

REGIONAL DIFFERENCES IN ANT COMMUNITY STRUCTURE AND CONSEQUENCES FOR SECONDARY DISPERSAL OF *COMMIPHORA* SEEDS

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Abstract. To understand the factors influencing secondary seed dispersal by ants we compared dispersal rates of *Commiphora* seeds between species in Madagascar and South Africa. We quantified secondary seed dispersal by ants and characterized the ant community using rice-baiting experiments at a Malagasy and a South African study site. The results showed significant differences, with seed dispersal rates of 48% at the Malagasy site and almost zero at the South African site. We found three possible factors causing the low seed dispersal rate at the South African site: (1) a lack of potential seed dispersers, due mainly to the small size of the ant species; (2) low ant activity; and (3) fewer aggressive interspecific interactions among ant species. High seed dispersal rates at the Malagasy site could be related to high ant activity and more aggressive interspecific interactions. Strong interspecific competition at the Malagasy site might force ants to carry food items rapidly into the safety of their colonies. Thus regional differences in the composition of ant communities appear to have consequences for the behavior of ants and, therefore, for secondary seed dispersal rates. Accepted 22 May 2002.

Key words: Secondary seed dispersal, ants, *Commiphora*, Madagascar, South Africa, ant community structure, competition.

INTRODUCTION

One of the current challenges in community ecology is understanding the ecology and evolution of mutualistic systems such as seed dispersal (Boucher *et al.* 1982, Bronstein 1994, Begon *et al.* 1996). In recent decades seed dispersal by frugivorous vertebrates has been intensively studied (Howe & Smallwood 1982, Janzen 1983, Howe 1986, Jordano 1992, Willson 1992, Chapman & Onderdonk 1998, Herrera 1998). However, it is becoming increasingly apparent that in many systems seeds are dispersed not only by these primary dispersers but also by secondary dispersers such as ants. Secondary seed dispersal can strongly affect seed distribution and seedling establishment (Roberts & Heithaus 1986, Kaufmann *et al.* 1991, Byrne & Levey 1993, Kaspari 1993, Levey & Byrne 1993). Nevertheless, we have only limited understanding of the factors which influence this type of dispersal.

To understand the factors influencing secondary seed dispersal by ants we compared seed dispersal bet-

ween two bird-dispersed tree species in the genus *Commiphora* at a Malagasy and a South African forest site. This system has already been intensively studied (Böhning-Gaese *et al.* 1995, 1996, 1999; Böhning-Gaese & Bleher 2000; Bleher & Böhning-Gaese 2000, 2001). Previous results revealed that primary dispersal rates by birds were considerably lower in the Malagasy than in the South African species. In both systems, many seeds drop to the ground with all or part of the aril still attached. These seeds may be attractive to ants. In Madagascar, secondary seed dispersal by ants has been shown to have an important impact on the spatial distribution of seeds and on seedling establishment (Böhning-Gaese *et al.* 1996, 1999). Preliminary studies indicate that it is of minor importance in South Africa. Therefore, the two objectives of this study were: (1) to quantify secondary seed dispersal rates by ants by conducting dispersal experiments in Madagascar and South Africa, and (2) to study the influence the ant community has on seed dispersal rates by focusing on the abundance of the dispersing ant species, on the presence of other ant species that could potentially disperse seeds, on ant activity, and on interspecific interactions.

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STUDY SYSTEM

The plant species used for the study were *Commiphora guillaumini* in Madagascar and *C. harveyi* in South Africa (de la Bathie 1946, van der Walt 1973). Both are dioecious trees. The fruiting season in the Malagasy species is from January to April (Rohner & Sorg 1986), in the South African species from March to June (Pooley 1994, Bleher & Böhning-Gaese 2000). The fruits of both species are spherical and include an unpalatable slightly green/red fleshy outer covering (exocarp and mesocarp) that splits when mature into two halves, exposing a single diaspore. The diaspore consists of a smooth black seed (Madagascar: 12.2 x 8.0 x 6.3 mm, n = 20; South Africa 7.1 x 5.7 x 5.1 mm, n = 20, Bleher & Böhning-Gaese 2000) that is partly enveloped by a red fleshy aril-like endocarp (hereafter called an aril). Arils in the Malagasy species are cup-shaped (de la Bathie 1946), the South African aril is similar, but has additionally four lobes (van der Walt 1973). Both arils are rich in lipids (Madagascar 81.1%; South Africa 60.1%, unpublished data) and have a similar fraction of proteins (Madagascar 3.4%; South Africa 3.1%, unpublished data). In Madagascar, frugivorous vertebrates cannot open the outer coverings before the fruit is fully mature, but have to wait until it splits and displays the diaspore. In South Africa, frugivorous vertebrates (e.g., hornbills) are able to open the outer coverings for access to seed and aril before the fruit reaches complete maturity and splits open (Böhning-Gaese & Bleher 2000, Bleher & Böhning-Gaese 2000). In both systems, considerable numbers of seeds drop to the ground with all or part of the aril still attached.

STUDY SITES

The Malagasy study was conducted in February and March 1991 and 1994 in the Kirindy Forest / CFPE, which is classified as a tropical dry deciduous forest. The Kirindy Forest is a 10 000 ha forestry concession of the Centre de Formation Professionnelle Forestière de Morondava (CFPF), situated 60 km north of Morondava. Average rainfall in the study area is 799 mm with the main rainfall season between December and March (Sorg & Rohner 1996). Detailed information on the Kirindy Forest / CFPF is given in Ganzhorn & Sorg (1996) and Böhning-Gaese *et al.* (1995, 1996, 1999).

The South African study was carried out in March and April 1999 in Oribi Gorge Nature Reserve (OGNR) on the KwaZulu-Natal East Coast. This

1850 ha nature reserve, located 110 km south of Durban and 22 km inland from Port Shepstone, is classified as coastal scarp forest (Cooper 1985). Average annual rainfall in the area is 1176 mm with the main rainfall season between October and March (Glen 1996). For further details on Oribi Gorge and coastal forests see Glen (1996) and Acocks (1988). At each site the study took place after the rainy season during the fruiting peak of the respective *Commiphora* species, when most fruits were ripe and therefore available to potential dispersers.

METHODS

Secondary seed dispersal by ants. To quantify secondary seed dispersal by ants systematic seed dispersal experiments were conducted in Madagascar in 1994 and in South Africa in 1999. The methods and results on secondary seed dispersal in Madagascar have already been published in Böhning-Gaese *et al.* (1999). However to make the comparison easier, we have chosen to describe the methods and results again. In Madagascar 96 seeds and in South Africa 114 seeds were placed randomly throughout the study area. All seeds were freshly collected and had complete arils or at least part of the aril left. They were presented on a rough spoon in Madagascar and a plate in South Africa. Plates and spoons were of nearly the same size. Sites were monitored after 90 minutes. We recorded the identity of the ant species visiting the seed, the behavior of the ants and the distance the seed was moved.

In addition, we performed specific feeding trials in South Africa on ant species that might act as potential secondary seed dispersers. To conduct these feeding trials we placed freshly collected seeds two and four meters from the colonies of the ant species that we tested as potential dispersers and recorded their behavior (feeding on the aril, transporting the seed).

All studies were conducted during daytime because almost all fruits split open and seeds dropped during daytime. Even seeds that were not dispersed by ants had their arils removed by ants *in situ* and were, therefore, not available to nocturnal ants.

Characterization of the ant community. The ant community in Madagascar has been studied using a large set of different methods (Olson & Ward 1996, Burkhardt *et al.* 1996). These studies demonstrated that baiting experiments are an adequate method of obtaining a representative sample of the ecologically

important species (Burkhardt *et al.* 1996). Thus to characterize the composition of the ant communities, ant-baiting experiments were conducted in Madagascar in 1991 and in South Africa in 1999. At each study site, nine random transects of 250 m were established, with baiting positions every ten meters. Baits consisted of cooked rice mixed with oiled sardines on a spoon or plate (see above). After 90 minutes we recorded the identity and number of the ant species found foraging on the spoon/plate or surrounding the baiting position trying to get access. We defined a bait position as occupied if an ant species was found on or surrounding the bait. In addition, we noted whether ants transported rice and whether antagonistic interactions occurred.

All baiting experiments were conducted during daytime to record the activity of diurnal ant species (for explanation see above).

All ant species were collected, identified, and deposited in the Natural History Museum in Karlsruhe, Germany. All ant species were measured. Because total body length measurements are difficult to standardize, only alitrunk (mesosoma) length (AL) was measured. Measurements are means of 2–4 workers of each species; in distinctly poly- or dimorphic species the length of the largest specimens is indicated separately. Ant species are distributed into three categories: (1) AL < 1.0 mm; (2) AL = 1.0–2.5 mm; (3) AL > 2.5 mm.

RESULTS

Secondary seed dispersal by ants

The secondary seed dispersal rate differed between the sites in Madagascar and South Africa. In Madagascar, 46 out of 96 (47.9 %) seeds were dispersed by ants, in South Africa none were dispersed ($n = 114$). In Madagascar, 93.5 % of the dispersed seeds were transported by *Aphaenogaster swammerdami* and in all other cases by *Pheidole* sp. Ma-1. The workers of *A. swammerdami* carried the seeds to their colony, with a mean dispersal distance of 4.4 ± 1.5 m (mean \pm SD, range = 1.6–10.4 m, $n = 41$ observations). In the colony, they removed the arils and discarded the seeds undamaged on refuse piles at the edge of the colony. Three times we observed *Pheidole* sp. Ma-1 carrying the seeds into their colony. The dispersal distances were 0.3 m, 1.2 m and 1.3 m. The fate of these seeds is not known (Böhning-Gaese *et al.* 1999). In South Africa, ants were not observed to disperse seeds during systematic seed dispersal experiments but several spe-

cies fed on arils *in situ*. Specific feeding trials indicated that one species, *Pheidole* sp. SA-3, dispersed seeds with recorded dispersal distances of 1.8 m and 2.2 m ($n = 2$ observations).

Furthermore, at the Malagasy site even the smallest ant species tried to move the diaspore, whereas at the South African site even fairly large species did not try to do so.

Characterization of the ant community

Abundance of dispersers. The abundance of the seed dispersing ant species as characterized by rice-baiting experiments was considerably higher at the Malagasy site than at the South African site. *A. swammerdami* and *Pheidole* sp. Ma-1 were both common species in Madagascar. *A. swammerdami* occupied $61.8\% \pm 26.8\%$ (mean \pm SD, $n = 9$ transects) of all feeding positions during rice-baiting experiments, *Pheidole* sp. Ma-1 $21.3\% \pm 15.7\%$ ($n = 9$). At least one of the two species occupied $68.0\% \pm 28.1\%$ ($n = 9$) of the feeding positions. In contrast, in South Africa, *Pheidole* sp. SA-3 was rare. It occupied only $1.3\% \pm 4.0\%$ ($n = 9$) of the feeding positions.

Potential seed dispersers. The ant species found differed almost completely between the Malagasy and South African study sites (Table 1); only one species was shared (*Tetramorium delagoense*). To identify ant species that could potentially disperse seeds we compiled species lists from the rice feeding experiments (Table 1). A potential seed disperser was defined as one attracted to the aril of *Commiphora* sp., transporting its food and being able, from its size and foraging behavior, to carry off the seed. An ant species was classified as being attracted to the aril if it was observed to feed on the displayed arils either during the systematic seed dispersal experiments or during the specific feeding trials. As potential seed dispersers, only ant species that fed on the aril and transported rice grains were included. To ensure that ants were able to carry off the seed, we considered only species that had either a minimal alitrunk size of 2.5 mm and were solitary foragers, or an alitrunk size of 1–2.5 mm and used a mass-recruitment system. These size specifications were deduced from those ant species that had been observed to disperse *Commiphora* seeds. Besides the actual dispersers, no species in Madagascar and only one species (*Myrmecaria* sp. SA-1) in South Africa were scored as potential seed disperser according to our definition. The South African species was rare, occupying only $0.9\% \pm 1.8\%$ ($n = 9$ transects)

TABLE 1. Ant species recorded with rice-baiting experiments in the Kirindy Forest / CFPP (Madagascar) and in Oribi Gorge Nature Reserve (South Africa). For measurements see METHOD. Species are distributed into three size categories [AL = Alitrunk]: (1) AL < 1.0 mm, (2) AL = 1.0–2.5 mm, (3) AL > 2.5 mm. Species with a mass-recruitment (m.r.) system are indicated by „+“, actual dispersers are marked as „+“ and potential seed dispersers as „p.d.“; (s) indicates soldiers in dimorphic species

Ant species / site	AL (mm)	Size categories	m. r.	Disperser
Madagascar				
DOLICHODERINAE				
<i>Tapinoma</i> sp. Ma-1	0.8	1	+	
FORMICINAE				
<i>Camponotus</i> sp. Ma-1	4.2	3	+	
<i>Camponotus</i> sp. Ma-3	2.2-2.9(s)	2-3(s)	+	
<i>Camponotus (Mayria) quadrimaculatus</i> Forel	1.5-2.15(s)	2	+	
<i>Camponotus (Mayria) immaculatus</i> Forel*	1.65	2	+	
<i>Camponotus (Myrmopytia) imitator</i> Forel	3.5-4.0(s)	3	+	
<i>Camponotus</i> sp. Ma-9	4.6(s)	3	+	
<i>Camponotus cf. niveosetosus</i> Mayr	2.05	2	+	
<i>Paratrechina</i> sp. Ma-1	0.75	1	+	
MYRMICINAE				
<i>Aphaenogaster swammerdami</i> Forel	3.1	3	+	+
<i>Crematogaster grevei</i> Forel	0.85	1	+	
<i>Crematogaster</i> sp. Ma-2	0.5	1	+	
<i>Crematogaster</i> sp. Ma-3	1.05	2	+	
<i>Meranoplus mayri</i> Forel	1.35	2	+	
<i>Monomorium robustior</i> Forel	0.7	1	+	
<i>Monomorium</i> sp. Ma-2 (<i>monomorium</i> -group)	0.45	1	+	
<i>Pheidole</i> sp. Ma-1	1.1-1.6(s)	2	+	+
<i>Pheidole</i> sp. Ma-4	0.55-1.0(s)	1-2(s)	+	
<i>Pheidole</i> sp. Ma-6	0.55-0.9(s)	1	+	
<i>Pheidole</i> sp. Ma-7	0.8-1.1(s)	1-2(s)	+	
<i>Pheidole</i> sp. Ma-8	0.45	1	+	
<i>Pheidole</i> sp. Ma-9* ²	0.8	1	+	
<i>Pheidole</i> sp. Ma-10* ³	1.1(s)	1-2(s)	+	
<i>Tetramorium delagoense</i> Forel #	0.65	1	+	
<i>Tetramorium aff. plesiarum</i> Bolton	0.85	1	+	
<i>Tetramorium quadrispinosum</i> Emery	1.2	2	+	
PONERINAE				
<i>Anochetus</i> sp. nov.	2.6	3	-	
<i>Hypoponera</i> sp. Ma-1	0.8	1	-	
<i>Leptogenys cf. truncatirostris</i> Forel		3	-	
<i>Pachycondyla wasmannii</i> Forel	3.4	3	-	
PSEUDOMYRMECINAE				
<i>Tetraoponera</i> sp.		3	-	
South Africa				
FORMICINAE				
<i>Anoplolepis</i> sp. SA-1	1.25-2.0	2	+	
<i>Camponotus</i> sp. SA-1	3.25(s)	3	+	
<i>Lepisiota</i> sp. SA-1	0.85	1	+	

Ant species / site	AL (mm)	Size categories	m. r.	Disperser
<i>Paratrechina</i> sp. SA-1	0.7	1	+	
<i>Plagiolepis</i> sp. SA-2	0.45	1	+	
MYRMICINAE				
<i>Crematogaster</i> sp. SA-1	1.25	2	+	
<i>Crematogaster</i> sp. SA-2	0.95	1	+	
<i>Monomorium binatu</i> Bolton	0.5	1	+	
<i>Monomorium</i> sp. SA-2 (<i>aff. bequaerti</i> -complex)	0.4	1	+	
<i>Myrmicaria</i> sp. SA-1	2.2	2	+	p.d.
<i>Oligomyrmex</i> sp. SA-1	0.35	1	+	
<i>Pheidole</i> sp. SA-1	0.95-1.05(s)	1-2(s)	+	
<i>Pheidole</i> sp. SA-2	0.75-1.0	1-2(s)	+	
<i>Pheidole</i> sp. SA-3	1.4-2.05(s)	2	+	+
<i>Pheidole</i> sp. SA-4	0.95-1.4(s)	1-2(s)	+	
<i>Pheidole</i> sp. SA-5	0.95	1	+	
<i>Tetramorium avium</i> Bolton	0.8	1	+	
<i>Tetramorium delagoense</i> Forel #	0.65	1	+	
<i>Tetramorium erectum</i> Emery	1.1	2	+	
<i>Tetramorium grassii</i> Emery	0.9	1	+	
<i>Tetramorium regulare</i> Bolton	0.7	1	+	
<i>Tetramorium simillimum</i> Smith, F.	0.75	1	+	
<i>Tetramorium weitzackeri</i> Emery	0.8	1	+	
PONERINAE				
<i>Leptogenys attenuata</i> Smith, F.	2.7	3	-	
<i>Plectroctena conjugata</i> Santschi	3.7	3	-	

* Might be conspecific with *C. quadrimaculatus*,

*₂ only workers collected, possibly conspecific with *Pheidole* sp. MA-10,

*₃ only soldiers collected, possibly conspecific with *Pheidole* sp. MA-9,

the only species shared between both sites.

of the feeding positions. In feeding trials, *Myrmicaria* sp. SA-1 was observed to remove the aril completely and transport it into the colony without moving the seed.

Activity and interactions between ant species. Ant activity as indicated by occupied feeding positions was higher at the Malagasy site than at the South African site. In Madagascar nearly all feeding positions were occupied, whereas the South African feeding positions were significantly less attended (Wilcoxon test: $z = 2.45$, $P = 0.014$, $n = 18$; Fig. 1).

Higher ant activity at the Malagasy site might lead to more aggressive behavior in the ant community. Indeed more interspecific interactions and fights were observed than at the South African site. Considering only occupied feeding positions in both coun-

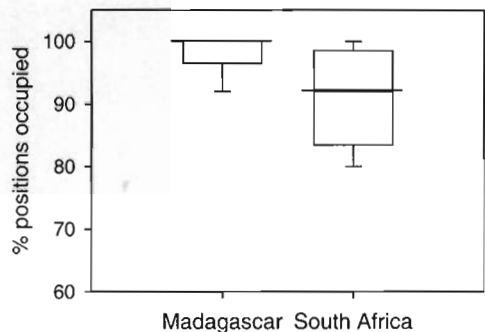


FIG. 1. Ant activity (Box-and-Whisker-Plot) measured as the percentage of occupied feeding positions in Madagascar and South Africa. $n = 9$ transects for each study site.

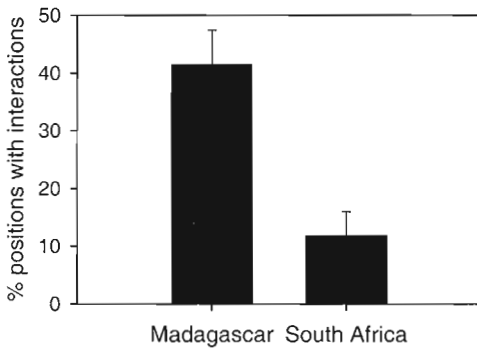


FIG. 2. Interspecific interactions measured as the percentage of occupied feeding positions (mean \pm 1 SE) in which a second species tried to get access to food at sites in Madagascar and South Africa. $n = 9$ transects for each study site.

tries, usually only a single species was found on the baits (Madagascar 1.13 ± 0.11 species; South Africa: 1.15 ± 0.09 species: t -test: $t = 0.5$, $P = 0.64$, d.f. = 16). However, at the Malagasy site a second species surrounded the baits in considerably more cases than at the South African site (t -test: $t = 4.1$, $P = 0.0009$, d.f. = 16; Fig. 2). In most instances the surrounding species lingered close by, trying to gain access. Additionally, we observed significantly more fights among ant species at the Malagasy site than at the South African site (Wilcoxon test: $z = 2.4$, $P = 0.018$, $n = 18$; Fig. 3).

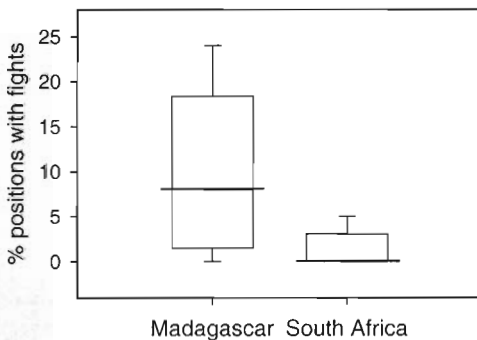


FIG. 3. Aggressive interactions (Box-and-Whisker-Plot) between species measured as the percentage of occupied feeding positions at which fights occurred at sites in Madagascar and South Africa. $n = 9$ transects for each study site.

DISCUSSION

The comparison of secondary seed dispersal by ants between sites in Madagascar and South Africa demonstrated large regional differences. Secondary seed dispersal rates were high at the Malagasy study site and low at the South African site. At the Malagasy site two abundant ant species, at the South African site only one rare species dispersed the seeds.

One explanation for the low dispersal rates in South Africa could be a lack of adequately-sized seed dispersers. Indeed only one species, *Myrmecaria* sp. SA-1, is a potential disperser according to our definition.

However, the lack of potential dispersers seems not to be the only reason behind the different seed dispersal rates of the Malagasy and the South African sites. First, *Myrmecaria* sp. SA-1 did not transport the seeds although, from its size and behavior, it should be able to do so. Second, at the Malagasy site even the smallest ant species tried to move the diaspores, whereas at the South African site even fairly large species did not try to do so.

Thus a second explanation for the higher seed dispersal rate at the Malagasy site might be its higher ant activity, which results in more aggressive interactions (Figs. 1 and 3). The data suggest strong interspecific competition at the Malagasy site that might force ants to carry food items rapidly into their colonies to prevent them from being stolen. Other studies have documented an especially high level of interspecific competition among ants at the Malagasy study site (Burkhardt *et al.* 1996). The main disperser, *A. swammerdami*, appeared to suffer exceptionally from interspecific competition. For example, *A. swammerdami* was not able to monopolize rice baits in the presence of *Pheidole* species (Burkhardt *et al.* 1996). In South Africa, competition seemed relatively weak. The lower risk of food monopolization by other ant species might lead to ants feeding on the arils *in situ*, instead of carrying them off with the seeds. The fact that ants in South Africa did, nevertheless, transport the rice grains might be explained by the grains being smaller and lighter and thus having lower transportation costs. The lower risk of food monopolization and the lower transportation costs could also be the explanation for the fact that *Myrmecaria* sp. SA-1 was observed to remove the aril completely and to transport it into the colony without moving the seed.

To conclude, we found regional differences between sites in Madagascar and South Africa in ant

community composition, especially in ant species size, in ant activity, and in the frequency of interspecific interactions. These regional differences seem to have consequences for ant behavior and thus on secondary seed dispersal rates. The results indicate that ant community composition, ant behavior, and secondary seed dispersal are closely linked. As we investigated only two study sites these results, of course, apply primarily to these sites. Therefore to make generalizations further studies at other sites are needed.

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