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Do frugivores enhance germination success of plant species? An experimental approach

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ABSTRACT

Frugivorous birds are among the most important consumers of fleshy fruits particularly in sub-tropical and tropical forest ecosystems. Whether or not such plant–frugivore interactions contribute to germination enhancement is still a subject of much debate. We tested the effect of gut treatment by four captive species of avian frugivores in comparison to manually depulped seeds and whole fruits on seedling emergence and germination probability of seeds from sixteen plant species in South Africa. Moreover, we determined whether fruit weight of each plant species affected germination patterns. Across plant species, a total of 2795 seeds were planted, of which 50% germinated. Both seedling emergence and germination probability neither differed among the bird species nor in comparison to manually depulped seeds or whole fruits. Further, seedling emergence and germination probability were both unaffected by fruit weight. However, the germination probability of all treatments increased similarly with increasing number of weeks after planting. Overall, these results suggest that seed depulping, neither by gut treatment nor manually improved germination of seeds, irrespective of their fruit weights. Thus, the major contribution of frugivores to forest regeneration may be more confined in transporting seeds away from the mother plant than in germination enhancement *per se*.

1. Introduction

Frugivorous vertebrates play a key role in the dispersal of seeds for many fleshy fruiting plants across global forest ecosystems (Farwig and Berens, 2012; Jansen, 1981; Stiles, 2000). Approximately 90% of tropical and up to 50% of temperate plant species largely depend on frugivorous vertebrates for dispersing their propagules (Howe and Smallwood, 1982). Avian frugivores in particular, have been shown to be among the most important of these dispersers, capable of transporting seeds far away from the vicinity of mother plants (Howe and Smallwood, 1982). This increases the survivorship of seeds and seedlings as it enables them to escape disproportionate mortality (Howe, 1986) and allows plants to colonize new habitats (Howe and Smallwood, 1982). Thus, frugivores and the process of seed dispersal in particular play a pivotal role in shaping the ecology, evolution and dynamics of plant diversity globally (Traveset, 1998).

When studying plant–frugivore interactions, it is important to consider not only the quantitative but also the qualitative aspects of this mutualism by establishing the probability that the swallowed and dispersed seeds will germinate after passage through the guts of different frugivorous animals (Howe and Smallwood, 1982; Schupp, 1993). Whether or not the treatment of seeds in the guts of animals affects germination is still a subject of much research. For example, several studies have found a significantly positive effect of gut treatment on germination (e.g. Barnea et al., 1990, 1991; Clergeau, 1992; Murray et al., 1994). Potentially, pulp removal in the guts of frugivores eliminates germination inhibitors present in the pulp (Traveset, 1998). Pulp removal can also reduce the susceptibility of seeds to microbial and fungal infections (Jackson et al., 1988). Moreover, some studies have suggested that frugivores can increase the permeability of seeds to both water and gases by modifying their seed coats (Barnea et al., 1991; Clergeau, 1992; Izhaki and Safriel, 1990), consequently enhancing germination (Traveset, 1998).

In contrast, other studies have shown that frugivores can actually inhibit germination, i.e. by the chemical and mechanical abrading of seed coats in their guts or by traces of feces on the excreted seeds (e.g. Crossland and Vander Kloet, 1996; Nogales et al., 1995; Valido and Nogales, 1994). This may consequently attract microbial and fungal infections on the seeds, hence impeding the germination of gut treated seeds (Crossland and Vander Kloet, 1996; Traveset, 1998). Finally, a few other studies have found no effect of gut treatment on germination, effectively suggesting that frugivores may simply be legitimate transporters of dispersed seeds without enhancing or reducing their germination probability (Barnea et al., 1992; Clout and Tilley, 1992; Howe and Vande Kerckhove, 1979).

The survival of seeds passing through the guts of frugivorous animals has also been shown to vary with fruit or seed size (Traveset and Verdú, 2002). Fruit or seed size can affect the time that seeds are retained in the guts of animals, with the larger and heavier seeds

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reported to have quicker retention time than the smaller and lighter seeds due to their specific gravity (weight/volume; Garber, 1986; Gardener et al., 1993).

The variation in gut retention time (Clergeau, 1992; Izhaki et al., 1995) and in the overall effects of gut treatment on germination patterns suggest that the digestive systems of frugivorous animal species differs greatly, both morphologically and physiologically (Schupp, 1993; Traveset, 1998). Therefore, examining different species of frugivores might reveal the traits that affect germination. In particular, it remains important to establish whether variations occur among different species of animals consuming the same fruits and if such variations could be attributed to the differences in animal species or plant traits such as fruit weight.

For this reason, we studied the germination pattern of sixteen woody plant species after passage through the guts of four generalist avian frugivore species in KwaZulu Natal, South Africa. Taking into account the mean weights of the fruits, we examined (i) seedling emergence and (ii) germination probability of each plant species following gut treatment by each frugivore species. We expected (a) different species of frugivores to affect both the seedling emergence (i.e. time to first seedling emergence) and germination probability (i.e. cumulative proportion of germination) differently based on the assumption that their gut treatment effects differ, (b) gut treatment to generally enhance germination due to both fruit pulp removal and the abrasive effect within their guts, and (c) fruit or seed weight to have a positive effect on both seedling emergence and germination probability given that larger seeds have quicker retention times and are thereby less susceptible to abrading than smaller seeds.

2. Material and methods

2.1. Fruit sampling from woody fruiting plant species

Between 2010 and 2011, fruits from different native and non-native woody fruiting plant species ($n = 16$) that interacted with native avian frugivores (Chama et al., 2013; Jordaan et al., 2011) were collected in the field. Fruits from the native plant species ($n = 14$) were collected from Vernon Crookes Nature Reserve (VNCR) while those from non-native ($n = 2$) were collected in Pietermaritzburg. Fruits were collected during the fruiting season of plant species (Appendix). After collection, fruits were stored in clean plastic jars in a refrigerator and used within 48 h of collection. The fruit weight of each plant species was recorded prior to the onset of the experiment, i.e. as the mean weight of 20 fruits per plant species.

2.2. Frugivore species

Four of the five captive and predominantly generalist species of native frugivorous birds (Chittenden, 2007) at the University of KwaZulu Natal (UKZN) in Pietermaritzburg, South Africa, were used in this experiment. These included (i) Speckled Mousebird (*Colius striatus*; 55 g; $n = 5$) (ii) Red-winged Starling (*Onychognathus morio*; 140 g; $n = 4$), (iii) Purple-crested Turaco (*Tauraco porphyreolophus*; 285 g; $n = 2$) and (iv) Knysna Turaco (*Tauraco corythiax*; 310 g; $n = 4$). The frugivores were housed in outside flight aviaries (1 × 2.12 × 2.66 m) either in pairs or groups depending on their body masses. They were fed a maintenance diet comprising mixtures of (i) fruit (apples, bananas, carrots, oranges, papaya, and pears) and (ii) Aviplus Softbill/Mynah crumble and pellets on a daily basis. Water was also provided *ad libitum*.

2.3. Feeding experiments

Birds were relocated from the outside aviaries into a separate room. They were each placed in separate cages for an adaptation period of two days, during which they were fed a maintenance diet similar to what they were fed in the outside aviaries. The temperature in the room was constantly maintained at 25 ± 1 °C. On the day of the experiment, birds were provided only with whole fruit collected from one of the sixteen plant species (Appendix). At least 30 ripe fruits from a species were fed to each individual bird. Fruits from each individual plant species were administered independently and only after the experiment was finished on one species were fruits from other species introduced one after the other. Feeding experiments started at 06:00 am. The length of the experiment for each bird and each plant species varied between 3 and 48 h, largely depending on their capacity to consume and defecate the minimum total of at least 20 seeds per plant species. As it was not always possible for some individuals from each of the four bird species to consume and defecate 20 seeds, we pooled the seeds defecated by all individuals of the same bird species in order to reach this minimum sample size. If it was not possible to collect this number of seeds on the first day, the experiment was repeated on the following day until the seeds defecated by all individuals of one bird species reached at least 20. Defecated seeds (henceforth referred to as 'gut treated' seeds) were collected from the trays placed under each cage every 3 to 6 h and in the morning after the last experimental day.

2.4. Germination experiments

Gut-treated seeds were stored at ambient temperature until sown within one to three days after collection. Seeds for each plant species were sown in six different treatments, i.e. one treatment for each bird species (gut treatment), plus one treatment with manually depulped seeds and one with whole fruit. Manually depulped seeds consisted of seeds whose pulp was manually stripped and washed with water prior to the experiment to reduce or eliminate potential inhibition effects on the germination of the seeds (Cipollini and Levey, 1997), while whole fruits (i.e. with intact pulp) served as control. For each treatment and each plant species, similar quantities of seeds ($n \geq 20$) were planted together in one tray. Seeds were sown at regular intervals and covered in trays (265 × 180 × 75 mm) containing sterilized potting soil at a depth of 0.5 cm. Seeds of all treatments for each plant species were sown simultaneously and under similar conditions to allow for comparison of seedling emergence and survivorship. The trays were placed in the greenhouse at UKZN where they were regularly watered with the aid of automated over-head sprinklers. The positions of these trays were randomly interchanged between the treatments once every week. Germination was recorded once every week in the first three months, after which it was recorded only once every four weeks up to the twelfth month. When monitoring germination, we recorded seedling emergence (i.e. when the cotyledon or embryonic-first-leaf shoot was first seen emerging from the soil) in days from planting. Further, we recorded germination probability during each record. Germination probability thereby was the cumulative proportion of all germinating individuals per number of seeds planted for each plant species. Two of the sixteen plant species (*Croton sylvaticus* and *Sapium ellipticum*) had between two and three seeds per fruit and/or fruit endocarp. Under such circumstances, the fruit and/or endocarp was considered a seed and only one germination event from each fruit and/or endocarp was recorded (Bradford and Westcott, 2010) and tallied to calculate the total germination for the pulped seed per plant species. The week from planting was used as a covariate when analysing the effects of seed treatment on germination probability.

2.5. Statistical analysis

We tested whether seed treatment had an effect on (i) seedling emergence and (ii) germination probability with linear mixed effects models and z-tests adjusting for multiplicity. Analyses on seedling emergence, i.e. the day of first leaf shoot, were done with the subset of plant species that had germinated in all treatments after 12 months ($n = 10$); analyses on germination probability were conducted on the full set of plant species ($n = 16$). Planned contrasts were incorporated