

VARIATION OF DISPERSAL AGENTS? FRUGIVORE ASSEMBLAGES AND FRUIT HANDLING IN A TYPICAL 'BIRD-DISPERSED' TREE (*LANNEA ACIDA*, ANACARDIACEAE)

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Abstract. Particular combinations of traits related to the consumption of fruits and dispersal of seeds by specific groups of frugivores have led to the postulation of 'dispersal syndromes'. *Lannea acida* (Anacardiaceae) is a West African tree with small purple drupes characteristic of the bird-dispersal syndrome. Given fruit type and size, however, the fruits should be attractive to a wider range of arboreal frugivores. To test this, we monitored frugivore assemblages, feeding activity during crop maturation, and fruit handling by frugivores. Fruits were harvested by 22 bird and five mammal species. Birds were the most common frugivores in the canopy of *L. acida* but fed predominantly on unripe, green fruit, and therefore probably acted as seed predators. Primates tended to visit trees after the onset of fruit maturation. Nearly all seeds found in feces of olive baboons (*Papio anubis*) were undamaged and had a significantly higher germination success compared with undispersed seeds from fresh ripe fruits. Non-granivorous birds that otherwise may be legitimate seed dispersers can become quantitatively important seed predators when consuming unripe fruits, for example during times of fruit scarcity. The role of birds in pre-dispersal seed predation for plant fitness requires further investigation. On the other hand, primates are often considered crucial dispersers for large-seeded tree species, but their importance for plants with small fruit should not be understated. Accepted 22 September 2008.

Key words: birds, dispersal syndrome, frugivore assemblage, fruit traits, pre-dispersal seed predation, primates, seed dispersal, unripe fruits, West Africa.

INTRODUCTION

Plant-frugivore interactions can be influenced by, among other factors, different fruit traits (Jordano 2000, Herrera 2002). For example, fruit type (e.g., berry, drupe, nut) and the size of fruits and seeds may constrain fruit handling and seed dispersal by animals. Hence, small fruit and large fruit with small seeds are generally consumed and dispersed by a greater number of frugivores than large fruit with large seeds (reviewed in Jordano 2000).

Frugivores may also differ in their effectiveness as seed dispersers (reviewed in Schupp 1993). One prerequisite for high-quality dispersal is that a frugivore should neither consume fruits before seed maturity nor destroy the seeds during fruit handling. Most fruits undergo dramatic biochemical changes during maturation, making ripe fruit more attractive to frugivores than unripe fruit (Steenfurt 1988, Schaefer *et al.* 2003). Fruit maturity can be indicated through

fruit color (Schaefer *et al.* 2004). 'Green' often signals unripeness and unpalatability (Herrera 2002, but see Knight & Siegfried 1983). Many frugivorous birds seem to avoid green and unripe fruit (Knight & Siegfried 1983, Sanders *et al.* 1997, Schaefer & Schaefer 2006). In fruit choice experiments, birds generally preferred ripe over unripe, and brightly colored (red, orange, and black) as well as UV-reflecting fruit over white and dull (green and yellow) fruit (McPherson 1988, Sanders *et al.* 1997, Honkavaara *et al.* 2004). Red and black are globally the most common fruit colors of bird-dispersed plant species (Willson & Whelan 1990, Herrera 2002). Red and black exhibit stronger contrasts against foliage than other colors, making fruit more conspicuous for avian frugivores (Giles & Lill 1999, Schmidt *et al.* 2004, but see Honkavaara *et al.* 2004).

Fruit color in combination with other morphological fruit traits has been related to fruit consumption by specific groups of dispersers, and has led to the postulation of 'dispersal syndromes' (van der Pijl 1982, Charles-Dominique 1993). Fruits typically

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dispersed by birds are small, brightly colored drupes or berries (Knight & Siegfried 1983, Balasubramanian 1996, Herrera 2002). Fruits associated with seed dispersal by mammals tend to be larger and dull colored (brown, yellow, or green) (Knight & Siegfried 1983, Herrera 2002, but see Gautier-Hion *et al.* 1985).

Lannea acida A. Rich. (Anacardiaceae) is a tree of up to 14 meters in height that is relatively common in West African savannas and along forest edges. Female trees produce small (~ 10 mm long), single-seeded, ellipsoid drupes which appear green to the human eye when unripe and dark purple when ripe. Several dozens are clustered in infructescences. Fruiting starts at the end of the dry season/beginning of the wet season and lasts one to two months (von Maydell 1990, Arbonnier 2000, Kunz pers. observ.). Trees are completely leafless during most of the fruiting period, providing excellent observation conditions.

According to the dispersal-syndrome hypothesis, we expected birds to play the major role as seed dispersers for the tree by regularly feeding on ripe crops. Given the fruit type and size, however, *L. acida* fruits should also be attractive to a wide range of arboreal frugivores. The aim of our study was thus twofold: to survey the frugivore assemblage of *L. acida* and to identify effective seed dispersers for the tree. Specifically, we were interested in the qualitative component of seed dispersal: the timing of frugivore feeding visits in relation to crop maturity and their treatment of fruits and seeds.

STUDY SITE

The study took place in the Comoé National Park (CNP) (8°30'–9°36'N, 3°07'–4°25'W), north-eastern Ivory Coast. The park covers approximately 11 500 km² at an altitude of about 250–300 m above sea level. The southern park area is situated within the 'Guinea-Congolia/Sudania regional transition zone', whereas the northern part belongs to the 'Sudanian regional centre of endemism' (White 1983). We collected data in the south-western section of CNP where the vegetation consists of a mosaic of different savanna formations (approximately 91 %), forest islands (7 %), and gallery forest (2 %) along the two main rivers (FGU-Kronberg 1979). Savanna and gallery forest are separated by a band of grass vegetation with only few woody species, henceforth referred to as 'plain'. The vegetation is described in detail

elsewhere (Poilecot 1991, Porembski 1991, 2001; Hovestadt *et al.* 1999). The climate in the study area is characterized by a dry season from November to March/April. Mean annual precipitation from January 1994 to December 1999 was 1053 mm, and mean annual temperature was 26.3°C.

The CNP harbors a rich flora and fauna. So far, 498 bird species (Salewski 2000, Salewski & Göken 2001, Rheindt *et al.* 2002) and 152 mammal species have been recorded (Poilecot 1991, Mess & Krell 1999, Fischer *et al.* 2002), including recent observations of nine diurnal non-human primate species (Fischer *et al.* 2000). Seventy percent of the 292 woody plant species produce fleshy fruit for consumption by animals (Hovestadt 1997).

METHODS

The study had two parts. To identify the seed disperser assemblage of *L. acida*, we first recorded frugivores feeding in different trees (10 trees in 1991 to 1993, and four in 1998 to 1999). We then observed two focal trees in 1999 and 2000 in more detail to obtain data on fruit and seed handling by frugivores and the frugivores' timing of feeding visits to *L. acida* trees in relation to crop maturity.

Vertebrate fruit consumers in L. acida trees. To determine frugivore assemblage feeding in *L. acida*, we randomly selected and consecutively observed trees bearing ripe fruits (as judged from the dark fruit color) in 1991 to 1993. We observed each tree for one to two days between 06:00 h and 10:00 h. During this time of day bird feeding activity is highest and primates in the study area are also foraging. Observation distance was 20–100 m from a focal tree. Where natural coverage was sparse, we hid behind artificial blinds of dark-green fabric. All vertebrates feeding on fruit were noted. Trees were discarded from the study when no frugivores were recorded during the first morning, presuming that fruits were not yet attractive. Total observation time of the 10 remaining trees was 17.5 hours (60–150 minutes per tree). Because the Shinozaki curve (Fig. 1), calculated using BIODIV (Messner 1996), showed no saturation in the number of bird species recorded as a function of the number of trees observed, we continued sampling frugivores in 1998 to 1999, adding four other trees, including our two focal trees, for 7.25 hours of observations.

Species feeding in the two *L. acida* focal trees that we monitored for details on fruit handling (see be-

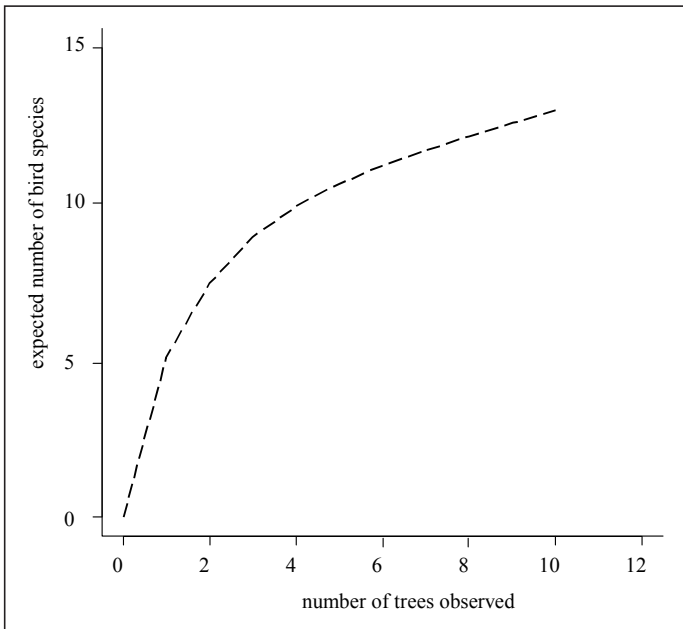


FIG 1. Shinozaki curve showing the total number of bird species recorded as a function of the number of *L. acida* trees observed in 1991–1993.

low) are also included in the species list. Identification of bird and mammal species was verified using Mackworth-Praed & Grant (1970–1973), Serle & Morel (1977), Brown *et al.* (1982–1992). Bird names follow Borrow & Demey (2001).

Fruit handling. In 1999 and 2000, we concentrated observations on two fruiting focal trees (Laac1, Laac2) to determine the timing of the feeding visits relative to crop maturation, and to record fruit treatment by different frugivores. We selected the focal trees with respect to good visibility of the crown and the fact that they were about equal in height (estimated 13 and 14 m). The trees were situated within 30 m of each other at the forest edge in the vicinity of the former field station of the University of Würzburg, Germany (8°45.056'N, 3°49.029'W). In this area, diurnal non-human primates (white-crowned mangabey *Cercocebus atys lunulatus* Temminck, Lowe's monkey *Cercopithecus campbelli lowei* Thomas, lesser white-nosed monkey *C. petaurista* von Schreber, olive baboon *Papio anubis* Lesson) were habituated to the presence of researchers, and were thus more likely to visit a tree under observation than elsewhere in the park.

At the onset of the study, fruit crops of the two focal trees were unripe (green). Crop maturity was

visually estimated once a week using binoculars. We multiplied the average number of fruits of 16 randomly-chosen infructescences by the mean number of infructescences of four randomly-selected branches of similar size. We then extrapolated this average fruit number per branch to the total number of similar-sized branches of the crown.

A single maturity state of the crop was noted when $\geq 90\%$ of the visible fruits had the same fruit coloration (green = unripe, greenish-purple = ripening, purple to dark purple = ripe). When $>10\%$ of the crop had a different coloration, a second maturity state was listed, with the dominant state being listed first. For example, the overall crop maturity was defined as 'ripening-ripe' when $> 50\%$ to $< 90\%$ of the fruits were ripening (greenish-purple) while $>10\%$ to $< 50\%$ were ripe (purple to dark purple).

Monitoring of a tree terminated when the crop was reduced by $\geq 95\%$ compared to the first visual estimation, or when the remaining fruits were withered and seemed no longer attractive to frugivores. Consequently, we observed Laac1 from 21 March to 21 April 1999 (63 hours) and from 21 March to 5 April 2000 (53 hours). Monitoring of Laac2 took place from 21 March to 11 April 1999 (45 hours), whereas the tree's crop was depleted soon after study onset in 2000 (six observation hours).

We monitored each tree from a distance of about 20 m using binoculars. Observations were undertaken for three to five hours a day and were about evenly distributed between 06:00 h to 19:00 h. When both focal trees were fruiting and attractive to frugivores, we alternated observations between the two focal trees (within a day or over consecutive days).

Lannea spp. fruits were not reported to be eaten by bats at Lamto reserve, Ivory Coast (Thomas 1982), although three *Lannea* species are present in the area (Schmidt 1973), yet *L. microcarpa* fruits are consumed by flying foxes in northern Benin (Djossa *et al.* 2008). We thus checked for the activity of bats and other nocturnal frugivores and observed both focal trees in 1999, and Laac1 again in 2000, during early night hours (between 20:00 h and 23:00 h) at the beginning and peak of fruiting. Night vision gear was used, and four nights of observations totaling five hours in Laac1 and four hours in Laac2 were undertaken.

During daytime and nighttime observations, we scanned the tree every five minutes for one minute and recorded the individual number and identity to species level of all birds and mammals foraging in the crown. Each foraging individual seen in a given scan was assessed as one record. We ascribed fruit handling by birds to either pecking of pulp (peckers/fruit thieves), crushing of fruits and dropping of seeds (mashers/fruit thieves), or swallowing of whole fruits (swallowers) (following Levey 1987). After squirrel feeding events, we checked fresh leftovers on the ground for signs of treatment (tooth marks, gnawed seeds). In primates, we observed whether fruits were swallowed entirely, or seeds were spat out during feeding in the tree.

We calculated the mean number of hourly records of swallower birds, squirrels, and primates per tree and year. Wilcoxon's signed-rank test and Friedman's ANOVA were respectively applied to test for differences in visitation rates within and across groups of frugivores (SPSS version 15.0, confidence limits set at 95%). We used exact tests for small sample sizes (SPSS Exact Extension). The level of significance of *a posteriori* comparisons was adjusted using the sequential Bonferroni technique (Rice 1989).

Fruit availability in the vicinity of the focal trees. In March and April 1999 and 2000, between day 10 and 20 of each month, we checked a 400-m strip for

the presence of other fruiting tree and shrub species in the direct vicinity of the focal trees in each of the following habitats: gallery forest (strip width 10 m), savanna (width 20 m), plain (width 50 m). Strip width followed visibility and tree density. We used binoculars when necessary. In addition, we recorded fruit availability along the forest edge (400 m, width about 2–3 m) where the two focal trees were located. When we recorded fruit species potentially suitable for consumption by birds (species with small fruit, or with larger fruit having soft husk and pulp) we noted whether mature fruits were present at the plant. Food plants were identified from the following sources: Hutchinson *et al.* (1954–1968), von Maydell (1990), Arbonnier (2000), Kasperek (2000), and a seed reference collection established in previous years by T. Hovestadt and P. Poilecot. S. Porembski (University of Rostock, Germany), and E. Robbrecht (National Botanic Garden of Belgium) verified plant material in question. Plant nomenclature follows the African Flowering Plants Database (<<http://www.ville-ge.ch/cjb/bd/africa/index.php>>).

Seed germination. Even though seed traps were installed below the canopy of Laac1 in 1999 and 2000, seeds dropped by birds were not available in adequate quantities for germination experiments and statistical analyses. We thus used seeds from fresh fruits to test for seed germination ability at different stages of maturity. Between the end of March and mid-April 1999 we randomly collected 60 unripe (green) and 60 ripe (dark purple) fresh fruits from each of two *L. acida* trees. Seeds were cleaned from pulp by hand to simulate pulp removal during ingestion and were briefly rinsed with water.

Data on dispersal of *L. acida* seeds by primates were obtained from fecal samples of olive baboons (Kunz & Linsenmair 2008a). During the fruiting period of *L. acida* in 1998 to 2000, we collected baboon feces opportunistically. Each sample was washed through 1-mm sieves and the extracted seeds were visually examined for damage. In 1999, undamaged seeds from baboon feces were stored for up to four days in a dark, dry place at ambient temperature until 120 seeds were obtained for germination experiments.

All seeds were placed on a double layer of filter paper in groups of 10 per petri dish. We exposed half the number of the petri dishes per maturity state, or treatment (undispersed, or dispersed by baboons) to full sunlight and the other half to shade (provided by a reed covering). We watered seeds *ad libitum* and

checked them daily for penetration of the seed coat by the radicle. Germinating seeds were removed.

Experiments with undispersed ripe seeds and seeds from baboon feces were conducted from 9 April to 23 June 1999. Experiments with unripe seeds started two days later and lasted until 25 June 1999.

Differences in germination success were tested using the Chi²-test with Yates correction.

RESULTS

Vertebrate fruit consumers in L. acida trees. Fourteen bird species, the red-legged sun squirrel (*Heliosciurus rufobrachium* Waterhouse) and the olive baboon were observed feeding on fruit of *L. acida* trees in 1991–1993 (Appendix 1). Observations of four additional trees in 1998–1999 yielded two more bird species.

Including frugivores feeding in Laac1 and Laac2 during observations of fruit handling, this totals 22 bird species and five mammal species (Appendix 1). Bird species noted most often were the village weaver (*Ploceus cucullatus*), violet-backed starling (*Cinnyricinclus leucogaster*), common bulbul (*Pycnonotus barbatus*), and the African thrush (*Turdus pelios*). There was no evidence of nocturnal visitors.

Fruit handling. We classified six of the 22 bird species as pulp peckers, while at least 13 species swallowed

entire fruits (Appendix 1). Fruit treatment by three species was not reliably identified. Fruit crushing in the bill (Levey 1987) was not observed, nor did we see birds regurgitating seeds. The four most common bird species visiting the trees (as above) were all fruit swallowers.

The sun squirrel preyed upon seeds by gnawing small holes in the pulp and testa to feed on the cotyledones and embryo. Primates swallowed *L. acida* fruits entirely. Olive baboons and white-crowned mangabeys sometimes also stuffed *L. acida* fruits in their cheek pouches, possibly for later fruit processing, though we never observed intensive seed spitting during or after consumption of *L. acida* fruits.

Altogether, variation in visitation rates per week, year, and tree were high (Table 1, Fig. 2).

Sun squirrels were not recorded in Laac1 in 1999 and were otherwise rarely observed. Primates were recorded irregularly. Mean records per week in Laac1 in 1999 were six times higher than in 2000. Primate species feeding in Laac1 included *C. a. lunulatus* and *P. anubis* in 1999, and *C. a. lunulatus*, *C. c. lowei*, *C. petaurista* in 2000.

Records of primates in Laac2 were rare, and the only primate species observed feeding was *C. a. lunulatus*.

Overall, birds were recorded most often and most regularly (Table 1, Fig. 2). However, bird visits h⁻¹

TABLE 1. Records of frugivores in *L. acida* focal trees in 1999 and 2000.

	Birds				Mammals				
	<i>P. barbatus</i>	<i>T. pelios</i>	<i>C. leucogaster</i>	<i>P. cucullatus</i>	<i>H. rufobrachium</i>	<i>C. a. lunulatus</i>	<i>C. c. lowei</i>	<i>C. petaurista</i>	<i>P. anubis</i>
Laac1									
1999									
n°. of records in focal tree (63 hrs)	43	24	48	80	0	44	0	0	54
mean records h ⁻¹	0.89	0.37	0.72	1.73		0.76			0.70
± sd	± 1.45	± 0.59	± 1.24	± 4.24	0	± 1.62	0	0	± 1.40
2000									
n°. of records in focal tree (53 hrs)	193	62	47	41	10	7	5	2	0
mean records h ⁻¹	3.70	1.20	0.90	0.80	0.18	0.12	0.09	0.03	
± sd	± 1.90	± 1.10	± 0.90	± 0.90	± 0.32	± 0.21	± 0.23	± 0.09	0
mean records h ⁻¹ (1999 & 2000)	2.30	0.79	0.81	1.27	0.09	0.44	0.05	0.02	0.35
Laac2									
1999									
n°. of records in focal tree (45 hrs)	4	10	4	54	6	1	0	0	0
mean records h ⁻¹	0.06	0.15	0.06	1.75	0.12	0.01			
± sd	± 0.17	± 0.34	± 0.17	± 3.23	± 0.31	± 0.04	0	0	0

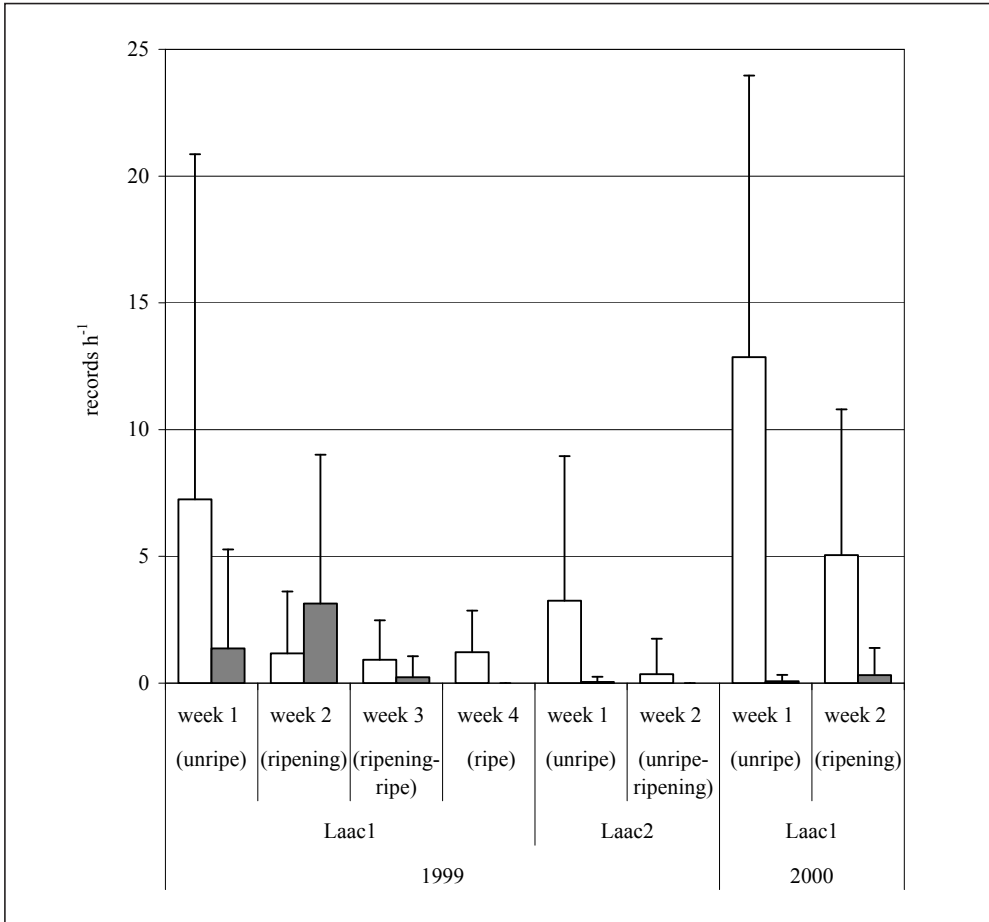


FIG. 2. Mean hourly records of birds and primates in the *L. acida* focal trees Laac1 and Laac2 during fruiting periods in 1999 and 2000. Birds are represented by white columns, primates by grey ones. Crop maturity (unripe, ripening, ripe) is given for each observation week. Laac1 was observed from 21 March to 21 April 1999 and 21 March to 5 April 2000. In 2000, fruits dried before full maturation and no birds and mammals were recorded after week 2. Observations of Laac2 took place from 21 March to 11 April 1999. No visitors were recorded after week 2. In 2000 (not displayed), the tree was depleted shortly after study onset.

were only significantly higher than that of primates and sunsquirrels in Laac1 and in 2000 (Friedman's ANOVA $\chi^2 = 68.21$, $df = 2$, $p < 0.001$, $n = 36$ hours in which at least one individual in one taxon was recorded, *a posteriori*: $Z_{\text{birds-squirrels}} = -5.2354$, $p = 0.001$; $Z_{\text{birds-primates}} = -5.2368$; $p = 0.001$; p -values in both cases were obtained after applying sequential Bonferroni technique). Visitation rates of primates and sun squirrels to Laac2 were too low for statistical analyses.

Birds were recorded visiting trees for feeding significantly more often when crops were unripe than when crops were ripening/ripe (Fig. 2, Table 2). In Laac1 in 1999, the number of primate feeding records increased in week two with the onset of maturation, though the difference in the mean number of hourly records was not significant between the two time periods ($Z = -0.507$, $p > 0.05$). However, while white-crowned mangabeys were recorded only in week 1 (unripe crop, three times observed) and on

the first day of week 2, olive baboons were first observed in week 2 (crop ripening) and revisited the tree until the end of week 3 (six times observed).

Fruit availability. Most woody plant species recorded fruiting in the gallery forest, savanna, and plain around the two focal trees in March and April 1999 and 2000 had fruit not characteristic of the 'bird syndrome' (gallery forest: *Cynometra megalophylla*, *Dialium guineense* Fabaceae; savanna / plain: *Anogeisus leiocarpa*, *Combretum* sp. Combretaceae, *Parkia biglobosa*, *Piliostigma thonningii*, *Tamarindus indica* Fabaceae, *Khaya senegalensis*, *Pseudocedrela kotschy* Meliaceae, *Securidaca longipedunculata* Polygalaceae, *Crossopteryx febrifuga*, *Mitragyna inermis* Rubiaceae, *Afraegle paniculata* Rutaceae).

Yet two fig trees (*Ficus* spp. Moraceae) in the savanna had unripe or withered fruit in March and April, and in the gallery forest the climber *Canthium* sp. had unripe fruits in April. Only the bird-dispersed climber species *Arbus precatorius* (Fabaceae), in which seeds mimic fruits and are displayed in a dry dehiscent pod, had ripe fruits. Along the forest edge, one additional small *L. acida* tree and five (1999) to four (2000) *L. welwitschii* trees were fruiting. Mature *L. welwitschii* fruits, however, were not available until April.

Seed germination. Four (2.9 %) of the 139 olive baboon feces collected during the fruiting periods of *L. acida* in 1998 to 2000 contained *L. acida* seeds (range 4–185). Most *L. acida* seeds were undamaged to the human eye ($n = 244$), or only had shallow scratches on the testa ($n = 2$). No seed pieces indicating baboons chewed on *L. acida* seeds turned up in fecal samples.

All seeds exposed to full sunlight failed to germinate, irrespective of maturity state, or treatment (fresh unripe $n = 60$, fresh ripe $n = 60$, or ingested by baboons $n = 60$). Unripe seeds from fresh fruits did not germinate in the shade ($n = 60$). Germination rate of ripe *L. acida* seeds from baboon feces in the shade (83.3 %, $n = 60$) was significantly increased compared with seeds extracted from fresh ripe fruits (3.3 %, $n = 60$) under the same light conditions ($\chi^2 = 78.190$, $df = 1$, $p < 0.001$). Germination of ripe seeds in the shade was rapid (range 4–22 days).

DISCUSSION

The small drupes of *L. acida* provided food for a high number of bird (at least 22) and mammal (a mini-

mum of five) species in the Comoé National Park (CNP). Elephants and chimpanzees, which are also known to consume *L. acida* fruits (McGrew *et al.* 1988, Hovestadt 1997), were not recorded in our study although they were present in the park at the time. The number of potential *L. acida*-seed-dispersing species in CNP, as well as the overall number of frugivorous species observed in the tree, is comparable to other studies in Africa. For example, in forest fragments in Kenya 21 frugivorous bird species were recorded in 11 tree species the fruits of which were characteristic of the bird-dispersal syndrome (Githiru *et al.* 2002). In Tanzania, 11 bird species were observed removing seeds of *Leptonychia usambarensis* (Sterculiaceae) (Cordeiro & Howe 2003). In South Africa, the maximum number of frugivorous species in a single fig species was 13 (Bleher *et al.* 2003). However, higher numbers of frugivorous bird species in a single tree species were also observed (36 species in *Prunus africana* (Rosaceae), Farwig *et al.* 2006).

As hypothesized, birds were the most common vertebrate group consuming *L. acida* fruits in CNP. Birds ranged in size from small tinkerbirds (Capitonidae), of about 10 cm, to large hornbills (Bucerotidae) (80 cm bill tip to tail tip), and included species that are generally considered as insectivorous, as well as some granivorous (-insectivorous) species. Most birds swallowed the fruits entirely, and thus can potentially act as seed dispersers for the tree. However, only four fruit-swallowing bird species regularly visited the focal trees (*P. barbatus*, *T. pelios*, *C. leucogaster*, *P. cucullatus*). Among them, *P. barbatus*, *T. pelios* and starlings (*C. leucogaster*, *Lamprolornis* spp.) are major seed disperser for many woody plant species in CNP (Hovestadt 1997). Bulbuls, in general, play an important role in seed dispersal in many tropical regions of the world (Lieberman & Lieberman 1986, Barnea *et al.* 1990, Kitamura *et al.* 2002, Cordeiro & Howe 2003, Weir & Corlett 2006).

In the present study, however, birds visited the two focal trees predominantly during the first week of the study when crops were still unripe. When fruit crops were not depleted before full maturity (Laa1 in 1999), *P. barbatus* was the only bird observed feeding after week 2, when ripe fruits were available (except one record of *T. pelios* and *P. cucullatus*, each during this time). *P. barbatus* is the bird with the smallest gape width among the four most often recorded swallower species (measurements of 3–4 specimens per species in the Natural History Museum Berlin; M. Abs, pers. comm.), making it thus

unlikely that birds are constrained by the larger size of ripe *L. acida* fruits (mean width of 120 unripe fruits = 8.1 ± 0.6 mm and 8.5 ± 0.6 mm in 20 ripe fruits, B. Kunz unpubl. data).

Ripe *L. acida* fruits are dark purple, a color strongly preferred by many birds (Willson & Whelan 1990, Herrera 2002, Schmidt *et al.* 2004), whereas unripe, green fruits are often avoided (Knight & Siegfried 1983, Sanders *et al.* 1997, Schaefer & Schaefer 2006). In *L. acida*, however, fruit color does not seem to be crucial for fruit choice by birds. Other factors, such as time of fruiting, fruit abundance, and overall fruit supply (Foster 1990, Hasui & Hofling 1998, Giles & Lill 1999, Izhaki 2002, Schaefer & Schaefer 2006) may also affect fruit choice in birds. Feeding on unripe fruit can be a way of dealing with seasonal food scarcity (Foster 1977, Schaefer & Schaefer 2006). Our data suggest that ripe fleshy fruit suitable for consumption by birds like bulbuls and thrushes might be locally scarce in March and April in CNP, as apparently was the case in the vicinity of the focal trees. Monthly phenology data from savanna and forest transects in a wider area in the southern part of the CNP support this assumption (Kunz, unpubl. data). *L. acida* trees, on the other hand, are relatively common in CNP (one adult individual ha^{-1} , Hovestadt 1997). In 2000 we had difficulties finding *L. acida* trees with ripe fruits for fruit size measurements, and empty infructescences indicated that crops of *L. acida* trees other than the focal ones were also heavily used while unripe (B. Kunz, unpubl. data).

In some plant species, seeds from apparently unripe fruit may be able to germinate without any treatment (e.g., Broschat & Donselman 1987), but unripe *L. acida* seeds failed to germinate.

We thus presume that birds mainly acted as seed predators for the two focal trees during the study period, given the early stage of fruit production at which birds consumed the fruits. However, ingestion by birds can have variable effects on seed germination of ripe seeds (Lieberman & Lieberman 1986, Barnea *et al.* 1990). We were unable to find data on the effects of gut passage by birds upon germination ability of unripe seeds. Further studies are required in which different bird species are exposed to unripe and ripe *L. acida* fruits under controlled conditions, and in which seeds ingested by birds are tested for viability.

Lannea fruits seem to be included in the diets of African primates where available (Lieberman *et al.*

1979, Norton *et al.* 1987, Kasperek 2000, Poulsen *et al.* 2001, Warren 2003). Given the short fruiting period, *Lannea* fruits make up an important part of baboon diet in CNP relative to other fruit species, accounting for 3% of baboon feeding observations across a 24-month study period (see Kunz & Linsenmair 2008b). In contrast to most birds, primates were recorded infrequently in *L. acida* trees. However, whenever a group of primates visits a tree it consumes a comparatively large quantity of fruits. A baboon group of mean size in CNP (15 individuals, Kunz & Linsenmair 2008b), eats 5200 *L. acida* fruits on average per feeding visit, representing 9% of all fruits removed from an average crop (Kunz, unpubl. data). Because we have no evidence that baboons chewed *L. acida* seeds (i.e., no seed fragments turned up in fecal samples) we suppose that baboons disperse the vast majority of *L. acida* seeds they consume. The fact that we found only a relatively small number of *L. acida* seeds in baboon fecal samples, despite the high estimated number of seeds consumed per group per visit to a fruiting tree, might be the consequence of the infrequent and irregular feeding visits to *L. acida* trees, different amounts of fruit consumed by different baboon individuals on different days and, naturally, incomplete sampling of all the feces deposited by the baboons, rather than indicating generally low dispersal rates by baboons.

Feeding visits by baboons to fruiting *L. acida* individuals are not frequent enough to deplete entire tree crops. Thus it seems unlikely that feeding competition with primates is leading to changes in bird fruit-choice. Further, primates, i.e. baboons, seem to visit trees more often after the onset of maturation. Germination success of *L. acida* seeds dispersed by olive baboons was high and enhanced in comparison with seeds from fresh ripe fruits. This could, however, be an artifact of differences in fruit choice between primates and researchers. Many frugivorous primates do not take fruits at random (Howe & van de Kerckhove 1981, Garber & Kitron 1997, Stevenson *et al.* 2005, Kunz & Linsenmair 2007). If baboons predominantly consume fruits that are at the very peak of (seed) maturation, germination success of ingested seeds should be higher than those of seeds from randomly selected ripe fruits.

Most species of Anacardiaceae have drupaceous fruit and are mainly distributed within the tropics and subtropics (Hutchinson *et al.* 1954-1968). In accordance with the concept of the 'dispersal syndrome' (Charles-Dominique 1993, Herrera 2002),

smaller fruited-species of the Anacardiaceae with red-colored drupes seem to be commonly dispersed by birds, e.g. *Pistacia* spp. (Jordano 1989, Izhaki *et al.* 1991, Traveset 1994), *Rhus trichocarpa* (Nishi & Tsuyuzaki 2004, Osada 2005), or *Schinus terebinthifolius* (Hasui & Hofling 1998), though consumption of these fruits by mammals is not excluded. Larger fruits of this family seem to be frequently consumed by mammals, including elephants, primates, and bats, e.g. *Spondias* spp. (Galindo-Gonzalez 1998, Stevenson *et al.* 2005), *Antrocaryon* spp. (Nchanji & Plumptre 2003, Wang *et al.* 2007), or *Trichoscypha* spp. (Nchanji & Plumptre 2003). *L. acida* has fruit characteristic of the bird-dispersal syndrome and in fact many bird species consume its fruits. Although the sample size of focal trees was small, the study showed that birds, which otherwise may be legitimate seed dispersers, can predominantly consume green, unripe fruits from individual plants at least in certain years, thereby potentially acting as pre-dispersal seed predators. So far, pre-dispersal seed predation by birds has mainly been considered in terms of seed-eating species, e.g., parrots (Galetti & Rodrigues 1992, Norconk *et al.* 1997). Though many birds tend to avoid green and unripe fruit in choice experiments, the effect of these traits on fruit choice by birds may change with varying natural conditions. The role of non-granivorous birds as seed predators for the fitness of fleshy fruited plants thus requires more careful investigation in long-term studies. On the other hand, primates are often considered crucial dispersers for large-seeded tree species (e.g., Howe 1984, Kitamura *et al.* 2002), but their importance for plants with small fruit should not be overlooked.

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APPENDIX. Species observed feeding on fruits or seeds of *L. acida* in Comoé National Park, Ivory Coast. Bird names and diets follow Borrow & Demey (2001); Diet: f = fruits, s = seeds, i = insects, n = nectar, o = omnivorous; FT (fruit treatment): W = swallower, K = pulp pecker, SE = seed eater, ? = unclear; Records: [x]: species were observed in 1999–2000 in trees other than the two focal ones.

	Common name	Scientific name	Diet	FT	Species recorded in 1991-93	1998-00
Birds						
Musophagidae	Green Turaco	<i>Tauraco persa</i>	f	W		x
	Western grey plantain-eater	<i>Crinifer piscator</i>	f	W		x
Phoeniculidae	Black wood-hoopoe	<i>Rhinopomastus aterrimus</i>	i	?	x	
Bucerotidae	Piping hornbill	<i>Bycanistes fistulator</i>	f, i	W	x	[x]
	Black-and-white-casqued hornbill	<i>B. subcylindricus</i>	f, i	W	x	
Capitonidae	Yellow-rumped tinkerbird	<i>Pogoniulus bilineatus</i>	f	W		x
	Yellow-fronted tinkerbird	<i>P. chrysoconus</i>	f	W	x	x
	Vieillot's barbet	<i>Lybius vieilloti</i>	f		x	
Pycnonotidae	Western bearded greenbul	<i>Criniger barbatus</i>	f, i	W	x	
	Common bulbul	<i>Pycnonotus barbatus</i>	f, i	W	x	x
Turdidae	African thrush	<i>Turdus pelios</i>	f, i	W	x	x
Platysteiridae	Senegal batis	<i>Batis senegalensis</i>	i	W?		x
Nectariniidae	Splendid sunbird	<i>Cinnyris coccinigaster</i>	n, i	K	x	
Zosteropidae	Yellow white-eye	<i>Zosterops senegalensis</i>	i, n, f	K	x	
Sturnidae	Bronze-tailed glossy starling	<i>Lamprotornis cf. chalcurus</i>	o	W		[x]
	Lesser blue-eared starling	<i>L. chloropterus</i>	o	W		[x]
	Violet-backed starling	<i>Cinnyricinclus leucogaster</i>	o	W	x	x
Ploceidae	Black-necked weaver	<i>Ploceus nigricollis</i>	s, i	K	x	
	Heuglin's masked weaver	<i>P. heuglini</i>	s, i	K	x	
	Village weaver	<i>P. cucullatus</i>	s, i	W		x
Fringillidae	Yellow-fronted canary	<i>Serinus mozambicus</i>	s	K	x	x
Emberizidae	Cabanis's bunting	<i>Emberiza cabanisi</i>	s	K		x
Mammals						
Sciuridae	Red-legged sun squirrel	<i>Heliosciurus rufobrachium</i>	s	SE	x	x
Cercopithecidae	White-crowned mangabey	<i>Cercocebus a. lunulatus</i>	o	W		x
	Lowe's monkey	<i>Cercopithecus c. lowei</i>	o	W		x
	Lesser spot-nosed monkey	<i>C. petaurista</i>	o	W		x
	Olive baboon	<i>Papio anubis</i>	o	W	x	x