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Dung beetles as secondary seed dispersers: impact on seed predation and germination

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ABSTRACT. Dispersal of seeds away from the parent plant may facilitate escape from density-dependent seed mortality. However, many post-dispersal events can have a profound influence on the survival of dispersed seeds. By incorporating seeds in the dung that dung beetles process for consumption and oviposition, dung beetles could enhance seed survival if they remove seeds from areas of high predation risk and place them in locations that avoid subsequent predation and that are suitable for germination. The role of dung beetles in seed survival was investigated over 15 mo in Kibale National Park, Uganda. Depths of seeds buried by beetles, levels of predation on buried and unburied seeds, and germination success of seeds buried to different depths were examined. Results suggest that by burying seeds dung beetles increase the probability that seeds will escape predation and germinate. Of seeds placed in dungpiles, 69% remained at the surface, while 25% were buried from 1–3 cm in depth. Larger seeds were buried more shallowly than smaller seeds. Buried seeds were less likely to be removed by predators than seeds at the surface. Germination of seeds buried at 1- and 3-cm depths was significantly higher than seeds buried at 10 cm. For the species tested, many seeds were buried by dung beetles between 1 and 3 cm and at this depth there was a high probability of escaping predators and germinating. This demonstrates the potential ecological importance of dung beetles in facilitating seed survival and provides data to consider the role of dung beetles in the evolution of seed attributes.

KEY WORDS: dung beetles, Kibale National Park, Uganda, regeneration, seed dispersal, seed size.

INTRODUCTION

Dispersal of seeds away from the parent plant may facilitate escape from density-dependent seed mortality. However, many post-dispersal factors can have

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a profound influence on the survival of dispersed seeds (Estrada & Coates-Estrada 1986, Howe 1993, Roberts & Heithaus 1986; Schupp 1988a,b). Factors such as water availability, soil type and light availability may be the first determinants of whether a dispersed seed can germinate and survive in a given microhabitat (Clark *et al.* 1993, Molofsky & Augspurger 1992, Sork 1987; Vander Wall 1993, 1994). If a seed is deposited in a suitable microsite, seed predation may then become the most important factor determining seed survival (Chapman 1989, Howe & Smallwood 1982; Janzen 1969, 1971; Schupp 1988a,b), since seed predation can approach 100% for some species (Chapman & Chapman 1996, Terborgh *et al.* 1993, Whelan *et al.* 1991). Not surprisingly, therefore, variation in the intensity and type of seed predation is viewed as a strong selective pressure influencing various plant traits (Chapman 1995, Chapman & Chapman 1996, Osunkoya 1994, Thompson 1985, Willson & Whelan 1990).

For seeds that are deposited in large numbers in frugivore dung, secondary dispersal has the potential of decreasing density-dependent competition among seedlings and decreasing the probability of discovery by seed predators. Secondary movement of large seeds can occur when rodents scatterhoard seeds, and subsequently fail to return for the buried seeds (Bond & Breytenbach 1985; Forget 1990, 1992, 1993, 1996; Vander Wall 1993, 1994). However, rodents are typically seed predators, and thus a plant may pay a high cost for their secondary dispersal service. In contrast, dung beetles are not seed predators and can relocate seeds by incidentally including them in buried dung, or by moving them when they disturb the general area as they dig holes and move the soil (Andresen 1994, Estrada & Coates-Estrada 1991). Dung beetles use mammalian dung directly for food, to provision their nests, or as oviposition sites (Cambefort & Walter 1991, Halffter & Matthews 1966, Hanski 1991). Secondary dispersal of seeds by dung beetles has the potential of positively affecting seed survival by helping seeds avoid predation and in turn enhancing germination potential (Estrada & Coates-Estrada 1986, 1991; Wicklow *et al.* 1984). Given the significance of seed predation on seed survival, secondary seed dispersal may be among one of the most important events influencing the reproductive success of plants (Byrne & Levey 1993, Kaspari 1993, Levey & Byrne 1993, Portnoy & Willson 1993).

Dung beetles show species-specific variation in their dung-processing strategies. Some species roll dung balls away from the dungpile and bury them ('rollers'), others deposit dung in a burrow directly beneath the dungpile ('burrowers'), while a third group stay within the dungpile ('dwellers') (Doube 1991, Halffter & Matthews 1966). Species also differ in their arrival time at dung piles, amount of dung taken, distance the dung is moved, and the depth to which they bury the dung (Halffter & Edmonds 1982, Halffter & Matthews 1966). These factors, in turn, influence seed survival. For example, the probability of escape from density-dependent mortality can be influenced by the

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amount of dung and seeds removed from the site of deposition and the distance the dung is moved. Likewise, burial depth of seeds may influence seedling emergence, and the arrival times of beetles probably determine which beetle species gets the most dung and seeds, thus influencing how the seeds are processed.

Seed size may modify the effect of dung beetles on seeds deposited in dung. For example, since seeds are contaminants in the food resource of dung beetles, large seeds may be less likely to be included by beetles in the dung they bury. The relationship between dung beetles and seed survival may also be complicated by the effect of seed size on seedling emergence at different depths. Because seed size is correlated with the amount of nutritive tissue available to the embryo (Foster 1986, Westoby *et al.* 1992), larger seeds may be more likely to emerge from deeper depths than smaller seeds. Whether burial depth is advantageous or disadvantageous will depend upon the costs and benefits to the seed of burial at a particular depth. If a seed is not buried deeply enough it may be exposed to increased predation, but if a seed is buried too deeply it may be unable to germinate and reach the surface of the soil. Theoretically, an optimum burial depth should exist for a particular seed size.

The aim of this study was to examine whether dung beetles significantly affect the survival and germination of seeds in frugivore dung. Several experiments were set up in Kibale National Park, Uganda, each one designed to test a specific question, including; (1) How deeply are seeds buried by dung beetles?, (2) Does seed burial decrease seed predation?, and (3) Does burial depth influence the likelihood of seed germination?

METHODS

Study site and species

The study was conducted between July 1994 and October 1995 in Kibale National Park, a moist evergreen forest located *c*. 24 km east of the Ruwenzori Mountains in Western Uganda (Chapman & Chapman 1997, Chapman *et al.* in press, Skorupa 1988). Rainfall is seasonal and bimodal, averaging 1670 mm per year (1977–1995; annual range=157–186 cm) with peaks in March to May and September to November.

Dung beetle movement of larger seeds in Kibale (> 5 mm long axis) is primarily accomplished by one large (14–20 mm total body length) species of burrowing beetle, *Diastellopalpus semirubidus* (Nummelin & Hanski 1989). This species tunnels under the dung pile (occasionally moving some horizontal distance under the soil or making its original tunnel a short distance away from the dungpile) and deposits large amounts of dung in caches beneath the soil. When a *D. semirubidus* individual arrives at a dungpile, it immediately begins tunneling under the dung and later emerges many times to take large chunks of dung, often unintentionally including seeds, into its tunnels. A large species of roller, *Garreta crenulatus* (17 mm total length), also visits frugivore dung at

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Kibale and moves large amounts of dung, but it typically constructs its balls from small pieces of dung and tends to exclude the larger seeds. However, the contribution of this species to the dispersal of small seeds (e.g., *Ficus* spp.) may be important.

Since the probability of seed germination is influenced by passage through animal guts (Wrangham *et al.* 1994), all seeds used in this study were taken from chimpanzee dung (*Pan troglodytes*; collected between January and May of 1994). Seeds were dried and stored in a covered basket in a cool, dry place until needed. Species were chosen to permit comparisons of how dung beetles treat seeds of different sizes and based on their availability in chimpanzee dung. Seeds of species used were: *Monodora myristica* (Annonaceae, mean seed length=19 ± 1.7 mm (SE are reported throughout); mean seed width=12 ± 1.2 mm), *Mimusops bagshawei* (Sapotaceae, length=16 ± 1.6 mm; width=10 ± 0.9 mm), *Uvaria* sp. (Annonaceae, length=10 ± 1.6 mm; width=7 ± 0.7 mm), *Cordia abyssinica* (Boraginaceae, length=9 ± 0.8 mm; width=8 ± 0.7 mm), and *Aframomum* sp. (Zingiberaceae, length and width were difficult to measure, *c.* 2–3 mm in diameter; mean weight=0.03 g). Hereafter species are referred to by their generic names.

How deeply are seeds buried by dung beetles?

From July to December, 1994, experiments were conducted to determine the depth at which dung beetles bury seeds. Over this period, 28 soil-filled buckets (32 cm deep and 30 cm in diameter) were buried in the ground with the top flush with the forest floor. When burying the bucket, soil layers were kept relatively intact, with the hardest-packed clay-like soil in the bottom third of the bucket, looser soil in the middle, and the root mat and topsoil in the top of the bucket. Leaf litter was removed before placing the dung to standardize between buckets and facilitate later definition of the surface layer.

Dung with a known number of seeds of three species was placed on top of the soil in the bucket. Since experiments were conducted over a number of months, seasonal effects were examined: no seasonal differences in removal rates were detected (Shepherd 1996), however. For these experiments, fresh baboon (*Papio anubis*) dung was collected no more than 1 wk in advance of placement of the buckets in the forest and stored in plastic bags. Dung freshness has been demonstrated to be important for its attractiveness to dung beetles, largely because old dung tends to desiccate in the field (Halffter & Edmonds 1982). Dung stored for short periods of time in plastic retains much of its smell and texture, although it is not known whether some of its attractiveness to beetles may be lost. Seeds of three plant species were used in this experiment: *Monodora*, *Mimusops*, and *Uvaria*. Seeds of the focal species and other large seeds were removed from dung before a known number of focal seeds were placed in the dung for experimentation, but smaller seeds (e.g., *Ficus* spp.) were often impossible to remove and were left in the dung.

After burying the bucket, approximately 100 g of dung (chosen to roughly

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approximate a typical baboon defecation) mixed with 8 *Monodora*, 15 *Mimusops*, and 20 *Uvaria* seeds were placed on top of the soil in the centre of the bucket. Seed numbers were chosen based on the average numbers of seeds found in chimpanzee dung, a representative large frugivore (Wrangham *et al.* 1994; 1849 samples analyzed in that study).

Buckets were left in the field for approximately 24 h (range=22–25 h), then dug up and brought back to the laboratory. In all cases, at least 2/3 of the original dung had been removed by dung beetles. Seeds immediately visible in the churned up soil and remaining dung were counted before the bucket was moved. In the laboratory, layers of soil 1 cm deep were sequentially taken out of buckets, and each layer sifted through a 0.5 cm mesh screen to retrieve buried seeds. To quantify the dispersion of seeds away from the centre of each bucket, two subsets of each 1 cm layer were taken: one from an inner core 20 cm in diameter and one from the remaining 12 cm outer ring.

To determine whether species differences exist in seed distribution in the buckets, pairwise comparisons of cumulative mean percentages of seeds at each successive depth were made. Mean percentages were calculated for each depth by dividing the number of seeds found at a depth in each bucket by the total number of seeds originally placed in the bucket, and then calculating the mean over all buckets for that depth.

Does seed burial decrease seed predation?: Long-term fate of buried seed

A series of seed removal experiments was used to determine whether burial of seeds by dung beetles affects removal by seed predators. Sixteen *Mimusops*, 14 *Monodora*, and 3 *Uvaria* seed removal stations were established between 11 November 1994 and 20 January 1995. Seventeen *Cordia* seed removal stations were established between 30 April 1995 and 8 May 1995. The number of removal stations established was determined by the availability of seeds. Each removal station consisted of seeds of one of the four species experimentally buried at three different depths. Each station was left for 14 d. Stations were placed at least 20 m apart and marked with flagging tape *c.* 1.5 m above the station.

In a natural situation, seeds would be buried by dung beetles along with dung. However, if dung beetles were allowed to bury the dung with seeds, it would have been impossible to control the depth at which seeds were buried. Since the scent of dung may attract rodents (Andresen 1994, Estrada & Coates-Estrada 1986; Janzen 1982a,b), seedless dung was set at each station approximately 48 h before experimental burial of seeds; its location was marked with a wire stake. Within 48 h dung beetles had removed the majority of the dung and they were typically not seen in the area of the station. Because of shifts in ranging patterns of baboons, dung was more difficult to find during the time of these experiments, so only 50 g were used for each experiment and dung was stored in plastic bags for up to 3 wk in advance of the experiment. Scarcity

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of baboon dung during *Cordia* trials led to 13 stations being baited with chimpanzee dung and five stations with baboon dung.

For each removal station for *Monodora*, *Mimusops*, and *Uvaria*, six seeds of one of the species were placed at each of three depths: surface, 1 cm, and 3 cm. Only seeds at the surface and 1 cm were tested in the experiments involving *Cordia* since almost no seeds were removed from 3 cm for the species examined previously and smaller seeds are harder to find the deeper they are buried. Seeds were buried 3.5 cm apart by digging a vertical hole, approximating to the size of the diameter of the long axis of the seed, placing the seed in the hole such that the long axis was horizontal and the top of the seed was at the appropriate depth, and loosely packing the soil dug from the hole on top of the seed. Surface seeds were placed on top of the soil in a specific grid position. At stations where there was continuing dung beetle activity, the centre stake was moved 15 cm or less from its original position to reduce the chance that continuing dung beetle activity would move seeds. Stations were left undisturbed for 2 wk and seeds were then retrieved from each of the depths.

To consider the possibility that residual dung beetle activity caused unwanted movement of buried seeds or that we were unable to find all buried seeds, control stations were established exactly as the experimental stations, but covered after the initial 48 h period with a 0.5 mm wire mesh cage (*c*. 15 cm × 15 cm × 5 cm) anchored with 30 cm iron stakes such that the edges of the cage extended 0.5 cm into the soil. These stations were designed to be impervious to rodent seed predators, only allowing seed movement by dung beetles. For *Monodora*, *Mimusops*, and *Uvaria*, an equal number of such control stations were paired with experimental stations by placing them at locations adjacent to the experimental stations, but 20 m apart. Because nearly all seeds in all control stations were found for the other three species, fewer control stations (n=10) were established for *Cordia*. All *Mimusops* and *Cordia* control seeds were found. Only one *Monodora* control seed was missing, a surface seed at a station with heavy dung beetle disturbance subsequent to burial. A large burrow was observed where the seed had been, and it is believed that this seed was buried by dung beetles. Two *Uvaria* control seeds were missing, one at the surface and one at 1 cm.

Does seed burial decrease seed predation?: Short-term fate of surface seeds

Dung beetles do not immediately remove dung and seeds from the surface, and therefore all seeds in dung spend some time on the soil surface. In the long-term experiments described in the previous section, seedless dung was placed prior to experimental burial of seeds as a potential cue to rodents. To allow an assessment of initial removal of seeds while still avoiding dung beetle disturbance of the seeds, a pile of 18 seeds was placed 10 cm way from the dung pile used in the long-term experiments. Stations were left undisturbed for 48 h, then the remaining seeds were counted.

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A total of 81 short-term surface removal stations (18 seeds each) were established (*Monodora* n=17, *Mimusops* n=30, *Uvaria* n=6, *Cordia* n=28) concurrently with dung placement for the long-term seed removal stations.

Does burial depth influence the likelihood of seed germination?

To quantify the probability that seeds can germinate and emerge from the depths to which they are buried by dung beetles, germination trials were conducted using three common depths as determined from preliminary depth profile experiments. Seventy-five seeds of each of the four species (*Monodora*, *Mimusops*, *Uvaria*, and *Aframomum*) were planted in mid-September 1994 at 1, 3 and 10 cm in lightly packed topsoil-filled plastic bags (8 cm in diameter and 20–25 cm tall; total=900 bags, soil collected from the neighbouring forest). The bags had six drainage holes and were placed on a thin layer of sand on an outdoor wooden table with sides *c.* 15 cm high, covered by a tin roof (1.5 m above the table).

Since many seeds may germinate better when passed through the gut of a frugivore (Mayer & Poljakoff-Mayber 1982, Wrangham *et al.* 1994) seeds were carefully chosen from a large collection taken from chimpanzee dung. Those with obvious insect or other mechanical damage (e.g., beetle exit holes) were discarded. To determine whether seed size was related to germination potential at different depths, the maximum length of each seed was measured to the nearest 0.1 cm. Each seed was randomly assigned a depth and a table position.

Seeds at the 1 cm and 3 cm depths were planted using a finger marked to the appropriate depth. Seeds at 10 cm were planted by gently forcing a 4 cm diameter hollow plastic tube into the centre of the soil in a bag to a depth of 10 cm, removing with it a plug of soil, planting the seed in the hole that remained, and then filling the hole with the soil in the tube. All seeds were planted with the longest axis of the seed horizontal, and depths were measured from the top of the seed. Bags were watered, weeded and monitored for germination weekly. The purpose of this experiment was to determine whether successful germination could occur from different depths, and thus germination was defined as the point at which a seedling appeared at the soil surface.

In March 1995, *Cordia* seeds were added to the germination trials since no *Uvaria* had germinated by that time. A total of 170 *Cordia* seeds were planted, 60 at 1 cm, 53 at 3 cm, and 57 at 10 cm. Seeds were monitored until 3 October 1995.

RESULTS

How deeply are seeds buried by dung beetles?

Significant differences were found in the cumulative percentage of seeds found at each successive depth between pairs of all three species: *Monodora* (the largest seed species) and *Mimusops* (the mid-range seed species), $P<0.0001$;

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Mimusops and *Uvaria* (the smallest seed species), P<0.0001; and *Monodora* and *Uvaria*; P<0.0001 (two-sample Kolmogoroff-Smirnov test; Figure 1). The differences between seeds of different species suggest that the patterns of seed burial may be influenced by seed size.

Not all of the seeds originally placed in the dung in the buckets were retrieved, possibly because of removal by potential seed predators or by movement of seeds outside the bucket diameter by dung beetles. The median percentage of seeds recovered was 100% for the seeds of the largest species *Monodora*, 93% for the mid-sized *Mimusops*, and 70% for the seeds of the smallest species *Uvaria*. All 28 buckets had some seeds missing. A larger proportion of the *Uvaria* seeds, the smallest seeded species, was missing than either *Monodora* or *Mimusops* (Mann-Whitney test; U=130, n=29, P<0.0001; and U=204, n=29, P=0.0007, respectively), but the difference between the proportion of *Monodora* and *Mimusops* seeds missing was not significant (U=329, n=29, P=0.12).

Of the seeds recovered from the bucket trials, a median percentage of 30% of the *Monodora*, 53% of the *Mimusops*, and 5% of the *Uvaria* seeds remained on the surface; 13% of the *Monodora*, 33% of the *Mimusops*, and 28% of the *Uvaria* seeds were found at depths of 1–9 cm, and 0% of the *Monodora*, 0% of the *Mimusops*, and 25% of the *Uvaria* were found at 10 cm or below (Figure 1). Although most of the seeds of all species remained at the shallower depths, *Monodora* seeds were found as deep as 13 cm, *Mimusops* were found to 18 cm and *Uvaria* seeds were found to 27 cm.

To determine whether most seeds were buried by dung beetles in the centre of the bucket beneath the dung pile or dispersed horizontally throughout the bucket, the percentage of seeds found in all inner fractions of buckets were compared to the percentage of seeds found in all outer fractions of buckets using a Wilcoxon signed-rank test (the inner and outer fractions of each bucket were paired). Significantly more seeds were found in the inner fractions than the outer fractions for all three species (*Monodora* z=–3.68, n=22, P=0.0002; *Mimusops* z=–3.99, n=27, P<0.0001; *Uvaria* z=–3.65, n=27, P=0.0003).

Seed length (considering all species) was a significant correlate of seed burial depth (r=–0.87, P<0.0001). This suggests that smaller seed species may tend to experience greater burial depth by dung beetles than larger seed species. Analyses conducted on each species separately showed that seed length does not relate to burial depth within any of the species (*Monodora* r=–0.105, P=0.76; *Mimusops* r=–0.084, P=0.30; *Uvaria* r=–0.055, P=0.78). However, this may reflect little variation in seed size within a species.

Does seed burial decrease seed predation?: Long-term fate of buried seeds

After 2 wk seeds buried at long-term removal stations were less likely to be removed than those placed on the surface. For *Mimusops* and *Monodora*, significant differences were found in the probability of removal among depths of 0, 1, and 3 cm (*Mimusops* % of seeds removed 0 cm = 62.5, 1 cm = 5.3, 3 cm = 0, χ^2= 128, df=2, P<0.0001; *Monodora* 21.4, 2.4 and 0% respectively for three depths;

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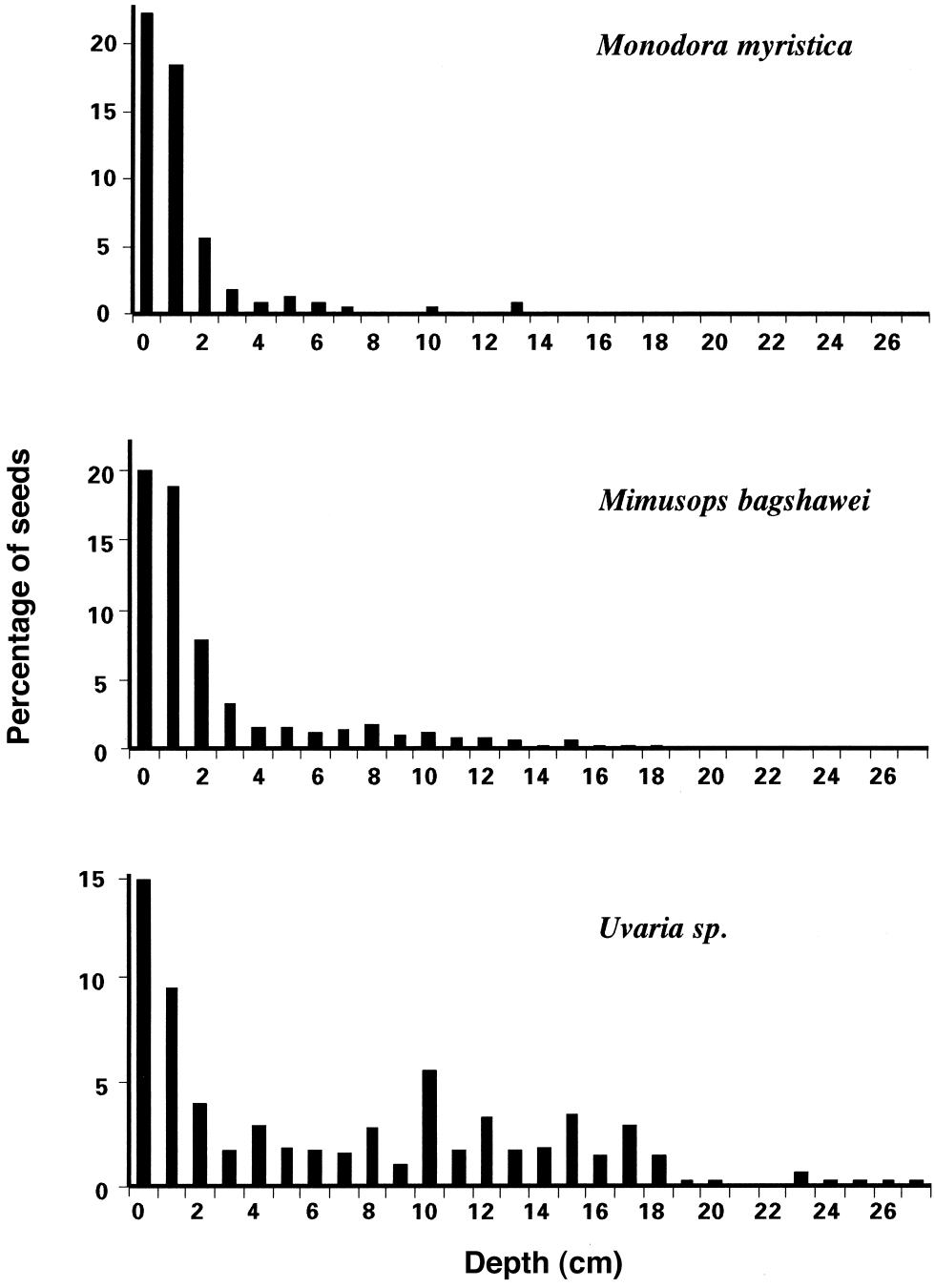


Figure 1. Mean percentage of the total number of seeds for *Monodora myristica* (n=8 seeds per bucket, mean seed length=19 ± 1.7 mm (SE)), *Mimusops bagshawei* (n=15 seeds per bucket, length=16 ± 1.6 mm), and *Uvaria* sp. (n=20 seeds per bucket, length=10 ± 1.6 mm) found at each depth after burial by dung beetles in Kibale National Park, Uganda (n=28 buckets per species).

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χ^2=30, df=2, P<0.0001). For *Cordia*, a significant difference in the number of seeds removed was found between depths 0 and 1 cm, the only depths examined (35.2 and 2.0% at 0 and 1 cm depths respectively; χ^2=38, df=1, P<0.0001). For *Uvaria* the number of stations established per depth were too few to allow statistical comparison. Removal differed among species at the surface (χ^2=33, df=3; P<0.0001, Figure 2). However, species differences (excluding *Uvaria* due to low expected frequencies) in numbers of seeds removed from 1 cm were non-significant (χ^2=1.94, df=2, P=0.38). Expected values were too low to analyze removal among species from 3 cm depth.

Often, overall seed removal levels are reported in the literature as a percentage of seeds removed from surface experimental stations (Osunkoya 1994, Schupp 1988b, Whelan *et al.* 1991). For the present study, it is analogous to examine percentages of seeds removed from the surface at long-term seed removal stations, ignoring the seeds at 1 cm and 3 cm. From the 50 stations for all species, 40% of all of the seeds on the surface were removed. From the 14 *Monodora* stations, 21% of the surface seeds were removed; of the 16 *Mimusops* stations, 63% were removed; of the three *Uvaria* stations, 39% were removed; and from the 17 *Cordia* stations, 35% of the surface seeds were removed.

Does seed burial decrease seed predation?: Short-term surface seed fate

After 48 h, the median value of seeds removed from short-term removal stations was 0% (*Monodora* 0%, *Mimusops* 0%, *Uvaria* 2.8% and *Cordia* 0%). No significant differences were found among the species in seed removal from short-term stations (Kruskal-Wallis, H=0.35, df=3, P=0.95). Overall, 38% of all stations, 30% of the *Mimusops* stations, 35% of the *Monodora* stations, 50% of the *Uvaria* stations, and 36% of the *Cordia* stations had at least one seed removed.

Does burial depth influence the likelihood of seed germination?

A total of 142 *Mimusops* (total number of seeds planted n=225, 75 at each depth), 7 *Monodora* (n=225), 23 *Aframomum* (n=225), 0 *Uvaria* (n=225), and 1 *Cordia* (n=170) seeds germinated and emerged from the soil. Only *Mimusops* and *Monodora* seeds germinated from 10 cm, suggesting that the larger-seeded species are more capable of germination from greater depths than smaller-seeded species. For *Mimusops*, 92% (69 out of 75) of the seeds planted at 1 cm germinated, 95% (66 out of 75) of the seeds planted at 3 cm germinated, and 9% (7 out of 75) of the seeds planted at 10 cm germinated (χ^2=146, df=2, P<0.0001). No significant difference was found between the numbers of *Mimusops* seeds that germinated at 1 cm and at 3 cm (χ^2=0.76, df=1, P=0.384). For *Aframomum*, 17 seeds germinated at 1 cm (23%), 6 at 3 cm (8%), and 0 at 10 cm (0%)(χ^2=22, df=2, P<0.0001). Significantly more Aframomum seeds germinated at 1 cm than at 3 cm (χ^2=6.2, df=1, P=0.01). For *Monodora*, three seeds germinated at 1 cm (4%), three at 3 cm (4%), and one at 10 cm (1%). Only 1 *Cordia* seed germinated, at 3 cm.

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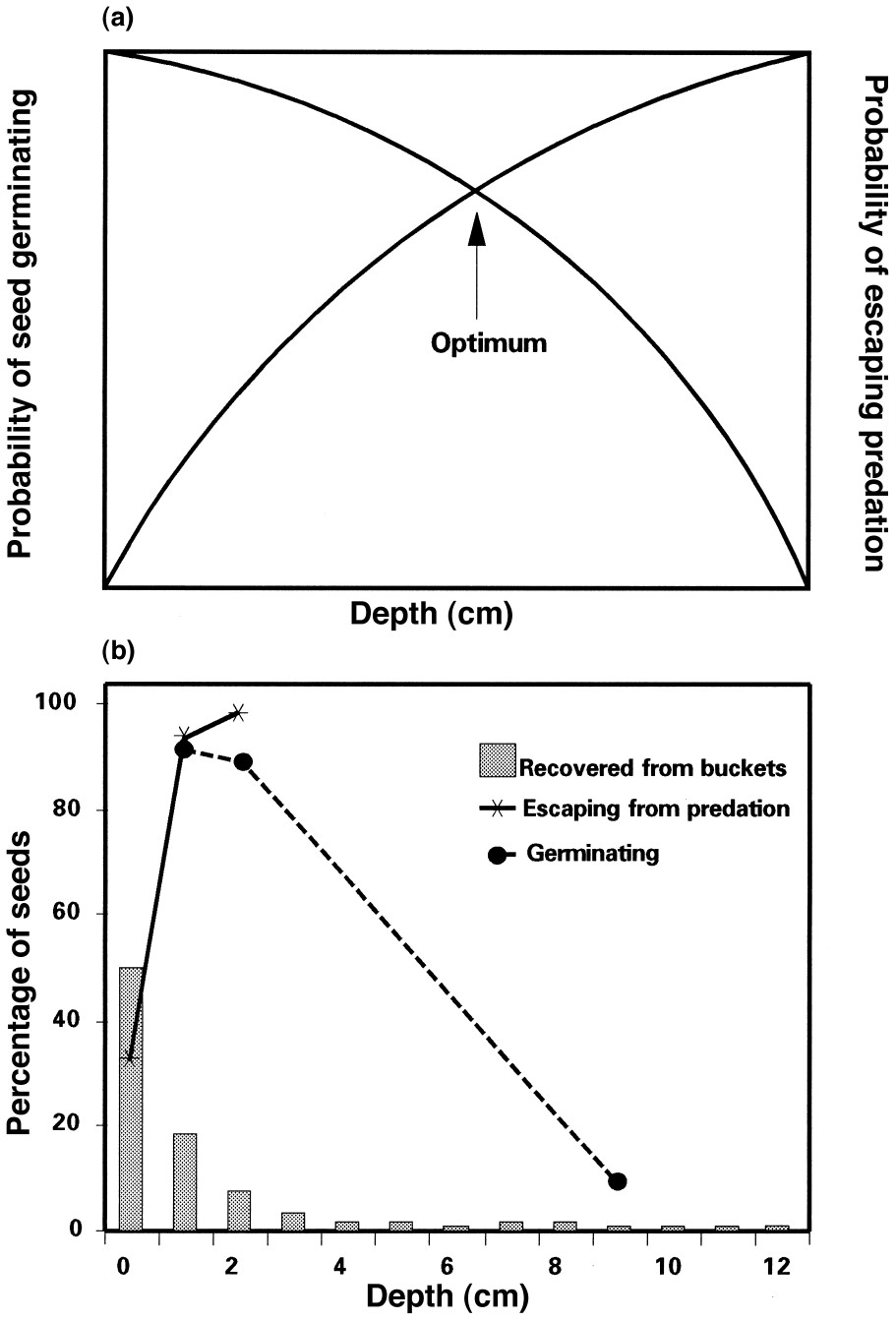


Figure 2. (a) The hypothetical relationship between seed predation and seed germination in relation to depth showing an optimal seed burial depth. This relationship could equally be convex in which case optimum depth will remain as depicted, but the percentage of seeds surviving and germinating would be considerably lower. (b) The relationship between seed burial depth by dung beetles, the probability of escaping seed predators, and the probability of seed germination for *Mimusops bagshawei* in Kibale National Park, Uganda.

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DISCUSSION

For dung beetles to significantly enhance the survival of seeds through their actions as secondary dispersers, several conditions must be met. First, dung beetles must remove seeds from deposition sites where the risk of seed predation is high. We documented high levels of seed removal from experimental stations. The levels reported in this study generally agree with published literature from other tropical areas, which indicate high levels of seed removal over short periods of time (Chapman 1989 – 52% after 5 d, Forget 1993 – 56% after 4 wk, Howe *et al.* 1985 – 58% after 6 wk; Osunkoya 1994 – 59% after 4 wk; Schupp 1990 – 76% after 4 wk; Schupp & Frost 1989 – 66% after 4 wk). However, removal rates often vary considerably among species, and can range from 0–100% (Chapman & Chapman 1996, Terborgh *et al.* 1993). In this study, the percentage of seeds removed from the surface at long-term seed removal stations differed greatly among species, with *Mimusops* (63%, 16 mm) experiencing the highest levels of removal, followed by *Uvaria* with 39% (10 mm), *Cordia* with 35% (9 mm) and *Monodora* with 21% (19 mm). Thus, seed removal increased with increased seed size up to a certain point (*Mimusops* 16 mm) and decreased thereafter.

Second, dung beetles must place seeds in locations where subsequent seed predation is relatively low. In experiments where soil-filled buckets were buried in the forest, topped with a dung pile containing seeds of three species, most seeds manipulated by dung beetles remained close to the surface (in the 0–3 cm range). These locations appear to be relatively safe from subsequent seed predation. Removal from 2-wk seed removal stations demonstrated that seed removal decreases with burial depth. Thus, for all three species, burial of seeds to only 1 cm greatly reduced the likelihood that seeds were removed. Nonetheless, evidence from one *Uvaria* station suggests that at least some rodents are able to detect seeds at 3 cm. This station had all of the surface seeds, most of the seeds at 1 cm, and all seeds at 3 cm removed. This suggests that although increased burial depth may decrease predator detection of seeds, failure of seed predators to remove seeds may not necessarily represent inability to detect those seeds.

The ability of rodents to detect buried seeds has been documented by Estrada & Coates-Estrada (1991) who found that captive rodents could on average detect 92% of seeds on the surface, 83% of seeds offered at 1–2.5 cm, 56% of seeds offered from 2.5–5 cm, and 17% from 5–8 cm. (Seeds were buried without dung.) Andresen (1994) found that captive rodents could detect 11% of seeds buried at 1 cm compared to 8% buried at 3 cm when seeds were buried without dung. When seeds were buried with dung, Andresen (1994) found much higher detection rates: 74% of the seeds were detected by the rodent from 1 cm and 18% were detected from 3 cm. Andresen (1994) also found a marked effect of burial depth on seed survival with 68% removal of seeds buried at 1 cm at field removal stations compared to 21 and 2% of seeds buried at 3

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and 5 cm respectively. Both of these studies show that burial of seeds by dung beetles to 1 to 5 cm ameliorates levels of seed predation. However, the results of the present study show a steeper increase in seed survival with burial depth than Estrada & Coates-Estrada (1991) and Andresen (1994), with a mean of 40% of seeds removed from the surface, compared to a mean of 5% removed from 1 cm and only 0.5% removed from 3 cm.

Lastly, dung beetles must place seeds in locations suitable for germination. More *Mimusops* (a medium-sized seed) and *Aframomum* (a small-sized seed) seeds germinated from a depth of 1 or 3 cm than from 10 cm. No statistical difference in numbers of seeds germinated was found for *Mimusops* between depths of 1 and 3 cm, but for *Aframomum*, seeds were more likely to germinate from 1 cm than 3 cm. Although sample sizes of germinating *Monodora* seedlings were too low to permit statistical comparisons, there seems to be a trend toward fewer seeds emerging from 10 cm than from 1 or 3 cm. These results suggest that increasing depth negatively affects seedling emergence. To our knowledge, the effect of burial depth on germination has not been quantified for moist tropical forest systems, but evidence from temperate regions suggests an optimal depth for germination and seedling emergence and that seeds germinate better when buried (Blackshaw 1990, Smith *et al.* 1992, Vander Wall 1993).

Whether seed burial by dung beetles is advantageous or disadvantageous will depend upon the costs and benefits to the seed of burial at a particular depth. If a seed is not buried deeply enough it may be exposed to increased predation, but if a seed is buried too deeply it may not be able to germinate successfully. Given that the probability of a seed escaping predation increases with increasing burial depth, and the probability of a seedling emerging decreases with increasing burial depth, a theoretical optimum depth for a seed species can be postulated (Figure 2). At this depth, a seed would be deep enough to minimize the risk of predation, but not too deep to prevent successful establishment. The data from this study suggest that for at least one of the species considered (*Mimusops*), this depth occurs at *c.* 1 cm and thus also falls within the range of the majority of dung beetle seed burial (Figure 2). This supports the assertion that dung beetles serendipitously elevate the probability of seed survival of some proportion of seeds dispersed in dung piles.

These findings suggest that dung beetles can play a significant ecological role; they may greatly increase the number of dispersed seeds that end up in locations where seed predation is low and germination potential is high. It is also possible to ask whether dung beetles are playing a significant evolutionary role in influencing seed characters. It is important to keep in mind that the ecological and evolutionary roles of a seed disperser should be considered separately: it is possible for an animal to be very important in an ecological sense, but only play a minor evolutionary role (Lambert 1997). The selective strength exerted by a secondary dispersal agent on plants is complicated by several

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factors. For example, the seeds of many plants are dispersed by several species of primary dispersal agents, each depositing seeds in different ways (e.g., spitting seeds or defecating seeds; Lambert 1997, Rowell & Mitchell 1991) and each associated with an array of factors influencing the fate of the dispersed seeds. A plant species with many dispersers may be expected to have an increased degree of variability in seed fate compared to a plant species with just one disperser (Herrera 1985). Another complicating factor is that since seeds are buried as contaminants of a dung beetle's food resource, dung with too many seeds may be energetically unfavourable to process. Thus, burial of seeds may be selected against if they decrease the quality of the dung. Finally, multiple sources of mortality (e.g., pathogens, insects, rodents) may act simultaneously on seeds deposited by primary dispersers (Holmes 1990, Howe 1993, Kerley 1991, Traveset 1990). Each type of mortality is associated with its own variation subject to different conditions, probably causing an increase in overall variation.

From the plant's perspective, spatial and temporal variation in seed fate acts to weaken the directional selective pressures by the factors affecting seed survival. If dung beetles consistently reduce the variability in seed survival by increasing the 'safety' of deposition sites, a case may be made for directional selection on plant traits that increases the probability of burial by dung beetles. On the other hand, if dung beetles add to the variability of the system, though their ecological importance is obvious, they are not playing a significant role in directional selection on the plant.

With such considerations in mind, the data collected from Uganda does suggest the possibility that dung beetles could act as a selective agent on seed traits, in particular seed size. Seed distributions in the bucket experiment differed among species, with small seeds being buried deeper than large seeds. Estrada & Coates-Estrada (1991) and Andresen (1994) similarly demonstrated that seed size was a significant predictor of burial depth for several Central and South American seed species. Direct comparison among species to determine the relationship of seed size to burial depth and seedling emergence is difficult in this study since only *Mimusops* and *Aframomum* germinated in sufficiently high numbers to permit analyses. The percentage of seeds germinating at 1 cm versus 3 cm was not significantly different for *Mimusops*, but differed for *Aframomum*. This suggests that burial depth and seed size interact to affect seedling emergence. This is also supported by the fact that equal numbers of *Monodora* seeds germinated at 1 cm and 3 cm, although the sample sizes were too small to compare statistically. Furthermore, *Mimusops* and *Monodora* germinated from 10 cm (albeit at a lower percent germination), while the smaller seeds of *Aframomum* did not. This is not surprising since larger seeds generally have greater resources for a developing seedling (Foster 1986, Westoby *et al.* 1992).

Seed size appears to be a trait that has the potential to be influenced by a

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variety of biotic selective agents associated with dispersal and seed survival. Previous studies have demonstrated that frugivores select which fruits to eat based partially on the size of the seed the fruit contains (Westoby *et al.* 1992, Chapman & Chapman 1996). Osunkoya (1994) demonstrated that seed size relates to survival, with predators taking small to medium sized seeds in preference to larger ones. In our study we have shown that dung beetle seed removal increases with increased seed size up to a certain point (*Mimusops* 16 mm) and decreases thereafter. Considering that seed size is embedded in a complex of attributes which together help define the life history of a plant species (Foster 1986, Foster & Janson 1985, Westoby *et al.* 1992), further investigation into how seed size affects dung beetle activity and how the behaviour of dung beetles is linked to other aspects of the dispersal process needs to be more fully investigated.

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