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SEED DISPERSAL BY BIRDS IN A SOUTH AFRICAN AND A MALAGASY *COMMIPHORA* SPECIES

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Abstract. The diversity of fruit-eating bird species in Africa is high and comparable to other continents; however, it is strikingly depauperate in Madagascar. To address the question of whether regional differences in the diversity of frugivorous bird species have an influence on seed dispersal we compared the tree visitation and seed dispersal rates of a South African and a Malagasy species of *Commiphora* (Burseraceae). In keeping with the higher diversity of frugivorous birds on the African continent, the South African *Commiphora* species was visited by 13, the Malagasy species by only four bird species. In each of the two countries only one primate species visited the trees. Ten of the South African but none of the Malagasy bird species dispersed seeds by swallowing them. Other species either dropped the seeds under the parent tree or occasionally carried them away in their bills. Consequently, the percentage of seeds dispersed away from the crown in South Africa was 66% and in Madagascar 9%. The results demonstrate that regional differences in frugivore diversity, and especially in seed handling behavior, can lead to pronounced differences in seed dispersal away from the parent tree. *Accepted 4 January 2000.*

Key words: Commiphora, *frugivore diversity, Madagascar, seed dispersal, South Africa.*

INTRODUCTION

A large number of plant species rely on animals for the dispersal of their seeds. The percentage of animal-dispersed tree species can be as high as 90% in the tropics (Howe & Smallwood 1982). In spite of the widespread occurrence of animal-dispersed plants it is not known whether plants depend on particular animal species for the dispersal of their seeds. At one end of the interaction continuum, plant species can be dispersed by a multitude of fruit-eating animal species (Howe & DeSteven 1979, Coates-Estrada & Estrada 1988, Fleming & Williams 1990, Pizo 1997). Thus, the extirpation of one or a small number of animal species might not have consequences for seed dispersal because animal species are redundant and other species would fill the gap (Wheelwright & Orians 1982, Howe 1984b, Herrera 1985). At the other end, plant species might be dependant on only a few obligate dispersers whose absence could therefore reduce seed dispersal (Bond & Slingsby 1984). Hence it is important to study such dispersal systems for the eventuality of a disperser becoming extinct.

Low rates of seed dispersal away from a parent tree might result in low rates of seedling establishment, as establishment and survival of seedlings is much lower under the crown than at a greater distance from the parent tree (Janzen *et al.* 1976, Augspurger 1983, 1984; Augspurger & Kelly 1984, Howe *et al.* 1985, Schupp 1988, Böhning-Gaese *et al.* 1999). Furthermore, seed dispersal could influence the abundance and chance of local extinction of a plant species (Howe 1977, 1984a) and affect the spatial distribution of trees (Hubbell 1979, Howe 1989). It is therefore important to ask whether regional differences in frugivore diversity, in the sense of species richness, have an effect on seed dispersal, and whether low frugivore diversity leads to low and potentially ineffective seed dispersal.

One approach to answering these questions is to compare frugivory and seed dispersal in South Africa and in Madagascar. Although Africa and Madagascar are separated only by 400 km of open sea, the diversity of frugivorous birds differs considerably. In Africa, the diversity of frugivorous birds is high and comparable with other continents (Fleming *et al.* 1987). Madagascar, however, is "strikingly depauperate" (Fleming *et al.* 1987, Goodman & Ganzhorn 1997), and compared with Africa lacks a multitude of frugivorous taxa such as Bucerotidae, Coliidae, Musophagidae and Capitonidae (Langrand 1990, Maclean 1993).

Ideally we wished to compare frugivory and seed dispersal in the same tree species in South Africa and Madagascar, but as 96% of the tree and shrub species in Madagascar are endemic (G.E. Schatz, pers.

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comm.) this was not possible. We therefore compared two species in the same genus (*Commiphora*, Burseraceae) with morphologically similar, typically bird-dispersed fruits. The questions addressed were: 1. Does local diversity of frugivorous bird species differ between the South African and Malagasy study sites? 2. Are there differences in tree visitation and seed dispersal rates between the South African and Malagasy *Commiphora* species? 3. Does a low diversity of frugivorous birds in the Malagasy study site lead to low seed dispersal?

THE TREES

The study was conducted on *Commiphora harveyi* in South Africa and *C. guillaumini*, a Madagascar endemic. Both species are dioecious trees, the South African species flowering from October to December (Pooley 1994) and the Malagasy species from October to November (Rohner & Sorg 1986). The fruiting season of *C. harveyi* lasts from March to June (Pooley 1994, B. Bleher, pers. obs.), of *C. guillaumini* from January to April (Rohner & Sorg 1986). Both species bear roundish fruits that consist of an unpalatable greenish-reddish fleshy outer covering (exocarp and mesocarp) that splits into two halves exposing a single diaspore (Fig. 1). The diaspore consists of a brilliant black seed (South Africa: 7.1 x 5.7 x 5.1 mm, n = 20; Madagascar: 12.2 x 8.0 x 6.3 mm, n = 20) which is partly enveloped by a red fleshy aril-like endocarp (hereafter called an aril). Arils in *C. harveyi* are cup-shaped with four lobes (van der Walt 1986) (Fig. 1), aril shape in *C. guillaumini* is similar but lobes are absent (de la Bathie 1946) (Fig. 1). Before the fruit reaches complete maturity and splits open in *C. harveyi*, some frugivorous tree visitors are able to open the outer coverings for access to seed and aril. In *C. guillaumini*, frugivores cannot open the outer coverings but have to wait until they split open by themselves and the diaspore is "displayed".

STUDY SITES

In South Africa, the study was conducted from February to July 1997 in Oribi Gorge Nature Reserve (OGNR) on the KwaZulu – Natal South Coast (Fig. 1). This 1850 ha nature reserve is located 110 km south of Durban, and 22 km inland from Port Shepstone, and 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 Acocks (1988) and Glen (1996).

In Madagascar, the study was carried out in February and March 1993 in a dry deciduous forest in western Madagascar (Fig. 1). The study site was the Kirindy Forest/CFPF, a 10 000 ha forestry concession of the Centre de Formation Professionelle 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). Further information on the Kirindy Forest/CFPF is given in Ganzhorn & Sorg (1996) and Böhning-Gaese *et al.* (1995, 1996, 1999).

METHODS

Frugivore diversity. The number of frugivorous bird species was obtained for Oribi Gorge, South Africa, from the unpublished bird list of the KwaZulu-Natal Nature Conservation Service, and for the Kirindy Forest/CFPF, Madagascar, from Langrand (1990). For determining the degree of frugivory for each species Maclean (1993) and Langrand (1990) were used. Bird species were categorized as mainly frugivorous in both countries when fruit was the first item listed in the diet and as partly frugivorous when fruit was taken but was not the primary food source.

Tree observations. To obtain information about frugivorous tree visitors we observed eight trees in South Africa and six trees in Madagascar for two days each. We selected trees with comparatively large numbers of fruits. However, this did not bias the results because the number of fruits did not affect the identity or the dispersal behavior of tree visitors (see results). Observations were conducted in three sessions from sunrise to 10:00 h, from 10:00 h to 14:30 h, and from 14:30 h to sunset (giving a total of 184 observation hours for *C. harveyi* and 156 hours for *C. guillaumini*). Observation sessions were randomly distributed over the study period. All visits by animals were recorded. For each visitor we noted the seed handling behavior and counted the number of seeds that were either dropped under the crown or dispersed away from the crown. The small number of other observations of animals only resting in the trees were removed from the data, so that analyses were limited to individuals that were observed foraging on arils. Night observations were conducted in four four-hour sessions in South Africa and in five three-hour sessions in Madagascar, using a night-vision scope.

Fruit traps. To obtain more accurate information on seed dispersal rates, fruit coverings and seeds were collected in fruit traps placed under the crowns of the same trees. In South Africa, five 1 m^2 traps were placed at random positions under each tree. Traps were installed in February before fruit production had started and were removed in July after it ceased. They were monitored three times a week. In Madagascar, large nets which covered the entire crown area were installed under the trees. Nets were open for four to five weeks from the middle of February until the end of March. They were installed after the first fruit coverings had dropped off the trees and were removed when there was still some fruit available. Nets were inspected four times daily. In both South Africa and Madagascar, the number of coverings and seeds were counted at each inspection. In addition to the seed dispersal data from tree observations, another estimate of the total percentage of seeds dispersed away from the crown could be obtained – as each fruit has two coverings and one seed – by calculating the difference between the number of seeds expected (half the number of coverings) and the number of seeds found in the nets. We observed neither rodents nor ants removing seeds from the traps.

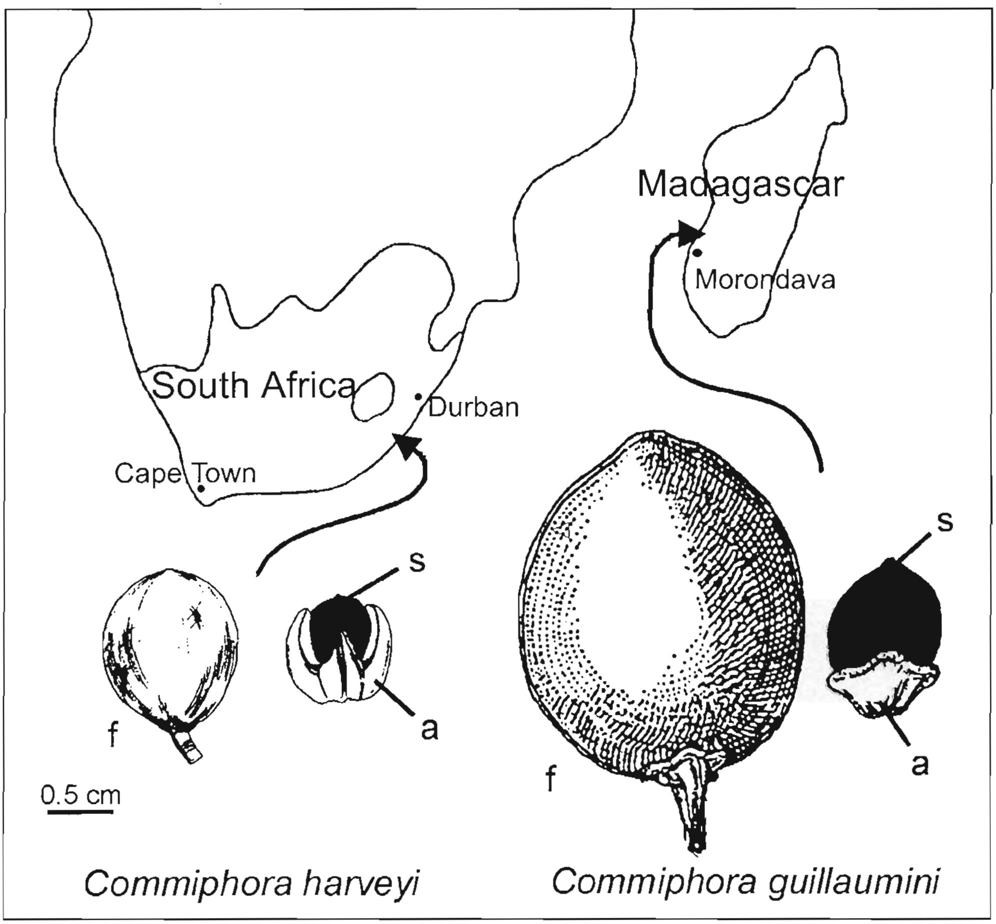

FIG. 1: Map of study sites (arrows) with respective fruits of the South African (*Commiphora harveyi*) and the Malagasy species (*C. guillaumini*). (f) whole fruit with outer coverings, (s) seed, (a) aril (redrawn after de la Bathie 1946 & van der Walt 1973).

RESULTS

The number of frugivorous bird species recorded for the study sites in South Africa and Madagascar reflects the general pattern of avian frugivore diversity in the two countries. In Oribi Gorge, 6.2% (14 out of 226) of all recorded bird species are mainly, and 22.6% (51 out of 226) partly frugivorous. In the Kirindy Forest/CFPF, 3.5% (4 out of 114) of all observed bird species feed mainly, and 8.8% (10 out of 114) partly on fruits.

In both countries, trees were visited primarily by birds. Birds constituted an average of 97.7% of all visitors in South Africa and 98.3% in Madagascar. We counted 25 ± 7 (if not otherwise noted mean ± 1 SE) visitors per tree per day to *C. harveyi* (range: 2.5–54.5, n = 8 trees), and 11 ± 4 to *C. guillaumini* (range: 4.0–25.5, n = 6; t-test: t = 1.5, df = 12, $P = 0.16$) (Fig. 2a), and the former was visited by more bird species than the latter. In South Africa, we recorded 13 bird and one primate species, with Crowned Hornbill (for scientific names see Table 1) being the most frequent visitor (Fig. 3a). Bird species ranged from 12 to 54 cm in body length. In Madagascar, we counted four bird and one primate species, with the Lesser Vasa Parrot being the most frequent visitor (Fig. 3a). Body length of bird species in Madagascar ranged from 10 to 54 cm. Most of the bird species are classified as mainly or partly frugivorous (Table 1). However, three of the bird species in South Africa and two in Madagascar are usually insectivores. We did not observe any nocturnal animals (e.g., fruit bats) feeding on arils.

The mean proportion of seeds per tree handled by visitors was similar in both countries, i.e., 87.1 ± 1.2% in South Africa (range: 80.3–91.1%, n = 8 trees), compared with 89.7 ± 3.3% in Madagascar (range: 74.2–95.9%, n = 6; t-test: t = –0.8, df = 12, $P = 0.43$) (Fig. 2b). However, whereas the total percentage of seeds dispersed away from the parent tree (as obtained from fruit trap data) was high in South Africa, with an average of 66.1 ± 5.2% (range: 43.6–81.4%, n = 8), the situation in Madagascar was completely different (Fig. 2c). Although 89.7% of all seeds were handled (Fig. 2b), only 9.0 ± 2.6% were dispersed (range: –1.0–15.2%, n = 6; t-test: t = 8.8, df = 12, $P < 0.0001$) (Fig. 2c). The negative dispersal rate of –1.0% for one tree indicates that more seeds were "imported" than "exported". However, this number might be an artifact because fruit coverings and seeds did not drop simultaneously, and seed dis-

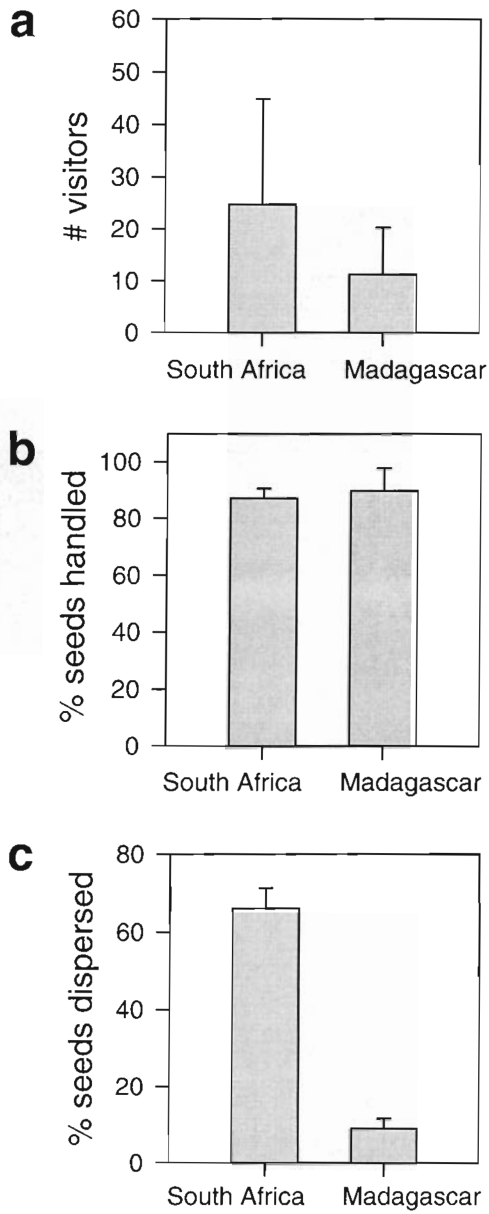

FIG. 2: Comparison of frugivory and seed dispersal in *Commiphora harveyi* (South Africa, n = 8 trees) and *C. guillaumini* (Madagascar, n = 6 trees). a: number of visitors per day and tree (mean ± 1 SE) (data from tree observations). b: total percentage of seeds handled per tree (mean ± 1 SE) (data from tree observations). c: total percentage of seeds per tree dispersed (mean ± 1 SE) (data from fruit traps).

persal rates could not be calculated with absolute precision (Böhning-Gaese *et al.* 1995).

The reasons for the differences in dispersal rates were the different seed handling behavior and dispersal rates of individual animal species (as obtained from tree observation data) in South Africa and Madagascar (Fig. 3b, c, Table 1). In South Africa, a total of ten bird species dispersed seeds by swallowing them and therefore carrying them away from the tree (Table 1). Seed dispersal rates per species, i.e. seed dispersal rates with respect to each species contributing to the dispersal of seeds, were highest for the Crowned Hornbill (43.1%, Fig. 3c). The three most important dispersers, the Crowned Hornbill, Redbilled Woodhoopoe and Redfronted Tinker Barbet, dispersed 75% of all seeds, the other species dispersed less than 10% of the seeds each. Two species in South Africa, the Forest Weaver and Southern Black Tit, removed the aril and dropped the seed under the crown, therefore not contributing to dispersal (Table 1). The Sombre Bulbul and Forest Weaver were occasionally observed dispersing seeds by carrying them away in

Table 1. List of bird and primate species recorded as visitors to *Commiphora harveyi* (South Africa) and *C. guillaumini* (Madagascar) with their respective diet and seed handling behavior. For each country the order of the species reflects decreasing visitation rates (see Fig. 2a). Average body length data of bird species obtained for South Africa from Maclean (1993) and for Madagascar from Langrand (1990). Diet data obtained for the South African species from Lawes (1991) and Maclean (1993), and for the Malagasy species from Harcourt & Thornback (1990) and Langrand (1990). mf = mainly frugivorous, pf = partly frugivorous, i = insectivorous, a = swallows and disperses seed, b = disperses seed in bill, c = removes aril and drops seed under crown, d = not able to open fruit.

Tree visitor	Scientific name	Body length (cm)	Diet	Handling	Abbr.
South Africa					
Birds:					
Crowned Hornbill	*Tockus alboterminatus*	52	mf	a	ch
Redbilled Woodhoopoe	*Phoeniculus purpureus*	33	i	a	rw
Blackbellied Starling	*Lamprotornis corruscus*	20.5	mf	a	st
Forest Weaver	*Ploceus bicolor*	17.5	pf	c, b	fw
Cape White-eye	*Zosterops pallidus*	11.5	pf	d	we
Blackheaded Oriole	*Oriolus larvatus*	24.5	pf	a	or
Sombre Bulbul	*Andropadus importunus*	21	pf	a, b	sb
Blackeyed Bulbul	*Pycnonotus barbatus*	21	mf	a	bu
Redfronted Tinker Barbet	*Pogoniulus pusillus*	12	mf	a	rt
Southern Black Tit	*Parus niger*	15.5	i	c	ti
Blackcollared Barbet	*Lybius torquatus*	19.5	mf	a	ba
Forktailed Drongo	*Dicrurus adimilis*	23.8	i	a	fd
Goldenrumped Tinker Barbet	*Pogoniulus bilineatus*	12	mf	a	gt
Primates:					
Samango Monkey	*Cercopithecus mitis*		mf	a	sm
Madagascar					
Birds:					
Lesser Vasa Parrot	*Coracopsis nigra*	35	mf	c, b	lv
Common Jery	*Neomixis tenella*	10	i	c	cj
Greater Vasa Parrot	*Coracopsis vasa*	50	mf	c	gv
Whiteheaded Vanga	*Leptopterus viridis*	20	i	c	wv
Primates:					
Sifaka	*Propithecus verreauxi*		mf	c	si

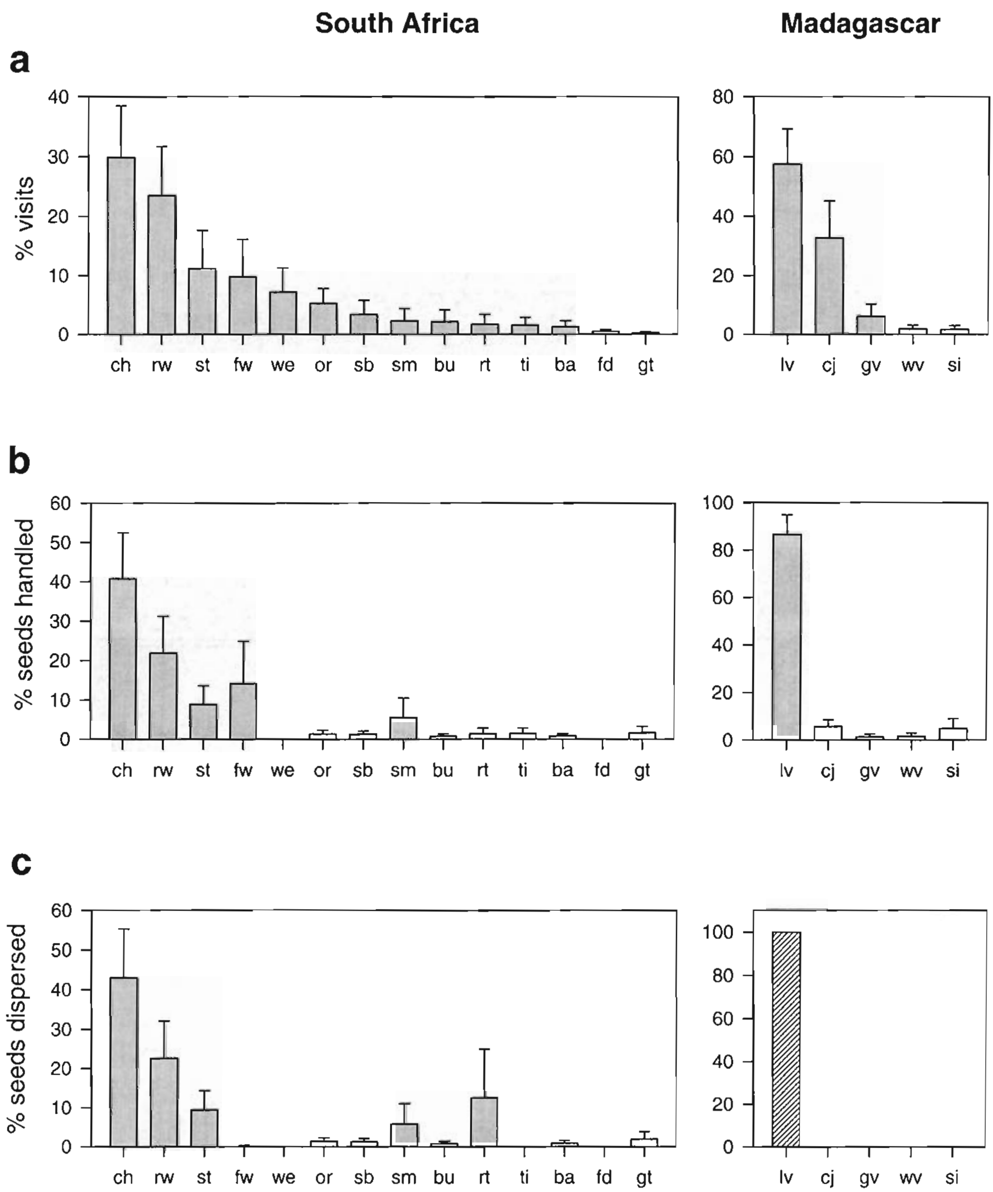

FIG. 3: Importance of different animal species in visiting trees, handling seeds, and dispersing seeds in *Commiphora harveyi* (South Africa, n = 8 trees) and *C. guillaumini* (Madagascar, n = 6 trees) (all data from tree observations). a: visitation rate by species per tree (mean ± 1 SE); b: seed handling rate by species per tree (mean ± 1 SE); c: seed dispersal rate by species per tree (mean ± 1 SE), e.g. Crowned Hornbills were responsible for 43% of all seeds dispersed. Gray bars: seeds dispersed by swallowing, shaded bars: seeds dispersed in the bill. In South Africa, Forest Weavers (fw) always, and Sombre Bulbuls (sb) in 16.7% of all dispersal events, dispersed seeds in the bill. Data are not normally distributed, however, as most medians show a value of zero, mean and standard error is used. For abbreviations of species names see Table 1.

their bills, but this did not represent their main handling method (Table 1). The Cape White-eye visited the trees but did not manage to open the fruits (Table 1).

All species recorded in the Malagasy trees stripped the arils off the seeds and usually dropped the seeds under the crown (Table 1). Seed dispersal took only place when Lesser Vasa Parrots took off from a tree with a seed still in their bills (on 47% of their visits). Therefore, seed dispersal rates were highest for the Lesser Vasa Parrot (100%, Fig. 3c), the only species observed dispersing seeds.

Average number of fruits produced per tree was larger in *C. harveyi* than in *C. guillaumini* (*C. harveyi*: median 3774 fruits per tree, range 1200–15231, n = 8 trees; *C. guillaumini*: median 678, range 345–4591, n = 6 trees; Wilcoxon test: z = -2.52, P = 0.0118). We tested whether fruit production had an influence on the number of visitors and the total percentage of seeds handled and dispersed. This was not the case, neither for South Africa nor for Madagascar ($P > 0.6$). Furthermore, fruit production did not affect the number of species visiting the trees, handling seeds and dispersing seeds ($P > 0.7$). As these results could be due to small sample size, we tested whether differences in the total percentage of dispersed seeds were influenced by fruit production and country (Fig. 4). Only country contributed significantly to the differences in the percentage of dispersed seeds (ANCOVA: $F_{2,11} = 43.91$, $P < 0.0001$, $R^2 = 88.9$, country: $F_{1,11} = 39.40$, $P < 0.0001$, log [fruit production]: $F_{1,11} = 2.28$, $P = 0.16$).

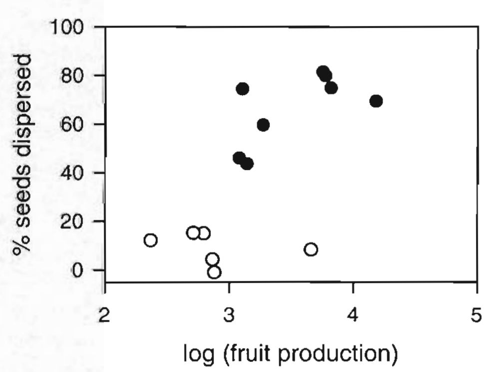

FIG. 4: Total percentage of seeds dispersed (as obtained from fruit trap data) as a function of (log) fruit production in *Commiphora harveyi* (South Africa, n = 8 trees, filled cicles) and *Commiphora guillaumini* (Madagascar, n = 6 trees, open circles).

DISCUSSION

The comparison of frugivory and seed dispersal by birds in South Africa and Madagascar demonstrated that regional differences in frugivore diversity, and especially in seed handling behavior significantly affected seed dispersal. As might be expected from the higher diversity of frugivorous birds in South Africa, the South African species *C. harveyi* was visited by 13, the Malagasy species *C. guillaumini* by only four bird species. Furthermore, 10 of the South African but none of the Malagasy species dispersed seeds by swallowing them. Consequently, seed dispersal rates in Madagascar were 7.4 times lower than in South Africa. The low dispersal rates of the Malagasy species were caused by a local lack of "legitimate" dispersers that swallow seeds and disperse them effectively away from the parent tree. Thus, the combination of frugivore diversity, which provides the plant with a certain variety of possible dispersers, and efficient handling is crucial for seed dispersal.

One might argue that only the effectiveness of seed removal but not of seed dispersal can be addressed in the present study as the fate of the removed seeds is not known. Several factors influence seed dispersal effectiveness after removal of seeds from the parent tree. One factor is that seeds being swallowed have to survive the passage through frugivore guts. In *C. harveyi*, the main disperser was the Crowned Hornbill. In general, hornbills are known to provide high-quality dispersal for many trees in African and Asian forests (see Kemp 1995). Their effectiveness as seed dispersers comes from the fact that they move seeds away from the parent trees and that most seeds are not damaged during ingestion (Leighton & Leighton 1983, Becker & Wong 1985, Gautier-Hion *et al.* 1985, Whitney *et al.* 1998). In the Malagasy *Commiphora* species, the Lesser Vasa Parrot as main disperser did not swallow seeds but dropped them to the ground after aril removal. Seeds were not damaged despite the fact that, in general, parrots are known rather to be seed predators than seed dispersers (Higgins 1979, Coates-Estrada *et al.* 1993). Therefore, in both countries the main disperser of *Commiphora* seeds very probably did not have a negative impact on the fate of the seeds following their removal from the parent tree.

What are possible alternative explanations, besides frugivore diversity, for the differences in tree visitation and seed dispersal rates between South Africa and Madagascar? Important variables influencing the composition of avian frugivore assemblages at fruiting plants are, e.g., fruit structure, size and abundance (Pratt & Stiles 1985). Fruit structure is very similar in both species, although there are differences in diaspore size. Smaller diaspores attract more species of birds, and have a higher probability of being dispersed away from the crown because they can be swallowed by birds with a smaller gape width (Wheelwright 1985, 1993; Jordano 1987a, b; Levey 1987). Diaspore size in *Commiphora* is mainly determined by seed size because the aril covers only part of the seed. The South African species has smaller seeds than the Malagasy species (average maximum diameter South African species: 5.7 mm, Malagasy species: 8.0 mm, Fig. 1). However, these differences in seed size are relatively small, and seeds of both species range in the lower end of the fruit size distribution for frugivores as recorded by, e.g., Wheelwright (1985: Fig. 1) or Pratt & Stiles (1985). Furthermore, observations made at the same study site in a second study year during the same season demonstrated that the somewhat larger seeds of the Malagasy *Commiphora* species were readily swallowed by the Madagascar Bulbul *Hypsipetes madagascariensis* and Crested Drongo *Dicrurus forficatus* (Böhning-Gaese *et al.* 1999). However, as these species are uncommon at the study site and dispersal events by them extremely rare, they are rather unimportant seed dispersers.

Another factor influencing dispersal rates might be differences between the two tree species in South Africa and Madagascar in the mean number of fruits produced. However, for both species the results show that this was not the case and that the total percentage of dispersed seeds, as well as the number of species visiting trees, handling seeds and dispersing seeds, did not depend on fruit production. These results are consistent with other studies that often reported little or no influence by the number of fruits produced on the percentage of dispersed seeds (Howe & Smallwood 1982, Jordano 1987a, Laska & Stiles 1994). Thus, fruit characteristics like structure, size, and abundance do not appear to be the reason for the profound differences in seed dispersal rates found between the South African and Malagasy *Commiphora* species. However, as we studied only one species in each country, these results apply only to the specific study site and tree species. To be able to make generalizations, further studies on other species have to be carried out.

Seed dispersal rates of 66% as found for *Commiphora harveyi* are comparable with other tropical tree species with similar phenology and fruit morphology. For example, seed dispersal rates were 91% for *Casearia corymbosa* in Costa Rica (Howe & Vande Kerckhove 1979), 76% for *Virola sebifera* in Panama (Howe 1981), 66% for *Virola surinamensis* in Panama (Howe & Vande Kerckhove 1981), 45% for *Cymbopetalum baillonii* in Mexico (Coates-Estrada & Estrada 1988), and 70–97% for *Bursera simaruba* in Mexico (Greenberg *et al.* 1995). Seeds of the South African *Commiphora* species were dispersed by ten bird species, *Casearia corymbosa* by 12 (Howe & Vande Kerckhove 1979), *Virola sebifera* by six (Howe 1981), *Virola surinamensis* by seven (Howe & Vande Kerckhove 1981), *Cymbopetalum baillonii* by 20 (Coates-Estrada & Estrada 1988), and *Bursera simaruba* by ten bird species (Greenberg *et al.* 1995). By comparison, seed dispersal rates of 9.0% recorded for the Malagasy *C. guillaumini* are extremely low, and its seeds were dispersed only by one bird species (see *Casearia corymbosa*, Howe 1977).

To our knowledge the only other published studies of frugivores visiting fruiting trees on Madagascar are those by Scharfe & Schlund (1996), Goodman *et al.* (1997) and Dew & Wright (1998). All three studies show that lemurs play a prominent role in seed dispersal in Madagascar. Fruits of a *Ficus* species were eaten by four bird and four lemur species (Goodman *et al.* 1997), fruits of *Poupartia sylvatica* by two bird and four lemur species and fruits of *Berchemia discolor* by six lemur species (Scharfe & Schlund 1996). The island is, in general, depauperate in frugivorous birds in comparison with other tropical areas (Langrand 1990, Goodman & Ganzhorn 1997, Goodman *et al.* 1997). This does not appear to result from the extinction of frugivorous bird species either in historical or in paleontological time (Langrand 1990, Goodman & Rakotozafy 1997). However, it can be linked to a lower general fruit availability and a reduced diversity and density of *Ficus* species, which is often an important keystone group for numerous tropical frugivores (Goodman & Ganzhorn 1997).

To conclude, our studies in South Africa and Madagascar demonstrated that low diversity of fruit-eating and seed-dispersing animal species can have profound consequences for seed dispersal. The low number of frugivorous bird species in Madagascar, and particularly the local absence of birds that swallow seeds, led to extremely low rates of seed dispersal. Other studies also confirm that a reduced frugivore community, e.g., through forest fragmentation, can lead to a reduced number of dispersers (Howe 1984a, Pizo 1997). Furthermore, low rates of seed dispersal can result in low rates of seedling establishment. Seeds of the Malagasy *Commiphora* species that were dropped under the crown had a 36 times lower probability of getting established as seedlings than seeds dispersed away from the crown (Böhning-Gaese *et al.* 1999). It remains to be seen if low rates of seedling establishment have consequences for the abundance and probability of extinction of a tree (Bond 1995). However, there is some evidence to indicate that dispersal-generated patterns of seedling establishment can have an influence on the spatial distribution of adult trees (Janzen 1970, Connell 1971, Hubbell 1979).

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