

REVIEW

Internal dispersal of seed-inhabiting insects by vertebrate frugivores: a review and prospects

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Abstract

The finding that some seed-inhabiting insects can survive passage through the entire digestive tract of seed-dispersing vertebrates is relatively recent, but evidence suggests that it does occur. Here, I document this phenomenon, discuss its qualitative and quantitative dimensions, and offer suggestions for further research. The few documented cases that I review include plant species belonging to different families, with varied fleshy fruit types, number of seeds per fruit and seed size. The vertebrate frugivores involved include passerines that feed on relatively small fruits, and galliforms, and perissodactyls and primates that feed on larger fruits. The seed-inhabiting insects involved are the larvae of seed-infesting wasps, parasitoid wasps and seed-infesting beetles. The phenomenon has been verified in open, rural ecosystems in North America and Southern Europe, and in tropical and subtropical forests in South America. These varied scenarios suggest that the qualitative dimension of the phenomenon is considerably greater than known thus far. A simple method for detecting new events is proposed. However, research must also focus on the identity and biology of seed-feeding insects of wild fleshy fruits and their parasitoids. High survival rates of seed-inhabiting insects after vertebrate gut passage are predominant. This phenomenon generally appears to favor insect dispersal.

Key words: digestion-resistant insects, endozoochory, frugivory, tetratrophic interactions, tritrophic interactions.

INTRODUCTION

In plant-disperser-fruit pest triads in general, a multiple interaction occurs among 3 organism types, a plant, a seed-dispersing vertebrate and a phytophagous insect or a pathogen, with different evolutionary consequences of varying intensity (Herrera 1984a; Buchholz & Levey 1990; Traveset 1993a; Willson & Traveset 2000; Silvius 2005). More precisely, in fleshy fruit-disperser-insect

frugivore triads, the plant benefits from defending itself from the insect that damages the seed or the whole fruit, and the seed is dispersed; the disperser benefits from eating the pulp of ripe fruits; and the insect benefits from consuming the fruit without being killed by the disperser. Plants defend their ripe fruits from insects in different ways (e.g. phenology of fruit ripening, secondary compounds) (Herrera 1982; Traveset 1993b), and fruit-infesting insects follow a number of strategies to avoid being killed by dispersers (e.g. abandoning the fruit before it ripens, preventing it from ripening, or altering its physical and chemical properties to make it undesirable for frugivorous vertebrates) (Herrera 1989; Krischik *et al.* 1989).

Insect fruit predators can adapt to developing and living inside a seed, thus remaining isolated and protected from the environment by the seed coat (see Herrera 1989).

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Therefore, these insects could be expected to survive passage through the digestive tract of seed-dispersing vertebrates. This peculiar phenomenon of phoresy has only recently been confirmed, but it has already been verified in several plant, vertebrate and insect species in several ecosystems and continents (Nalepa & Piper 1994; Guix & Ruiz 1997; Bravo & Zunino 1998; Olmos *et al.* 1999; Bravo 2008; Hernández 2009a). A surprising case of an evolutionary tetrad in which a parasitoid of a seed-infesting insect resists bird ingestion and gut passage can now also be added (Hernández & Falcó 2008).

In the present paper, passive internal dispersal of fruit-inhabiting insects facilitated by endozoochorous seed dispersal is reviewed, taking into consideration the biological, ecological and evolutionary characteristics and implications of this interaction, and suggesting further research to increase our knowledge of the phenomenon. The passive internal dispersal of aquatic invertebrates by migratory waterbirds (e.g. Green & Sánchez 2006) and the dispersal of seed-infesting insects by imperfect harvesting (e.g. weevil-infested acorns scatter-hoarded by corvids or rodents that eventually escape predation) (see Guix & Ruiz 2000) are not covered here, as they do not involve endozoochory.

SUMMARIZED DESCRIPTION OF KNOWN CASES

Table 1 summarizes known cases of seed-inhabiting insects surviving passage through the entire digestive tract of vertebrate frugivores, and shows the plant, vertebrate and insect taxa involved, as well as the insect survival rates and the biomes from which these systems are reported.

Roses, birds and wasps

The larvae of the wasp *Megastigmus aculeatus* (Swederus, 1795), widely distributed in the Holarctic region, feed on the endosperm of *Rosa* spp. seeds (Syrett 1990; Nalepa & Grissell 1993; Roques & Skrzypczyńska 2003; Bruun 2006). Female wasps oviposit a single larva per seed in young green hips in spring-summer, just after petal fall. The larvae develop until the seed has hardened and then typically overwinter in diapause; adults usually exit the seed the following spring-summer (Nalepa 1989; Nalepa & Grissell 1993; Amrine 2002). Nalepa and Piper (1994) demonstrated that wasps emerged after passage through the gut of a northern mockingbird (*Mimus polyglottos* Linnaeus, 1758). In the experiment, a captive bird was given pseudo-hips filled with crushed banana and wasp-infested multiflora rose (*Rosa multiflora* Thunberg, 1784) seeds, which

were then removed from the droppings and examined for adult eclosion and emergence. Seeds were defecated 30–210 min after feeding. A total of 180 seeds were recovered from the total of 200 fed to the bird (90%). Survival rate was 53% for bird-ingested insects and 46% for controls (infested seeds that did not pass through the bird gut). Therefore, bird ingestion did not contribute to mortality.

In a rural habitat in north-west Spain, Hernández (2009a) collected common blackbird (*Turdus merula* Linnaeus, 1758) and thrush (mainly song thrush *Turdus philomelos* Brehm, 1831) droppings, and observed larval survival and adult emergence of *M. aculeatus* from dog rose (*Rosa canina* Linnaeus, 1753) seeds contained in the droppings. Gut passage time in common blackbirds is usually 30 min, although some seeds can be retained for longer (see Traveset *et al.* 2008). Hernández (2009a) reports rose seed infestation rates of 4.9 and 5.0%, and wasp survival rates (emerged adults plus live larvae inside the seed) of 89 and 87% in early and late winter, respectively. However, adult emergence rate was noticeably lower in droppings collected in early winter (54%) than late winter (87%).

Palms, birds and beetles

In a rainforest in south-east Brazil, Guix and Ruiz (1995) found *Revena rubiginosa* (Boheman, 1836) weevils infesting the fruit of the palm tree *Syagrus romanzoffiana* ([Chamisso] Glassman, 1968), and an unidentified weevil infesting the fruit of a myrtaceous tree (*Eugenia* sp.). The fruits of both trees were eaten by toucans (red-breasted *Ramphastos dicolorus* Linnaeus, 1766 and channel-billed *Ramphastos vitellinus* Lichtenstein, 1823 toucans) and those of the palm also by rufous-bellied thrushes (*Turdus rufiventris* Vieillot, 1818), and weevil larvae survived passage through bird stomachs inside the seeds. However, seeds were regurgitated and not defecated owing to their large size and, therefore, larvae did not pass through the entire digestive tract of the birds. Therefore, the time of exposure to mechanical and chemical digestive agents was short (2–30 min).

The same authors verified the survival of *R. rubiginosa* larvae inside *S. romanzoffiana* seeds, passing through the entire gut of captive dusky-legged guans (*Penelope obscura* Temminck, 1815) (Guix & Ruiz 1997). Defecated seeds were collected and checked for exiting larvae (*Revena* weevils emerge from fruit as larvae and pupate in the soil). Of the 120 fruits offered to birds, 87 (73%) were ingested and their seeds collected from droppings. Gut retention time was approximately 6 h. Of the 87 defecated seeds, 78 (90%) had weevil larvae inside; survival rate was nearly 100%.

Table 1 Known cases of seed-inhabiting insects surviving passage through the entire digestive tract of frugivorous vertebrates, in chronological order

Plant taxa	Vertebrate taxa	Insect taxa	Insect survival rate	Location and habitat	Reference
<i>Rosa multiflora</i> Rosaceae	<i>Mimus polyglottos</i> Mimidae, Passeriformes, Aves	<i>Megastigmus aculeatus nigroflavus</i> (<i>M. nigroflavus</i> according to Roques & Skrzypczyńska 2003) Torymidae, Hymenoptera	53%	USA Hedgerows	Nalepa & Piper (1994)
<i>Syagrus romanzoffiana</i> Arecaceae	<i>Penelope obscura</i> Cracidae, Galliformes, Aves	<i>Revena rubiginosa</i> Curculionidae, Coleoptera	≈ 100%	Brazil Atlantic rainforests	Guix & Ruiz (1997)
<i>Ocotea diospyrifolia</i> Lauraceae	<i>Alouatta caraya</i> Atelidae, Primates, Mammalia	<i>Heilipus</i> sp. Curculionidae, Coleoptera	8%	Argentina Flooded forests	Bravo & Zunino (1998)
<i>Syagrus romanzoffiana</i> Arecaceae	<i>Tapirus terrestris</i> Tapiridae, Perissodactyla, Mammalia	<i>Revena rubiginosa</i> Curculionidae, Coleoptera	≈ 100%	Brazil Primary forests	Olmos <i>et al.</i> (1999)
<i>Ocotea diospyrifolia</i> Lauraceae	<i>Alouatta caraya</i> Atelidae, Primates, Mammalia	<i>Heilipus</i> sp. Curculionidae, Coleoptera	8%	Argentina Flooded forests	Bravo (2008)
<i>Ligustrum vulgare</i> Oleaceae	<i>Turdus</i> spp. (mainly <i>T. merula</i>) Turdidae, Passeriformes, Aves	<i>Bracon</i> sp. (parasitoid of a lepidopteran tortricid) Braconidae, Hymenoptera	≈ 100%	Spain Hedgerows, forest edges	Hernández & Falcó (2008)
<i>Rosa canina</i> Rosaceae	<i>Turdus</i> spp. (mainly <i>T. merula</i>) Turdidae, Passeriformes, Aves	<i>Megastigmus aculeatus</i> Torymidae, Hymenoptera	88%	Spain Hedgerows, forest edges	Hernández (2009a)

Palms, tapirs and beetles

In a primary forest in south-east Brazil, Olmos *et al.* (1999) showed that *R. rubiginosa* larvae inside *S. romanzoffiana* seeds survive passage through the lowland tapir (*Tapirus terrestris* Linnaeus, 1758) digestive system. Gut passage time was 2–3 days for a captive tapir. The authors examined 844 and 1092 palm seeds from new and old dung piles, respectively. Of the 844 seeds from new dung piles, 183 (22%) were alive (intact endosperm), 561 (66%) contained weevil larvae and 100 (12%) were empty seeds displaying exit holes. Of the 1092 seeds from old dung piles, 251 (23%) were alive, 413 (38%) contained larvae and 428 (39%) were empty. Survival rate appeared to be nearly 100%.

Laurels, monkeys and beetles

Bravo and Zunino (1998) extracted 63 laurel (*Ocotea diospyrifolia* (Meisner) Mez, 1889) seeds from 11 fresh black howler monkey (*Alouatta caraya* Humboldt, 1812) feces, collected in a flooded forest in north-east Argentina, and examined them for the presence of insect larvae. Gut passage time suggested for black howlers is 20 h (Milton *et al.* 1980). The rate of laurel seed infestation was 19%, and live *Heilipus* (Germar, 1824) weevil larvae were found in a few (8%) of these seeds (see nearly identical results by Bravo 2008 for another lot of black howler feces collected in the same location). According to Bravo (2008), female *Heilipus* place the eggs directly within the seeds, the larva consumes the entire cotyledons and embryo, and the pupa then develops within the seed when the endosperm is consumed.

Privets, birds, moths and parasitoid wasps

For the same kind of bird droppings used by Hernández (2009a) to characterize the *Rosa-Turdus-Megastigmus* triad in north-west Spain, Hernández and Falcó (2008) confirmed the emergence of 3 adult braconids (parasitoid wasps), belonging to an unidentified species of the genus *Bracon* (Fabricius, 1804), from privet (*Ligustrum vulgare* Linnaeus, 1753) seeds. A total of 218 privet seeds were found in 259 *Turdus* droppings, 29 (13%) of which showed signs of infestation by insects. Of the infested privet seeds, 5 (17%) contained cocoons of ectoparasitoid braconids, together with the remains of the respective phytophagous host, an unidentified tortricid caterpillar. Cephalic capsules of the lepidopteran larva were found in most of the other perforated seeds. Actual prevalence of the braconid parasitoid was perhaps higher as some caterpillars likely fed on more than 1 seed (each privet fruit in the study area contained 1–4 seeds).

The 5 cocoons corresponded to the 3 previously mentioned adult braconids and another 2 that probably emerged in the field before the droppings were collected.

SCOPE OF THE PHENOMENON AND SUGGESTIONS FOR FURTHER RESEARCH

How many and which species are involved in the phenomenon?

The few, but taxonomically and ecologically diverse, known cases of seed-inhabiting insects surviving passage through the digestive tract of frugivorous vertebrates strongly suggest that this phenomenon is more common than reported. Although fleshy-fruited shrubs or trees are involved in all cases, the plant families (Rosaceae, Areaceae, Lauraceae and Oleaceae) and fleshy fruit types (fleshy receptacle with achenes in rose, drupe in palm, berry in laurel and privet) are diverse, as are the number of seeds per fruit (1 in palms and laurels and 1–4 in privets to a mean of 10–20 in dog roses) and seed size (from less than 5 mm long in roses and privets to 1–2 cm long in palms and laurels) (Guix & Ruiz 1997; Bravo & Zunino 1998; Hernández & Falcó 2008; Hernández 2009a). The frugivorous vertebrates involved are passerines (mockingbirds, blackbirds and thrushes) that eat relatively small fruits, and galliforms (guans), perissodactyls (tapirs) and primates (howler monkeys) that eat larger fruits. The seed-inhabiting insects involved are larvae of seed-infesting wasps (torymids), parasitoid wasps (braconids) and seed-infesting beetles (curculionids), which, depending on the case, either pupate inside the seed or exit it and pupate outside. The reported cases occur in temperate ecosystems of North America and Southern Europe, and tropical and subtropical forests of South America.

Guix and Ruiz (2000) discuss how widespread the palm-vertebrate frugivore-weevil triad could be. They directly observed 22 species of vertebrates belonging to 9 families feeding on *S. romanzoffiana* fruit in south-eastern and south-western Brazilian forests, which could transport and evacuate weevils via endozoochory, and suggest that many other bird and mammal species could do this (including the lowland tapir, which is confirmed by Olmos *et al.* 1999). In Europe, other birds besides *Turdus* blackbirds and thrushes disperse dog rose seeds (e.g. the common woodpigeon *Columba palumbus* Linnaeus, 1758) and privet seeds (e.g. the European robin *Erithacus rubecula*

Linnaeus, 1758) (Snow & Snow 1988; Hernández & Falcó 2008), and could potentially transport live larvae of *M. aculeatus* and braconids via endozoochory. Hernández (2009a) indicates that hips form part of the winter diet of several species of canids and mustelids on this continent, such as red foxes (*Vulpes vulpes* Linnaeus, 1758) and beech martens (*Martes foina* Erxleben, 1777) and, therefore, proposes that torymids could also withstand digestive processing by these mammal species.

On a worldwide level, seed dispersal by vertebrate frugivores is very common in woody plants in neotropical (70–94% of woody species), Australian (82–88%) and African (approximately 80%) rainforests; Mediterranean scrubland and some tropical dry and humid forests and woodlands usually range between 50 and 70%; and temperate coniferous and broad-leaved forests vary within 30–40% (Jordano 2000). Approximately 36% of 135 extant families of terrestrial birds and 20% of 107 families of non-marine mammals are partly or predominantly frugivorous (Herrera 2002). Pre-dispersal damage to wild ripe fruit by non-vertebrate agents probably occurs frequently (Herrera 1982), but little is known about species of seed-feeding insects associated with most fleshy-fruited plant species (e.g. Jordano *et al.* 2004 for the Mediterranean region). Generally, most pre-dispersal seed predators in plants are insects in the orders Hemiptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera, which have life cycles synchronized with the availability of seeds from just one or a few closely related plant species (Hulme 2002; Hulme & Benkman 2002). Members of the family Braconidae are among the most commonly encountered parasitoids emerging as adult wasps from infested fruits; the genus *Bracon* is one of the largest in the family, with over 2000 described species (Wharton 2010).

Systematic studies are necessary in different geographic areas and environments to establish the true qualitative dimension of this phenomenon of phoresy. Collecting fresh feces from different species of seed-dispersing frugivorous vertebrates, drying them and keeping them in closed containers at similar temperatures to those in the collection site, checking them for a certain period of time for exiting seed-inhabiting insects and, finally, examining the seeds, could provide satisfactory results. Another simple alternative method is to extract the seeds from the feces straight away and check them directly. Complementary research is needed to determine the identity and biology of seed-eating insects and their parasitoids in wild fleshy fruits.

What proportion of insect populations is affected by the phenomenon?

The survival rate of seed-inhabiting insects after vertebrate gut passage varies widely in the reported cases as a whole (approximately 10–100%), but high survival rates are predominant. Survival rate could depend on several factors, such as the degree of isolation of the insect inside the seed, the degree of mastication and of chemical and mechanical abrasion in the vertebrate digestive system, as well as gut retention time, but these aspects need to be investigated. Traveset *et al.* (2008) examined seed trait changes after fruit ingestion by common blackbirds and the consequences for germination and seedling growth. They verified that the seeds of some species had thinner coats, showed increased permeability and became less resistant to breakage after gut passage. In this respect, the seeds involved in the cases reported here have hard coats and, therefore, a great potential for not being damaged by mammal teeth and for withstanding long periods of time in vertebrate guts.

Determining the quantitative importance of the phenomenon on a wider scale, that is, determining which part of the population of a given insect species in a given site successfully passes through the gut of frugivorous vertebrates, is a highly complex task as it implies carrying out additional studies, such as estimating the insect population size and determining what part of this population is ingested involuntarily by the different species of seed-dispersing vertebrates. In Europe, dog rose hips are an essential component of the winter diet of *Turdus* species, which are their main avian seed dispersers (Snow & Snow 1988; Hernández 2007, 2009a), and in South America, the lowland tapir is a major disperser of *S. romanzoffiana* seeds (e.g. Giombini *et al.* 2009), so these vertebrate frugivores could transport a considerable part of the respective seed-eating insect populations via endozoochory. The range of the seed infestation rate in the reported cases of the phenomenon is very wide (approximately 5–80%), and it should be taken into account that pre-dispersal seed predation by insects varies considerably depending on the locality, year, habitat, microhabitat and individual plant (Hulme 2002; Hulme & Benkman 2002; Fenner & Thompson 2005).

Mortality in seed-inhabiting insects, prior to being ingested by a seed-dispersing vertebrate, is also open to investigation. As has already been stated, seed-infesting insects can be killed by parasitoids, and populations of seed-inhabiting insects in general (including parasitoids) could be diminished by the action of pathogens and ver-

tebrate seed predators. Although most pre-dispersal seed predators are insects, some vertebrate species consume considerable quantities of seeds in fleshy-fruited shrubs and trees (e.g. Snow & Snow 1988 for birds; Hernández 2008 for climbing rodents). In north-west Spain, European greenfinches (*Carduelis chloris* Linnaeus, 1758), wood mice (*Apodemus sylvaticus* Linnaeus, 1758) and red squirrels (*Sciurus vulgaris* Linnaeus, 1758) obtain and eat rose seeds from hips (Á. Hernández, unpubl. data), but their impact on tolymid larvae is not known. In England, European greenfinches made 2% of feeding visits by birds to dog roses (Snow & Snow 1988). The main privet avian seed-eater is the Eurasian bullfinch (*Pyrrhula pyrrhula* Linnaeus, 1758) (Snow & Snow 1988 for England: 21% of feeding visits by birds; Á. Hernández, unpubl. data for north-west Spain), which could kill the insects inside the seeds.

Post-dispersal seed predation, after defecation by vertebrate frugivores, must also cause a certain degree of mortality in seed-inhabiting insects before they exit the seeds. Post-dispersal seed predation is, on average, more severe than pre-dispersal seed predation and also varies spatially and temporally; generalist herbivores, such as small rodents, become extremely important at this stage, but passerine birds and insects (ants, bugs and beetles) are significant post-dispersal seed eaters in some ecosystems (Crawley 2000; Hulme 2002; Hulme & Benkman 2002; Fenner & Thompson 2005; Hulme & Kollmann 2005). Wood mice, yellow-necked mice (*Apodemus flavicollis* Melchior, 1834) and bank voles (*Myodes glareolus* Schreber, 1780) are the main post-dispersal seed predators of dog roses and privets in Europe (Herrera 1984b; Kollmann *et al.* 1998; García-Castaño *et al.* 2006; Á. Hernández, unpubl. data).

Does the phenomenon contribute to the successful dispersal of the insects involved?

According to Suhonen *et al.* (2010), organism dispersal will be advantageous when the fitness benefits of moving to a new patch exceed any costs. To assess whether the survival of seed-inhabiting insects to passage through the digestive tract of vertebrate frugivores is advantageous for insect dispersal, in terms of distance, it is necessary to determine the movement capacity of the insects involved by their own means, and compare it with that of dispersal by the respective vertebrate frugivore. Several authors have stated that the wasp *M. aculeatus* is a feeble, limited flier, at least over long distances (see Nalepa & Piper 1994; Amrine 2002). The related *Megastigmus spermotrophus* disperses successfully if assisted by wind (Jarry *et al.* 1997). Although adult *Revena* weevils have wings, they have not been reported to fly, only walking on the ground and on vegetation, so they

probably do not disperse very far by themselves (Guix & Ruiz 1997, 2000). *Heilipus* weevils can fly (e.g. Peña 1998), but the distances they cover have not been reported. Adult *Bracon* parasitoids are frequently caught using Malaise traps for flying insects (e.g. Falcó *et al.* 2006), but much remains to be determined about dispersal by flight in parasitoid wasps in general (Asplen *et al.* 2009).

Medium-sized birds, such as blackbirds and thrushes, disperse most seeds beyond 100 m (Jordano *et al.* 2007), so they are probably good dispersers of tolymids inhabiting rose seeds and braconids inhabiting privet seeds. Canids and mustelids disperse most seeds beyond 600 m (Jordano *et al.* 2007) and could, therefore, disperse tolymids even further if they survived passage through the gut of these mammals. Wild guan home range is estimated to be approximately 10 ha, suggesting that these birds move far enough to efficiently disperse *R. rubiginosa* larvae that palm seeds might contain (Guix & Ruiz 1997). Lowland tapirs defecate seeds at latrines located up to 2 km from the nearest palm clump, which might enable this weevil species to colonize new palm patches (Fragoso 1997; Olmos *et al.* 1999). Black howler monkey home range is approximately 2 ha (Bravo & Sallenave 2003) and, as previously stated, its gut passage time is almost 1 day, which should make these primates efficient dispersers of resistant *Heilipus* larvae contained in laurel seeds. Therefore, the survival of seed-inhabiting insects to vertebrate gut passage generally seems to favor insect dispersal.

It would be enlightening to explore this phenomenon in the context of potential colonization of oceanic islands by insects. Darwin (1859) was already interested in chance, long-distance dispersal, particularly of plants, to islands (see Carlquist 1981 for a historical perspective), and according to modern scientists, species diversity on islands arises, to a large extent, from rare, selective colonization events (Kaiser-Bunbury *et al.* 2010). Migratory animals, specifically birds and mammals, can transport seeds both externally and internally over long distances across dispersal barriers (Nathan *et al.* 2008). In particular, migratory passerines typically disperse fleshy-fruited plants (Nathan *et al.* 2008; Hernández 2009b). Even resident birds like some corvid species can disperse seeds of fleshy fruits out to islands, as they travel over large stretches of open ocean to reach foraging areas (Burns 2005). Nevertheless, the size of an island, its habitats and its pre-existing biota are all important in determining the success of potential colonists (Paulay 1994). Island plant communities are usually dominated by fleshy-fruited species, possibly an adaptation to the dominance of frugivorous vertebrates on the islands (Burns 2005; Kaiser-Bunbury *et al.* 2010); that is, islands seem to be favorable places for

colonization by fleshy-fruited plants and their associated insects. Seed dispersal processes play an important role in determining the diversity and distribution of plants on islands (Burns 2005). Several long-distance overseas colonizations by birds have been recorded over the past 200 years, including frugivorous species (Newton 2003).

CONCLUDING REMARKS

From a biological, ecological and evolutionary perspective, a better understanding of internal dispersal of seed-inhabiting insects by vertebrate frugivores would be a scientific advance in the knowledge of interactions among species. In addition, it would contribute to ecosystem conservation and management. As example cases, seed-infesting wasps are biological controllers of invasive exotic roses (Amrine 2002; Bruun 2006) and seed-infesting beetles are an important source of palm seed mortality (Olmos *et al.* 1999; Alves-Costa & Knogge 2005).

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