



## Vertebrate Fruit Removal and Ant Seed Dispersal in the Neotropical Ginger *Renealmia alpinia* (Zingiberaceae)\*

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### ABSTRACT

Plants frequently display fruit characteristics that support multiple seed-dispersal syndromes. These ambiguous characteristics may reflect the fact that seed dispersal is usually a complex process involving multiple dispersers. This is the case for the Neotropical ginger *Renealmia alpinia* (Zingiberaceae). It was originally suggested that the aromatic fruits of *R. alpinia* located at the base of the plant are adapted for terrestrial mammal seed dispersal. However, the dark-purple coloration of the fruits and bright orange aril surrounding the seeds suggest that birds may play a role in *R. alpinia* seed dispersal. At La Selva Biological Station, Costa Rica, we used camera traps to record vertebrate visits to infructescences of *R. alpinia*. Most visitors were toucans and aracaris (Ramphastidae). However fruits were also removed by terrestrial mammals (coatis and armadillos). In addition to vertebrate fruit removal, some of the fruits dehisce and the seeds that fall on the ground are dispersed by ants. Fruitfall traps showed that 77 percent of fruits are removed by vertebrates. However, 15 percent of fruits fall to the base of parent plants to be potentially dispersed by ants. Experiments using a laboratory ant colony showed that ants are effective seed dispersers of *R. alpinia*. Ant seed manipulation increased germination success and reduced time to germination. In conclusion, primary seed dispersal in the Neotropical ginger *R. alpinia* is mostly performed by birds, additionally ants are effective dispersers at short distances. Seed dispersal in *R. alpinia* is a complex process involving a diverse array of dispersal agents.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

*Key words:* Costa Rica; Ectatomminae; La Selva Biological Station; ornithochory; Ponerinae; Ramphastidae.

SEED DISPERSAL IS A FUNDAMENTAL PROCESS involved in forest regeneration, plant demography, and the genetic and spatial structures of future plant generations (Pijl 1982, Nathan & Muller-Landau 2000). In the tropics, seed dispersal by animals is the dominant mode of propagule dissemination with a wide variety of fauna serving as seed dispersers (Nathan & Muller-Landau 2000).

This high diversity of potential dispersal agents makes it difficult to determine the identities and roles of different frugivores in the process of seed dispersal. When the actual seed dispersers of a plant are unknown, researchers use dispersal syndromes that describe the position of the plant's infructescences and fruit or seed traits (*e.g.*, size, color or scent) to infer which animals may act as potential seed dispersers (Janson 1983, Gautierhion *et al.* 1993, Link & Stevenson 2004). For example, fleshy, unscented fruits with bright colors are assumed to be typical of bird dispersal (Pijl 1982). Fleshy, odoriferous fruits located at the base of a plant may suggest dispersal by terrestrial mammals (Pijl 1982). Adaptations to seed dispersal by ants usually involve small diaspores covered by an oily structure, an elaiosome, used by the ants as a food source (Beattie 1985).

However, plants may simultaneously display characteristics that suggest more than one dispersal agent. These ambiguous characteristics may indicate that a particular plant species is dispersed by multiple agents, lending support to the idea that seed dispersal is often a complex process involving multiple animal species (Levey & Byrne 1993, Passos & Oliveira 2002, Vander Wall & Longland 2004, Jordano *et al.* 2007).

The Neotropical ginger *Renealmia alpinia* (Rottboell) Maas 1976 (Zingiberaceae) is a ubiquitous component of tropical rain forest flora in South America, Central America, Mexico, and the Lesser Antilles (Maas 1977, Sarkinen *et al.* 2007). *Renealmia alpinia* is mainly found within secondary forests and open areas such as gaps or abandoned pastures (Maas 1977).

*Renealmia alpinia* infructescences display contrasting characteristics that suggest seed dispersal by multiple taxa. This plant species produces 12–55 cm long infructescences displayed at the base of the plant (Fig. 1A). Fruits are aromatic capsules, 1.5–3.5 cm long (Maas 1977). These characteristics suggest that seeds may be dispersed by terrestrial mammals (Ximenes *et al.* 1997). When fruits ripen, the capsule walls change from pink to dark purple. When open, the fruits display 100–200 seeds embedded in a bright orange aril. These fruit characteristics have been used as evidence to suggest that birds may play a role in *R. alpinia* seed dispersal (Maas 1977).

Seed dispersal in *R. alpinia* may be even more complex. We observed that some of the ripe fruits may dehisce, dropping the seeds to the forest floor. Ants are attracted to the 2–4 mm diameter seeds and remove them from the plant base. Ants may deposit the seeds either on the floor or they may bring them into the nest. Therefore, it is possible that *R. alpinia* is a primarily vertebrate-dispersed plant, but ants may play a role in this dispersal system by moving fallen seeds at a small spatial scale.

To determine if fruits of *R. alpinia* are mainly removed by birds or terrestrial mammals and to assess if ants act as seed dispersers of this plant, the main objectives of our research were: (1) to record the identities and proportion of visits by each species of vertebrate removing fruits of *R. alpinia*; (2) to record the percent of fruits removed by vertebrates and the percent of fruits available to ants

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FIGURE 1. Most common vertebrates and invertebrates removing seeds of *Renealmia alpinia*. (A) Infructescences of *R. alpinia*. Light pink fruits are unripe and turn dark purple when ripe. (B) *Pteroglossus torquatus* (Ramphastidae), the most common bird recorded consuming *R. alpinia* fruits. (C) *Nasua narica* (Procyonidae), the most common mammal recorded feeding on *R. alpinia*. (D) *Ectatomma ruidum* (Formicidae; Ectatomminae). (E) *Odontomachus erythrocephalus* (Formicidae; Ponerinae), the two most common ants observed removing *R. alpinia* seeds from the forest floor. Scale bars in A–C = 10 cm. Scale bars in D–E = 4 mm. (Picture credits B and C TEAM network—Volcán Barva).

on the forest floor; and (3) to assess the dispersal distances, removal rates, and the effects of ants on the germination success of *R. alpinia* seeds.

## METHODS

**STUDY SITE.**—We conducted this study from December 2006 to November 2007 at the Estación Biológica La Selva (hereafter La Selva), Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica (10°26' N, 83°59' W). La Selva is classified as lowland tropical wet forest (Holdridge 1947) and receives an average of 4000 mm of rainfall per year (McDade *et al.* 1994). The La Selva reserve is a mosaic of old-growth forest, secondary forest, swamp forest, and abandoned pasture land (McDade *et al.* 1994). We conducted our study within secondary forest, habitat where *R. alpinia* is abundant.

**VERTEBRATE FRUIT REMOVAL AND FRUITS AVAILABLE FOR ANT SEED DISPERSAL.**—To record the fruit-removing vertebrates of *R. alpinia* and their frequencies of visits, we monitored a total of 10 infructescences on nine fruiting plants using motion-detecting digital cameras. Monitored plants were separated from one another by a minimum distance of 50 m. A single camera was placed 1.5 m from each ripe infructescence. At this distance these cameras are able to detect visits by small vertebrates, such as birds, rats or mouse opossums, as well as larger vertebrates. Cameras were able to record vertebrates feeding from fallen fruits or from fruits still attached to the infructescence. Infructescences were monitored until all fruits were

removed. Thereafter, digital photos were examined for the identities, number of independent visits, and activity times of fruit-eating vertebrates.

To determine the proportion of fruits removed by vertebrates and the proportion falling onto the floor and available for ant dispersal, we placed fruitfall traps (diameter = 25 cm, depth = 35 cm) at the bases of 27 *R. alpinia* infructescences distributed among 15 plants. The minimum distance between plants was 50 m. Every 21 d, and until all ripe fruits were removed, we recorded the number of fruits that were either removed, had dehisced, and fallen into the fruitfall trap or had rotted but remained attached to the infructescence for each plant. Differences among proportions were analyzed using a Friedman test, including each plant as a block. The Friedman test, as with other nonparametric statistical tests, explores differences among medians. Therefore, in this paper we report medians as a measure of central trend.

**ANT SEED REMOVAL AND DISPERSAL DISTANCES.**—To ascertain the most common ant species that remove seeds of *R. alpinia*, how far they move seeds from the source, and the final fates of removed seeds, we conducted seed-removal trials in the field. Trials were performed at 11 different individuals of *R. alpinia*. Plants were separated from each other by at least 25 m. For each trial, 50 arillate seeds (the approximate number of seeds contained in one locule of a capsule) were offered on the forest floor near the base of a fruiting *R. alpinia* plant. Each removal trial lasted for 60 min after the arrival of the first ant visitor that was able to remove seeds from the seed pile. We recorded the ant species that removed seeds and the number of seeds removed by each species. Seed-dispersal distances were recorded by tracking the ants until they either dropped the removed seeds or brought the seeds to a nest.

**NEST RETENTION TIME AND GERMINATION SUCCESS OF *R. ALPINIA* SEEDS MANIPULATED BY ANTS.**—During the ant seed-removal trials in the field, most of the seeds were removed by the ant *Ectatomma ruidum* (*see results*). For this reason we selected this ant species to conduct additional laboratory trials to determine how seed handling by ants affects *R. alpinia* germination success.

An ant colony of *E. ruidum* was collected in the field and brought to the laboratory. The ant colony was placed in four covered Petri dishes that served as nest chambers. Nest chambers were lined with plaster impregnated with the antifungal agent Methylparaben. All chambers were connected with plastic tubing to allow for ant movement between them. The whole nest was contained within a 46 × 23 × 17 cm plastic box.

Laboratory seed-removal trials started after the colony resumed normal foraging behavior and the queen began laying eggs. Ants were provided food (live termite larvae) and water *ad libitum*. For each laboratory seed-removal trial, we placed 50 arillate *R. alpinia* seeds 5 cm from the entrance of the nest. Fifty additional seeds from the same plant with intact arils were collected and used in further germination experiments. Seeds were offered to the ants for 6 h. After this time period, any seeds not taken from the offered seed pile were removed and discarded. Any seeds moved by ants

but not taken into the nest were collected for further germination experiments.

To determine the length of time that seeds were retained within the *E. ruidum* nest, we counted the number of seeds remaining in the nest every 6 h until all seeds were discarded outside the nest or for a total of 36 h. Seeds that were deposited in refuse heaps were collected for further germination experiments.

To ascertain how seed handling by *E. ruidum* affects *R. alpinia* seed germination success, we placed all seeds collected from the laboratory colony trials (seeds with intact arils, seeds moved but not taken into the nest, and seeds discarded in refuse heaps after passing through the nest) into Petri dishes lined with wet paper. Seed germination was recorded every 2 d for 45 d. In total, we monitored 1450 unmanipulated seeds from 17 plants, 128 moved seeds from 16 plants, and 132 seeds that passed through the nest from 15 plants. We recorded days to germination and the percent of seeds that germinated in each treatment. Differences in the proportion of seeds germinating for each treatment were analyzed using Gehan's generalized Wilcoxon survival analysis. We compared times to germination for each treatment with a Friedman test, controlling for potential maternal effects by including all seeds from the same plant as a block.

## RESULTS

**VERTEBRATE FRUIT REMOVAL AND FRUITS AVAILABLE FOR ANT SEED DISPERSAL.**—Camera traps recorded visits by vertebrates for a total of 336 d (min–max number of days observation/plant: 11–63 d). We recorded visits by both birds and terrestrial mammals (Table 1). Bird visitors included Collared Aracaris (*Pteroglossus torquatus*), Keel-billed and Chestnut-mandibled Toucans (*Ramphastos sulfuratus* and *R. swainsonii*), and the great tinamou (*Tinamus major*) (Table 1). We also recorded visits by nine-banded armadillos (*Dasypus novemcinctus*) and white-nosed coatis (*Nasua narica*) (Table 1). Most of the fruits were removed during the day, between 0515 and 1549 h. Some fruits were removed by armadillos in the early morning at 0112–0215 h (Table 1). The most frequent visitors were Collared Aracaris, comprising > 65 percent of the total visits and white-nosed coatis, comprising > 11 percent of the visits to infructescences (Fig. 1B, C).

Infructescences of *R. alpinia* may display ripe fruits for up to 2 mo. In our estimates of fruit removal using fruitfall traps, we found that 77 percent of the fruits were removed from the infructescences (Fig. 2). However 15 percent of the fruits fell on the floor to be potentially dispersed by ants (Fig. 2). In most of the plants, < 5 percent of the fruits decayed and remained attached to the infructescences ( $\chi^2 = 18.7$ ,  $df = 2$ ,  $N = 15$ ,  $P < 0.0001$ ; Fig. 2).

**ANT SEED REMOVAL AND DISPERSAL DISTANCES.**—During the ant seed-dispersal trials, all seeds were encountered by ants 1–23 min after being placed at the base of a fruiting *R. alpinia* plant ( $N = 11$  trials). The first ants that arrived to the seed pile were *Pheidole* workers and other unidentified small ants. These ants immedi-

TABLE 1. Time of day and number of visits by vertebrates to infructescences of *Renalemia alpinia* (Zingiberaceae). Foraging time represents the earliest and latest time of day when the removal was observed. Percent of visits from the total represents the contribution of each species to the total number of visits by vertebrates. Total number of independent visits = 26.

	Foraging time (h)	Percent visits of total	No. visits/plant (mean $\pm$ SD)	Min–max no. visits/plant
Frugivores				
Birds				
<i>Pteroglossus torquatus</i>	8.15–15.49	65.4	1.89 $\pm$ 1.90	0–5
<i>Ramphastos sulfuratus</i>	13.20	3.85	0.11 $\pm$ 0.33	0–1
<i>Ramphastos swainsonii</i>	11.30	7.69	0.22 $\pm$ 0.44	0–1
<i>Tinamus major</i>	5.15	3.85	0.11 $\pm$ 0.33	0–1
Mammals				
<i>Dasypus novemcinctus</i>	1.12–2.15	7.69	0.22 $\pm$ 0.67	0–2
<i>Nasua narica</i>	11.15–11.55	11.5	0.33 $\pm$ 0.71	0–2

ately started to masticate the arils surrounding the seeds, but they did not remove any of the seeds from the seed pile. The most frequent ant species able to remove *R. alpinia* seeds was *E. ruidum* (Ectatomminae). The second most common ant species that removed seeds was *Odontomachus erythrocephalus* (Ponerinae) (Table 2; Fig. 1 D, E). We also observed *Pachycondyla apicalis* (Ponerinae) and *Pheidole* spp. majors (Myrmicinae) removing seeds (Table 2).

Most of the seeds (62%) were removed by *E. ruidum* (Table 2). This species also displayed the longest seed-dispersal distances,

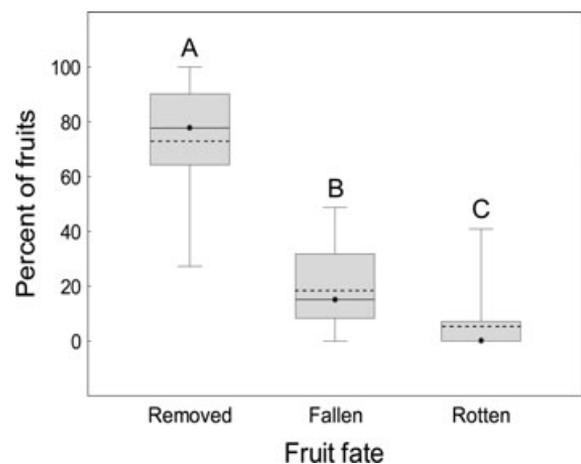


FIGURE 2. Percent of fruits removed by vertebrates, fallen from infructescences (and available for invertebrate dispersal), or that rotted and remained attached to the infructescence. Boxes group 75 percent of the data. Whiskers display min–max. Solid lines: Median. Dashed lines: Mean. Letters on the bars group similar categories ( $P < 0.05$ ). ( $N = 15$  plants. Total infructescences = 27, total fruits = 474).

TABLE 2. Ant seed removal, seed-dispersal distances (mean  $\pm$  SD), and percent of seeds deposited on the soil or brought to the nest in the Neotropical ginger *Renalmia alpinia*.

Ant species	No. of visits/plant	No. of seeds removed/plant	Total no. of seeds removed	Mean dispersal distance (m)	Min–max dispersal distance (m)	Seed fate	
						Percent left on soil surface	Percent brought to nest
<i>Ectatomma ruidum</i>	13.4 $\pm$ 10.5	10.7 $\pm$ 8.37	93	0.99 $\pm$ 0.75	0.01–2.3	39.8	60.2
<i>Odontomachus erythrocephalus</i>	4.91 $\pm$ 15.0	4.8 $\pm$ 15.0	53	0.37 $\pm$ 0.21	0.04–1.8	3.77	96.2
<i>Pachycondyla apicalis</i>	0.18 $\pm$ 0.40	0.09 $\pm$ 0.30	1	0.22	0.02	100	0
<i>Pheidole</i> spp. majors	0.64 $\pm$ 1.29	0.27 $\pm$ 0.65	3	0.08 $\pm$ 0.08	0.04–0.17	100	0

moving the seeds up to 2.3 m away from the offered seed pile (Table 2). *Odontomachus erythrocephalus* dispersed 34 percent of the total number of seeds removed (Table 2). This species displayed the second longest dispersal distances, transporting seeds up to 1.8 m away from the seed offer. The other ant species recorded dispersed only 4 percent of the total seeds removed and dispersed seeds short distances 0.02–0.17 m. Most of the removed seeds were taken inside ant nests (Table 2).

NEST RETENTION TIME AND GERMINATION SUCCESS OF *R. ALPINIA* SEEDS MANIPULATED BY ANTS.—Using a captive colony of *E. ruidum*, we found that within the nest, workers cooperate to remove arils from the seeds. Arils are consumed by adult ants and are also used to feed larvae. Most of the seeds taken into the nest were discarded in refuse heaps outside the nest after 12 h ( $N = 27$  trials using fruits from 15 different plants; Fig. 3). After 36 h < 2 percent of the seeds remained inside the nest (Fig. 3). All seeds were discarded after 72 h. None of the seeds were eaten or destroyed by the ants (Fig. 3).

Seed manipulation by *E. ruidum* enhances the germination success of *R. alpinia*. Seeds unmanipulated by ants had a germination success of only 17.8 percent (Fig. 4). Seeds that were moved but not brought into the nest had a germination success of 72.7

percent (Fig. 4). Seeds that were brought into the nest and later discarded in refuse heaps displayed the highest germination success, *i.e.*, 98.5 percent (Gehan's generalized Wilcoxon test; total  $N = 1710$  seeds,  $N_{\text{unmanipulated}} = 17$ ,  $N_{\text{moved}} = 16$ ,  $N_{\text{nest}} = 15$ ,  $\chi^2 = 704$ ,  $P < 0.00001$ ; Fig. 4).

Manipulation by ants also affected the time to germination of *R. alpinia* seeds (Fig. 5). Germination time for seeds brought into the nest was shorter than for seeds that were moved a short distance from the seed pile or not manipulated at all (Total  $N = 12$  plants, number of seeds:  $N_{\text{unmanipulated}} = 218$ ,  $N_{\text{moved}} = 82$ ,  $N_{\text{nest}} = 118$  seeds;  $\chi^2 = 8.17$ ,  $df = 2$ ,  $P < 0.017$ ).

## DISCUSSION

Aracaris and toucans are classic examples of large canopy-feeding frugivorous birds (Galetti *et al.* 2000). However, as shown by our results, ramphastids may also feed on the fruits of understory herbs such as *R. alpinia*. Aracaris and toucans actually comprised the majority of the visits to infructescences of this Neotropical ginger species (77%).

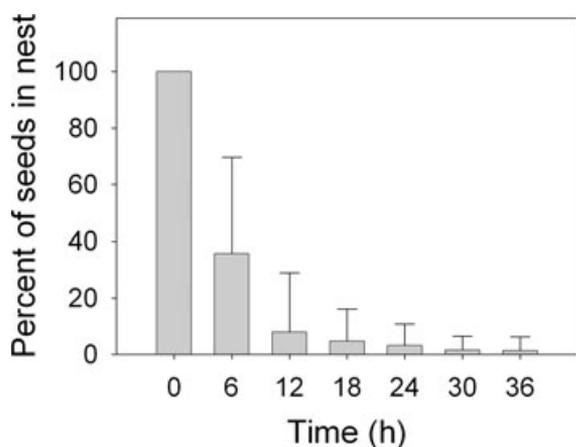


FIGURE 3. Percent of *Renalmia alpinia* seeds retained within an experimental ant colony of *Ectatomma ruidum* over time (mean  $\pm$  SD).

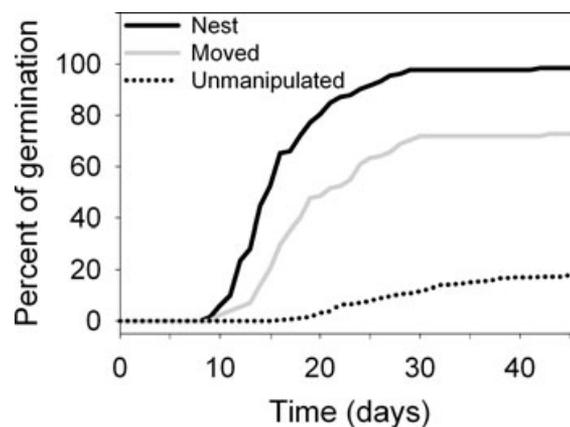


FIGURE 4. Germination success of *Renalmia alpinia* seeds after passing through an *Ectatomma ruidum* nest, being moved by *E. ruidum* or remaining unmanipulated by ants. Survival analysis,  $P < 0.05$ .

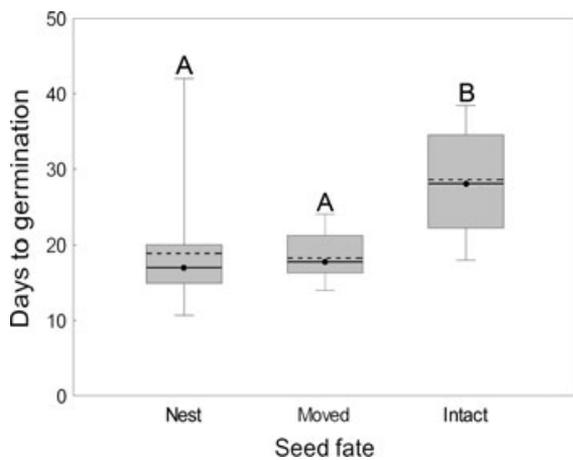


FIGURE 5. Time to germination of *Reinealmia alpinia* seeds after passing through an *Ectatomma ruidum* nest, being moved by *E. ruidum* or remaining unmanipulated by ants. Boxes group 75 percent of the data. Whiskers display min–max. Solid lines: Median. Dashed lines: Mean. Letters on the bars group similar categories ( $P < 0.05$ ,  $N = 12$  plants).

Although we did not measure seed-dispersal effectiveness by aracaris or toucans in the current study, previous research has demonstrated that ramphastids can disperse seeds over large distances (Galetti *et al.* 2000, Holbrook & Loiselle 2008). Seed passage through the guts of these birds may also enhance germination (Holbrook & Loiselle 2008). Therefore, it is likely that *P. torquatus*, *R. sulfuratus*, and *R. swainsonii* act as effective seed dispersers of *R. alpinia*.

The position of *R. alpinia* infructescences at the base of the plants allowed access to the fruits by terrestrial mammals. The most commonly recorded mammal feeding on *R. alpinia* fruits, *N. narica*, is likely an effective disperser of *R. alpinia* seeds since coatis pass small seeds through their guts unharmed and can disperse seeds over large distances (Alves-Costa & Eterovick 2007).

The camera traps used in this study were located at a distance and position that would allow us to record infructescence visits by rodents and marsupials. However, we did not record any visitations by these small mammals. In a previous study in the Brazilian Cerrado, Ximenes *et al.* (1997) suggested that fruits of *R. alpinia* are mainly consumed by small rodents. They based their conclusions on their trapping of four total individuals, two *Oecomys concolor* and two *O. bicolor* (Rodentia) during 260 trap-nights using fruits of *R. alpinia* as bait. This is not necessarily evidence that *R. alpinia* is a regular item in the diets of these two rodent species, as rodents could be trapped incidentally when exploring traps, not because of attraction to bait. During their study, Ximenes *et al.* (1997) recorded a proportion of fruit removal similar to that found in our study (74% vs. 75% in this study) and assumed that all fruits were removed by small rodents. Unfortunately they did not directly monitor visitors of *R. alpinia* infructescences. Therefore it is possible that the role of other vertebrates, such as birds, in *R. alpinia* fruit removal in the Brazilian Cerrado was underestimated. An alternative explanation is

that the discrepancies between our results and Ximenes *et al.* (1997) reflect actual differences in the composition of frugivore communities between the Brazilian Cerrado and La Selva Biological Station.

Our results show that a high proportion of *R. alpinia* seeds (15% of the fruits) may fall on the floor where ants subsequently locate and remove seeds a few minutes after fruits reach the ground. The proportion of seeds available to be dispersed by ants can be even higher, as aracaris and toucans occasionally drop intact seeds on the forest floor while feeding on the parent plant (Galetti *et al.* 2000).

Laboratory trials using a colony of *E. ruidum* showed that *R. alpinia* seeds manipulated by this ant species displayed higher germination success and shorter times to germination than seeds with intact arils. However, the effects of other ant species that we recorded removing *R. alpinia* seeds remain unknown. In a similar experiment, captive colonies of *Odontomachus laticeps* and *P. apicalis* were used to test the effects of ant seed manipulation on seed germination of the understory myrmecochorous herb *Calathea microcephala* (Marantaceae, Zingiberales) (Horvitz 1981). *Odontomachus laticeps* and *P. apicalis* carried at least half of the offered seeds into their nests and removed the arils from *C. microcephala* seeds. Similar to our results, interaction with ants increased the percent of germination and the germination speed of these seeds. Therefore it is likely that seed removal by *O. erythrocephalus* and *P. apicalis* also increases the germination success of *R. alpinia* seeds.

There is evidence that seed germination is also enhanced by ants in several nonmyrmecochorous plants (Pizo & Oliveira 1998, 2000; Passos & Oliveira 2002, 2003). These studies suggest that the benefits to seeds secondarily dispersed by ants in some cases are similar to those received by truly myrmecochorous seeds (Rico-Gray & Oliveira 2007).

Based on our field and laboratory experiments, ants are effective dispersers of *R. alpinia* seeds (*sensu* Schupp 1993). In the field we observed ants removing *R. alpinia* seeds rapidly from the source pile which likely protects seeds from predators and pathogens (Pizo & Oliveira 1998, Passos & Oliveira 2002). Another factor contributing to ant seed-dispersal effectiveness in *R. alpinia* is that the majority of seeds removed by ants in the field trials were brought to the nest rather than discarded on the forest floor. In laboratory experiments we observed that once inside the nest, *E. ruidum* completely cleaned the arils from all seeds, likely enhancing seed germination speed and success. Along with removing the aril from seeds, ants may also scarify the seeds allowing them to imbibe water and increasing germination likelihood (Horvitz 1981). In laboratory experiments, all *R. alpinia* seeds taken inside the ant nest were eventually deposited in refuse heaps outside the nest. Refuse heaps may contain nutrients such as nitrogen and phosphorus (Horvitz & Schemske 1986, Passos & Oliveira 2002). The nutrient-rich soil in refuse heaps may enhance seedling growth of some plant species (Passos & Oliveira 2002).

Our results show that birds, mammals and ants are highly variable in their contributions to seed removal in *R. alpinia*. These dispersal agents may also contribute to seed dispersal at different spatial scales. Large-sized birds and mammals can transport seeds over long distances. Long-distance dispersal promotes colonization

of new areas and gene flow between distant populations (Jordano *et al.* 2007). However, it may also increase the probability of seed deposition in habitats not suitable for plant establishment (Horvitz *et al.* 2002).

Short-distance dispersal by ants may contribute to *R. alpinia* population spread in localities already colonized by reproductive plants. Ant-mediated seed dispersal may also enhance directed dispersal, *i.e.*, the deposition of seeds in suitable microhabitats, thus increasing the probability of plant establishment (Rico-Gray & Oliveira 2007).

In conclusion, the seeds of *R. alpinia* are mostly dispersed by large birds. In addition, ants are dispersing seeds short distances and positively affecting germination in this primarily vertebrate-dispersed plant. This study illustrates, using *R. alpinia* as an example, how seed dispersal may be a complex process involving a diverse array of animal dispersal agents.

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## LITERATURE CITED

- ALVES-COSTA, C. P., AND P. C. ETEROVICK. 2007. Seed dispersal services by coatis (*Nasua nasua*, Procyonidae) and their redundancy with other frugivores in southeastern Brazil. *Acta Oecol.* 32: 77–92.
- BEATTIE, A. J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, Cambridge, UK.
- GALETTI, M., R. LAPS, AND M. A. PIZO. 2000. Frugivory by toucans (Ramphastidae) at two altitudes in the Atlantic forest of Brazil. *Biotropica* 32: 842–850.
- GAUTIERHION, A., J. P. GAUTIER, AND F. MAISELS. 1993. Seed dispersal versus seed predation—An inter-site comparison of two related African monkeys. *Vegetatio* 108: 237–244.
- HOLBROOK, K. M., AND B. A. LOISELLE. 2008. Using toucan-generated dispersal models to estimate seed dispersal in Amazonia Ecuador. *In* A. J. Dennis, E. W. Schupp, R. Green, and D. A. Westcott (Eds.). *Seed dispersal: Theory and its application in a changing world*. pp. 300–321. CAB International, Wallingford, UK.
- HOLDRIDGE, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* 105: 367–368.
- HORVITZ, C. C. 1981. Analysis of how ant behaviors affect germination in a tropical myrmecochore *Calathea microcephala* (P and E) Koernicke (Marantaceae). Microsite selection and aril removal by Neotropical ants, *Odontomachus*, *Pachycondyla*, and *Solenopsis* (Formicidae). *Oecologia* 51: 47–52.
- HORVITZ, C. C., AND D. W. SCHEMSKE. 1986. Ant nest soil and seedling growth in a Neotropical ant-dispersed herb. *Oecologia* 70: 318–320.
- HORVITZ, C. C., M. A. PIZO, B. BELLO, Y. BELLO, J. LECORFF, AND R. DIRZO. 2002. Are plant species that need gaps for recruitment more attractive to seed-dispersing birds and ants than other species? *In* D. J. Levey, W. R. Silva, and M. Galetti (Eds.). *Seed dispersal and frugivory: Ecology, evolution, and conservation*. pp. 145–159. CABI Publishing, New York, New York.
- JANSON, C. H. 1983. Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science* 219: 187–189.
- JORDANO, P., C. GARCIA, J. A. GODOY, AND J. L. GARCIA-CASTANO. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proc. Natl. Acad. Sci. USA* 104: 3278–3282.
- LEVEY, D. J., AND M. M. BYRNE. 1993. Complex ant plant interactions—rain-forest ants as secondary dispersers and post-dispersal seed predators. *Ecology* 74: 1802–1812.
- LINK, A., AND P. R. STEVENSON. 2004. Fruit dispersal syndromes in animal disseminated plants at Tinigua National Park, Colombia. *Rev. Chil. Hist. Nat.* 77: 319–334.
- MAAS, P. J. M. 1977. *Flora Neotropica*. Monograph No. 18. *Renealmia* (Zingiberaceae—Zingiberoideae), Costoideae (Additions) (Zingiberaceae). The New York Botanical Garden, New York.
- MCDADE, L. A., K. S. BAWA, H. A. HESPENHEIDE, AND G. S. HARTSHORN. 1994. *La Selva: Ecology and natural history of a Neotropical rain forest*. University of Chicago Press, Chicago, Illinois.
- NATHAN, R., AND H. C. MULLER-LANDAU. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15: 278–285.
- PASSOS, L., AND P. S. OLIVEIRA. 2002. Ants affect the distribution and performance of seedlings of *Clusia criuva*, a primarily bird-dispersed rain forest tree. *J. Ecol.* 90: 517–528.
- PASSOS, L., AND P. S. OLIVEIRA. 2003. Interactions between ants, fruits and seeds in a restinga forest in south-eastern Brazil. *J. Trop. Ecol.* 19: 261–270.
- PIJL, L. V. D. 1982. *Principles of seed dispersal in higher plants*. Springer-Verlag, New York, New York.
- PIZO, M. A., AND P. S. OLIVEIRA. 1998. Interaction between ants and seeds of a nonmyrmecochorous Neotropical tree, *Cabralea canjerana* (Meliaceae), in the Atlantic forest of southeast Brazil. *Am. J. Bot.* 85: 669–674.
- PIZO, M. A., AND P. S. OLIVEIRA. 2000. The use of fruits and seeds by ants in the Atlantic forest of southeast Brazil. *Biotropica* 32: 851–861.
- RICO-GRAY, V., AND P. S. OLIVEIRA. 2007. The ecology and evolution of ant-plant interactions. University of Chicago Press, Chicago, Illinois.
- SARKINEN, T. E., M. F. NEWMAN, P. J. M. MAAS, H. MAAS, A. D. POULSEN, D. J. HARRIS, J. E. RICHARDSON, A. CLARK, M. HOLLINGSWORTH, AND R. T. PENNINGTON. 2007. Recent oceanic long-distance dispersal and divergence in the ampho-Atlantic rain forest genus *Renealmia* L.f. (Zingiberaceae). *Mol. Phylogenet. Evol.* 44: 968–980.
- SCHUPP, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 108: 15–29.
- VANDER WALL, S. B., AND W. S. LONGLAND. 2004. Diplochory: Are two seed dispersers better than one? *Trends Ecol. Evol.* 19: 155–161.
- XIMENES, M., A. BIZERRIL, AND M. L. A. GASTAL. 1997. Fruit phenology and mammal frugivory in *Renealmia alpinia* (Zingiberaceae) in a gallery forest of central Brazil. *Rev. Bras. Biol.* 57: 305–309.