading the seed coats, which become more rapidly permeable to gases and water, or just by removing the pulp (or other structures that may contain germination inhibitors) in their digestive tracts. This has been found in our study in the case of *C. album*, seeds retrieved germinated significantly more (4%) than the non-eaten seeds (8–10%). For a long time it has been assumed that the fruits of some plants, especially those believed to have coevolved with their animal dispersers, obligatorily need to be ingested by them for seeds to germinate (Temple, 1977). However, little evidence exists that such reduction has been due to the requirement for seed ingestion by a particular frugivore. Probably the reduction in plant population densities is more related to the limited dispersal of seeds, with the consequence of higher seed/seedling mortality due to predators, pathogens, competition, etc. The seeds of *C. album* are probably preadapted to be dispersed by a wide assemblage of frugivores. Indeed, it has not been described a direct interaction with a single frugivore. Calviño-Cancela (2004) found that the overall probability of germination for a seed dispersed by gulls was 17.59% and was relatively low by blackbirds and rabbits (3.49 and 1.17%, respectively). In our study, we found a high overall probability of germination for seed dispersed by quails (10.3%). Germination of *C. album* seeds is low and seedling emergence almost restricted to open ground, imposing important limitations for recruitment on both quantity and spatial distribution (see also Calviño-Cancela, 2002). So far, frugivores seem, and now quails, to be essentials for germination, not as much for the effects of seed ingestion but for their ability to carry seeds to the more suitable sites.

The effect of a particular frugivorous species is largely unpredictable, varying among plant and presumably depending on seed traits, intrinsic to the plant species. In our case, quail, though to disperse a large number of seeds (30–40%), acting as a predator of *M. communis* and *P. lentiscus* inhibited seed germination by reducing the number of seeds that are able to germinate, probably by excessive abrasion. Moreover, quail significantly influences the germination patterns of *C. album*, enhancing germination (increasing either the germinability of seeds), acting as a good disperser of this species. Unravelling zoochorous dispersal mechanisms in a semi-natural environment may therefore offer both fundamental and necessary applicable ecological knowledge. Although future studies about aspect of plant–frugivore interactions (e.g. site where seeds are deposited, quality of nutrient conditions where seeds are defecated, etc.) are necessary, the incorporation of an avian-dispersed plant species into the diet of native frugivores can be an important step to disperse that species in coastal areas, so these interactions plants–frugivore studies should be

considered in developing conservation plans and restoration of natural vegetation.

ACKNOWLEDGMENTS

We thank the Doñana Natural Park and Dehesa de Gatos S.L. useful help, support and facilities. We also thank Sara Morales, Gema Ramos, and Javier Flores for assistance in the field and laboratory. Dr. Rachel F. Lo Faso revised the English version of the manuscript.

REFERENCES

- Álvarez-Cansino, L., Zunzunegui, M., Díaz Barradas, M.C., and Esquivias, M.P., Gender-specific costs of reproduction on vegetative growth and physiological performance in the dioecious shrub *Corema album*, *Ann. Bot.*, 2010, vol. 106, pp. 989–998.
- Baskin, C.C. and Baskin, J.M., *Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination*, San Diego: Academic, 1998.
- Bradbeer, J.W., *Seed Dormancy and Germination*, New York: Chapman and Hall, 1988.
- Brenchley, J.L. and Probert, R.J., Seed germination responses to some environmental factors in the seagrass *Zostera capricorni* from eastern Australia, *Aquat. Bot.*, 1998, vol. 62, pp. 177–188.
- Calviño-Cancela, M., Spatial patterns of seed dispersal and seedling recruitment in *Corema album*, Empetraceae: The importance of unspecialized dispersers for regeneration, *J. Ecol.*, 2002, vol. 90, pp. 775–784.
- Calviño-Cancela, M., Ingestion and dispersal: Direct and indirect effects of frugivores on seed viability and germination of *Corema album*, Empetraceae, *Acta Oecol.*, 2004, vol. 26, pp. 55–64.
- Clergeau, P., The effect of birds on seed germination of fleshy-fruited plants in temperate farmland, *Acta Oecol.*, 1992, vol. 13, pp. 679–686.
- Dalmáu, A., *Manual de la codorniz. Cría industrial y para la caza*, Ed. Dilagro, Lleida, 1994.
- D'hondt, B. and Hoffmann, M., A reassessment of the role of simple seed traits in mortality following herbivore ingestion, *Plant Biol.*, 2011, vol. 13, 118–124.
- Fredrickson, J., McKinley, J., Bjornstad, B., Long, P., Ringelberg, D., White, D., Krumholz, L., Suflita, J., Colwell, F., and Lehman, R., Pore-size constraints on the activity and survival of subsurface bacteria in a late cretaceous shale-sandstone sequence, northwestern New Mexico, *Geomicrobiol. J.*, 1997, vol. 14, pp. 183–202.
- Garber, P.A., The ecology of seed dispersal in two species of callitrichid primates, *Saguinus mystax* and *Saguinus fuscicollis*, *Am. J. Primatol.*, 1986, vol. 10, pp. 155–170.
- Gardener, C.J., McIvor, J.G., and Jansen, A., Survival of seeds of tropical grassland species subjected to bovine digestion, *J. Appl. Ecol.*, 1993, vol. 30, pp. 75–85.
- González-Redondo, P., Un caso de cambio en el manejo de los recursos cinegéticos: la historia de la cría en cautividad de la perdiz roja en España, *Rev. Esp. Estud. Agrosoc. Pesq.*, 2004, vol. 204, pp. 179–203.
- Harper, J.L., *Population Biology of Plants*, London: Academic, 1977.
- Jordano, P., Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus mahaleb*, *Ecology*, 1995, vol. 76, pp. 2627–2639.
- Jordano, P. and Godoy, J.A., Frugivore-generated seed shadows: A landscape view of demographic and genetic effects, in *Frugivores and Seed Dispersal: Ecological, Evolutionary, and Conservation Issues*, Levey, D.J., Silva, W., and Galetti, M., Eds., Wallingford, UK: CAB International, 2002, pp. 305–321.
- Levey, D.J. and Grajal, A., Evolutionary implications of fruit-processing limitations in cedar waxwings, *Am. Nat.*, Levey, D.J., Silva, W., Galetti, M. eds., vol. 138, pp. 171–189.
- MacKay, D.B., The measurement of viability, in: Roberts, E.H. Ed., *Viability of Seeds*, London: Chapman and Hall, 1972, pp. 172–208.
- Meyer, G.A. and Witmer, M.C., Influence of seed processing by frugivorous birds on germination success of three North American shrubs, *Am. Nat.*, 1998, vol. 140, pp. 129–139.
- Pakeman, R.J., Digneffe, G., and Small, J.L., Ecological correlates of endozoochory by herbivores, *Funct. Ecol.*, 2002, vol. 16, pp. 296–304.
- Pakeman, R.J. and Small, J.L., Potential and realised contribution of endozoochory to seedling establishments, *Basic Appl. Ecol.*, 2009, vol. 10, pp. 656–661.
- Pérez-Ramos, I.M., Marañón, T., Lobo, J.M., Verdú, J.R., 2007. Acorn removal and dispersal by the dung beetle *Thorectes lusitanicus*: Ecological implications, *Ecol. Entomol.*, 2009, vol. 32, pp. 349–356.
- Russi, L., Cocks, P.S., and Roberts, E.H., The fate of legume seeds eaten by sheep from a Mediterranean grassland, *J. Appl. Ecol.*, 1992, vol. 29, pp. 772–778.
- Temple, S.A., Plant–animal mutualism: Coevolution with dodo leads to near extinction of plant, *Science*, 1977, vol. 197, pp. 885–886.
- Traveset, A., Effect of seed passage through vertebrate frugivores' guts on germination: A review, *Perspect. Plant Ecol. Evol. Syst.*, 1998, vol. 1, pp. 151–190.
- Traveset, A. and Verdú, M., A meta-analysis of the effect of gut treatment on seed germination, in *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*, Levey D.J. and Silva, W.R., Eds., Gainesville, FL: Univ. of Florida Press, 2002, pp. 339–350.
- Villanúa, D., Casas, F., Viñuela, J., Gortázar, C., Garcia de la Morena, E., and Morales, M., First occurrence of *Eucoleus contortus* in a Little Bustard, *Tetrax tetrax*. Negative effect of red-legged partridges *Alectoris rufa* releases on steppe bird conservation?, *Ibis*, 2007, vol. 149, pp. 405–406.
- Wang, B.C. and Smith, T.B., Closing the seed dispersal loop, *Trends Ecol. Evol.*, 2002, vol. 17, pp. 379–385.
- Wheelwright, N.T. and Orians, G.H., Seed dispersal by animals: Contrasts with pollen dispersal, problems of terminology, and constraints on coevolution, *Am. Nat.*, 1982, vol. 119, pp. 402–413.
- Wessels, S.C. and Schwabe, A. Testing the potential seed availability in dung samples: Comparison of two seedling emergence methods, *Flora*, 2008, vol. 203, pp. 429–436.