

# Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds

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**Abstract** Seed dispersal by animals is an important ecological process shaping plant regeneration. In general, seed dispersers are highly variable and often opportunistic in their fruit choice. Despite much research, the factors that can explain patterns of fruit consumption among different animal groups remain contentious. Here, we analysed the interactions between 81 animal species feeding on the fruits of 30 plant species in Kakamega Forest, Kenya, during 840 h of observations. Our aim was to determine whether plant characteristics, fruit morphology, fruit colours and/or fruit compounds such as water, sugar, phenols and tannins explained the relative importance of fruit consumption by the two most important consumer groups, primates and birds. We found significant differences in fruit choice between both groups. Primates fed on larger fruits and on higher trees that had larger fruit crops, whereas birds were observed feeding on smaller fruits and on smaller plants producing fewer fruits. Fruit colours did not differ between fruits consumed by primates and those consumed by birds.

However, differences in the fruit choice among frugivorous birds were associated with differences in fruit colours. Smaller plants with smaller fruits produced red fruits which contrasted strongly with the background; these fruits were dispersed by a distinct set of bird species. The contents of water, sugar, phenols and tannins did not differ between fruits eaten by primates and those eaten by birds. Some phylogenetic patterns were apparent; primates fed preferentially on a phylogenetically restricted subsample of large plants with large fruits of the subclass Rosidae. We discuss why the observed primate dispersal syndrome is most likely explained by a process of ecological fitting.

**Keywords** Seed dispersal syndrome · Fruit colour · Nutrients · Frugivore · Food selection

## Introduction

Seed dispersal by animals is an important mutualistic interaction between fleshy-fruited plants and frugivorous animals (Howe and Smallwood 1982; Bascompte and Jordano 2007). This interaction compensates for the limited mobility of plants and determines the population dynamics and gene flow of plant populations (Howe and Miriti 2000). Dispersal by animals is particularly important in the tropics where up to 90% of tropical tree species have fleshy, vertebrate-dispersed fruits (Jordano 1992). Animals in turn benefit from fruit consumption by obtaining nutrients such as carbohydrates and lipids.

In general, the interactions between fruit-bearing plants and frugivorous animals are asymmetric and characterised by a low degree of specialization (Bascompte and Jordano 2007). Most plant species interact with many animal species (and vice versa), and those plant species that are

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dispersed by few animals tend to be dispersed by abundant and unspecialized animals. Recent studies on the structure of mutualistic networks suggest that these networks might be generated by two processes: ecological fitting and coevolutionary convergence (Bascompte and Jordano 2007). Interactions could arise by ecological fitting where animals disperse those plants they can most easily exploit without coevolution taking place. Alternatively, as soon as an interaction evolves and is successful, more species can attach to this interaction by convergent evolution of their traits (Bascompte and Jordano 2007). The consequence would be the evolution of dispersal syndromes, i.e. non-random suites of plant traits that are associated with specific disperser groups (Bascompte and Jordano 2007).

Although many studies report the existence of seed dispersal syndromes (e.g. van der Pijl 1969; Janson 1983; Gautier-Hion et al. 1985; Voigt et al. 2004), the dispersal syndrome hypothesis has also been rejected by a number of phylogenetically controlled studies (e.g. Fischer and Chapman 1993; but see Lomáscolo et al. 2008). As such, the existence and the specificity of seed dispersal syndromes remain contentious. For example, Gautier-Hion et al. (1985) and Dowsett-Lemaire (1988) contrast a combined “bird–monkey-syndrome” with an “elephant–rodent–ruminant-syndrome”, whereas others describe distinct dispersal syndromes for birds and primates (Janson 1983; Poulsen et al. 2002). According to the latter view, fruits pertaining to a primate dispersal syndrome are large, have a thick husk and are yellow, green, brown, orange or red (Janson 1983; Dew and Wright 1998), whereas fruits consumed by birds are small, with a thin husk and are black, blue, violet, or red (Janson 1983; Lomáscolo and Schaefer 2010).

The existence of distinct dispersal syndromes of birds and primates is not only of academic, but also of conservation interest because mammals and birds can differ in their effects on seed-mediated gene flow (Jordano et al. 2007). Moreover, primates are generally hunted more intensely than birds and are often rare or locally extinct in disturbed and degraded forests (Johns and Skorupa 1987; Corlett 2007; Nuñez-Iturri and Howe 2007). Therefore, it is important to assess if certain plant species are dispersed primarily by primates because regeneration of these species might decline with the local extinction of their dispersers.

Although dispersal syndromes are important from an evolutionary and conservation-oriented perspective, standardized, quantitative observations of the fruit choice of birds and primates are often lacking on a community level. Moreover, few studies have used a phylogenetically controlled approach to examine simultaneously which fruit traits or combination thereof define fruit syndromes. This gap in the literature is surprising given that fruit morphology, biochemistry, and colour can strongly filter fruit consumers (Dennis et al. 2007).

It was our aim to study fruit consumption of diurnal vertebrates in a tropical forest by standardised, quantitative observations while accounting for fruit consumption by nocturnal animals qualitatively. We specifically asked: are there plant species whose fruits are mainly dispersed by birds or primates? We then investigated whether plant characteristics (e.g. plant height, habitat), fruit morphology, fruit colour, or specific fruit compounds influenced the fruit choice of primates and birds differentially, thereby defining seed dispersal syndromes. Because colour perception is in the eye of the beholder, we modelled fruit colour according to the sensory sensitivities of birds and primates, respectively. We finally explored whether some bird species overlapped in their fruit choice with primates.

## Materials and methods

### Study area

From December 2007 until March 2008, the season of high fruit availability, we observed frugivores in Kakamega Forest, a mid-altitudinal tropical rainforest in western Kenya (0°14'–0°21'N, 34°47'–34°48'E). The forest comprises 12,000 ha at 1,500–1,700 m a.s.l. (Bleher et al. 2006). The rainy season is from April to November; the mean monthly temperature lies between 15 and 27°C. The forest is an eastern remnant of the Congo basin rainforests, and it is known for its high diversity of plant and animal species (KIFCON 1994; Bleher et al. 2006). Our study area covered approximately 250 ha in the northern part of the forest, in the region of Buyangu. This area is marked by a heterogeneous habitat structure including all successional forest stages from grassland, forest edge, to secondary and primary forest. Very large, typical seed dispersers such as elephants are now missing although some plants with very large fruits remain potentially pertaining to a syndrome of megafaunal fruits (see Guimarães et al. 2008), although none of these plants fruited during our study period.

### Plant species

We observed fruit consumption of 32 plant species (mainly trees, but also climbers, shrubs and herbs) with fleshy fruits. No frugivorous animals were observed on *Leea guineensis* and we observed only a single blue-headed coucal (*Centropus monachus*) on hill raspberry (*Rubus niveus*). We thus excluded both species from further analyses. We observed four different individuals of each plant species except for three rare species of which we observed the same individuals repeatedly on different days (Table 1). A mean species accumulation curve calculated over all 32 plant species shows that we did not observe the full visitor spectrum in

**Table 1** Observed plant species, number of observed plant individuals (*ind.*), and number of primate, bird and fruit bat visitors consuming fruits over 4 observation days

Species	Plant ind.	Primates	Birds	Swallow (primate)	Swallow (bird)	Peck (primate)	Peck (bird)	Fruit bats	Visits	Time	Fruits
<i>Allophylus abyssinicus</i>	4	0	9	0	6	0	1	0	0	0	0
<i>Antiaris toxicaria</i>	4	36	118	15	1	2	50	1	0.25	0.36	0.46
<i>Bridelia micrantha</i>	4	59	294	16	164	0	38	0	0.16	0.43	0.55
<i>Carissa edulis</i>	4	0	33	0	21	0	8	0	0	0	0
<i>Casearia battiscombei</i>	2	6	54	2	0	1	44	0	0.08	0.15	0.3
<i>Cissus oliveri</i>	3	0	23	0	15	0	1	0	0	0	0
<i>Clerodendrum capitatum</i>	4	0	18	0	8	0	10	0	0	0	0
<i>Coffea eugenioides</i>	4	0	8	0	3	0	5	0	0	0	0
<i>Culcasia falcifolia</i>	4	0	14	0	9	0	5	0	0	0	0
<i>Cyphostemma cyphopetalum</i>	4	0	55	0	19	0	28	3	0	0	0
<i>Draecaena fragrans</i>	4	0	5	0	1	0	4	0	0	0	0
<i>Ficus exasperata</i>	4	50	49	27	7	2	20	2	0.36	0.62	0.83
<i>Ficus cf. lutea</i>	4	30	602	21	192	0	329	0	0.06	0.13	0.25
<i>Ficus sur</i>	4	130	108	61	13	48	65	4	0.57	0.83	0.93
<i>Ficus cf. thonningii</i>	4	68	470	40	113	0	31	0	0.12	0.21	0.27
<i>Harungana madagascariensis</i>	4	0	68	0	46	0	2	0	0	0	0
<i>Jasminum fluminense</i>	4	0	33	0	15	0	15	0	0	0	0
<i>Maesa lanceolata</i>	3	0	21	0	12	0	4	0	0	0	0
<i>Manilkara butugi</i>	4	77	72	35	9	10	23	0	0.44	0.59	0.74
<i>Morus mesozygia</i>	4	82	32	35	3	0	19	0	0.76	0.88	0.95
<i>Peponium vogelii</i>	4	13	0	0	0	7	0	0	1	1	1
<i>Piper guineense</i>	4	0	10	0	6	0	2	0	0	0	0
<i>Pittosporum viridiflorum</i>	4	0	19	0	12	0	3	0	0	0	0
<i>Polyscias fulva</i>	4	1	97	1	57	0	13	0	0.01	0.01	0.01
<i>Prunus africana</i>	4	3	407	3	45	0	97	0	0.03	0.03	0.08
<i>Psychotria peduncularis</i>	4	0	8	0	3	0	5	0	0	0	0
<i>Rhamnus prinoides</i>	4	0	19	0	13	0	0	0	0	0	0
<i>Solanum mauritanium</i>	4	0	35	0	1	0	22	0	0	0	0
<i>Toddalia asiatica</i>	4	1	15	1	10	0	3	0	0.05	0.06	0.16
<i>Trilepisium madagascariense</i>	4	94	6	33	3	0	3	0	0.87	0.91	0.9

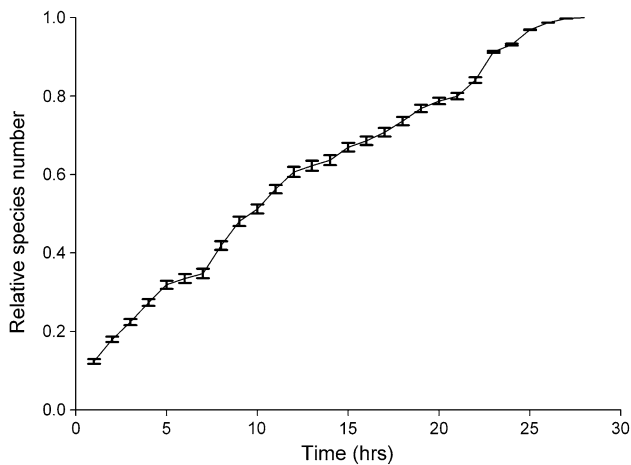
The number of visitors swallowing or pecking at fruits is indicated for birds and primates. Relative visitation rate by primates (*Visits*), relative time spent in the trees by primates (*Time*), and relative fruit consumption by primates (*Fruits*) were calculated as the mean of the daily ratios over the 4 observation days. All variables are scaled so that a value of 0 indicates that only birds visited, spent time or consumed fruits, whereas a value of 1 indicates that these actions were only carried out by primates. All species were observed for 28 h

most plants during our 28-h observation period for each species (Fig. 1). As such, our analyses are based on the relative attractiveness of plant species for primates and birds during the peak of fruit availability and not on the entire fruit consumer set that may visit a plant.

#### Plant characteristics

For each plant we measured plant height with a clinometer and categorised its habitat as 1 = undisturbed primary forest, 2 = disturbed primary forest, 3 = old secondary forest, 4 = young secondary forest, and 5 = grassland. We

estimated crop size by counting the number of ripe and unripe fruits on 5% of the plant and extrapolating this estimate of fruit density separately to each of the four quarters of a plant because fruit numbers were often not evenly distributed within a plant. We then summed fruit numbers of each of the quarters to obtain a total for each plant individual. All estimates were done by a single observer. At the beginning of the observation period, estimates were repeated by a second observer until a high repeatability was ensured. The variable fruit crop size was  $\log_{10}$ -transformed for further analysis to achieve heteroscedascity and to reduce errors in fruit estimates. Finally, we estimated the



**Fig. 1** Mean accumulation curve (and SE) of the fruit consumer species of 32 plant species over the observation period of 28 h. We observed different plant individuals, each for 7 h. Thus, differences in microhabitats among plant individuals and differences in ripening stages among fruits likely explain the more or less pronounced increases at 8, 15, and 22 h

ratio of ripe fruits to all fruits (ripeness) and arcsine-square root transformed it for analysis.

#### Fruit morphology

To obtain fresh fruits we collected fruits directly from the plants which also required climbing trees that fruited in the canopy. For logistical reasons we thus measured fruit characteristics mainly within individuals on one or two individuals per species and up to 20 fruits from each individual. We measured fruit length, diameter, and fresh mass. These variables correlated strongly; we performed a principal component (PC) analysis (PCA) of them. PC1 explained more than 95% of total variance and was included as fruit size index (FSI) to account for variation in fruit size. We calculated crop mass of ripe fruits per plant by multiplying the estimated number of ripe fruits (crop size) with the mean fresh fruit mass. This variable was  $\log_{10}$ -transformed to achieve heteroscedasticity. We categorised husk thickness as 1 = no protection, 2 = thin husk, 3 = thick husk/capsule and counted the number of seeds. We calculated a seed size index (SSI) analogue to FSI from seed length and seed diameter. Again PC1 explained 95% of the variance. We categorised infructescences as 1 = single fruit, 2 = one to ten fruits, 3 = ten to 20 fruits, 4 = >20 fruits and recorded the presence of a peduncle.

#### Fruit colour and colour perception

The reflectance of 20 ripe fruits, ten leaves, and associated structures such as non-green bracts and capsules were measured for each species with a spectrometer (AvaSpec2048

with a DH 2000 Deuterium-Halogen lamp, Avantes). Reflectance was measured from 300 to 700 nm as the proportion of a standard white reference tile (WS-2). We calculated a PCA on the spectra of ripe fruits (for clarity, we name the fruit colours as those seen by humans). The first three PCs explained more than 95% of the total variance and were included as quantitative variables describing fruit reflectance in the analyses independent of consumer vision (PC1, PC2, PC3). High PC1 values indicated relatively high UV reflection of fruits; low values show low relative UV reflection. Black and dark purple fruits scored high on PC2, whereas red fruits scored low on PC2 but had high values on PC3. Low values on PC3 indicated yellow and green fruits.

To estimate how birds perceive fruit colours, we modelled the probability of photon capture of the four cone types that birds use for colour vision. The avian eye model we used assumes that colour discrimination is mediated by noise originating in the cones (Vorobyev and Osorio 1998). The probability of photon capture by each cone can be transformed into a three-dimensional colour space that is characterised by the Cartesian coordinates  $x$ ,  $y$  and  $z$  (for calculations, see Endler and Mielke 2005). In general, avian colour vision is relatively conservative (Ödeen and Håstad 2003). Given that the exact spectral sensitivities of most birds are unknown and that most frugivorous birds belonged to the passerines, we used the spectral sensitivities of the blue tit (*Cyanistes caeruleus*) to model colour perception (our conclusions do not change qualitatively if we used the other violet-sensitive avian visual system).

In contrast to birds, Old World primates have three cones used for colour vision. We modelled primate perception of fruit colours using catarrhine spectral sensitivities determined by Bowmaker et al. (1991) and Osorio and Vorobyev (1996). We then projected the resulting values onto a two-dimensional plane with variables  $x$  and  $y$  following Kelber et al. (2003). We calculated the perception of brightness (that is variation in light intensity) by analysing the stimulation of the avian double cone and of the combined input of the middle- and long-wavelength cones in primates according to Kelber et al. (2003) and Siddiqi et al. (2004). Finally, we calculated the maximal chromatic and achromatic (luminance) contrast between fruits and their background (leaves or any of the associated structures) for birds and primates as the perceived difference in colour or luminance between fruits and background (Vorobyev and Osorio 1998).

#### Chemical fruit traits

After reflectance measurements fruits were dried at a temperature of <math>50^{\circ}\text{C}</math> to avoid mould. We calculated the water content by subtracting dry fruit mass from fresh fruit mass.

In contrast to primates, passerine birds cannot digest sucrose (Martinez del Rio and Stevens 1989). Glucose and fructose are thus the predominant sugars of bird-dispersed fruits but not of mammal-dispersed fruits (Baker et al. 1998). Owing to the strong prediction that glucose and fructose pertain to a bird dispersal syndrome, we focused on these two sugars and analysed the contents of glucose and fructose photometrically with enzymatic D-glucose/D-fructose Boehringer analysis kits (r-biopharm). This method is robust to the presence of anthocyanins. It does not measure sucrose, a sugar that occurs in some fruits dispersed by mammals such as Old World bats. Phenol concentration in fruits was measured using the Prussian blue method using gallic acid as standard (Price and Butler 1977). Tannin concentration was measured using the proanthocyanidin method using catechin as a standard (Porter et al. 1986). A limitation of both methods is that not all phenolic compounds show identical responses to oxidation. As such, the results of these tests should not be treated as yielding an estimate of the contents of phenols and tannins on a per mass basis but rather as equivalents of gallic acid and catechin, respectively. Nevertheless, these assays correspond well to behavioural data on fruit consumption both of avian seed dispersers as well as of fruit pests such as microbes and fungi in two different plant communities (Schaefer et al. 2003; Cazetta et al. 2008).

#### Frugivore observations

Plant individuals were observed continuously from 7 a.m. to 2 p.m. Observations were conducted from camouflaged hides with binoculars (10 × 50) to reduce biases caused by our presence. We determined the species' identity and the number of individuals of all fruit consumers as well as the duration of their visits. If species identification was difficult (e.g. different greenbul species) we recorded the genus or weight classes of fruit consumers. Weight classes were categorised following Kingdon (1997) and Dunning (1993): class 1, small birds (body mass < 18.5 g); class 2, e.g. bulbuls and weavers (body mass 18.5–40 g); class 3, e.g. barbets and thrushes (body mass 40–100 g); class 4, large birds (body mass 100–400 g); class 5, squirrels; class 6, hornbills; class 7, guenons; and class 8, colobus monkeys (Appendix 1 in Supplementary material). Finally, we recorded whether animals fed on ripe or unripe fruits and classified their fruit handling behaviour. That is we recorded whether animals swallowed fruits or carried them away, pecked at them or whether they dropped the fruit.

We conducted night observations to record the presence of nocturnal vertebrates feeding on fruits. At least one individual from each plant species was observed with infrared night vision glasses (5 × 52 and 2 × 24) for 2 h from night-fall. We integrated the number of nocturnal fruit consumers

in our calculations as an independent variable to account for their possible effect in defining fruit syndromes.

#### Response variables

We restricted analyses to visits of animals that fed on fruits. We evaluated the ratio of primates relative to bird visitors on three levels; the number of visits per plant individual, the duration of visits by each consumer group, and finally the estimated number of consumed fruits by each animal group. For the number of visits per plant, we calculated the ratio of primate visits in relation to the total number of bird and primate visits ( $V$ ) such that a ratio of 0% indicated that a plant species was only visited by birds, whereas a ratio of 100% indicated that it was only visited by primates.

We calculated the sum of duration of visits of all bird and primate individuals per plant. If the duration of a visit could not be determined with certainty (21% of total observations), we substituted it by the mean duration of the same animal species or weight class in the same plant. A ratio of duration of time spent by primates in relation to time spent by primates and birds ( $T$ ) was calculated.

Finally, we estimated the ratio of the number of fruits consumed by primates and birds, respectively. Often, we could not record exactly the number of consumed fruits because several animals fed concomitantly on the plant. We therefore used the mean number of fruits consumed per minute for each class of fruit consumers from Farwig et al. (2006) and Kirika et al. (2008a, b; Appendix 1 in Supplementary material). To estimate fruit consumption we calculated the mean fruit consumption per minute for each weight class and multiplied it by the total time (in minutes) spent by each animal species on each plant. We then calculated the ratio of the estimated number of fruits consumed by primates in relation to the estimated total number of fruits consumed by primates and birds for each plant ( $F$ ).

We calculated the mean of the daily ratio values. If a tree was not visited during one day, the mean was calculated of the remaining days. All ratio data were arcsine-square root transformed. As expected, all three ratio values ( $V$ ,  $T$ ,  $F$ ) were highly correlated (Pearson correlations all  $> r = 0.97$ ,  $P < 0.001$ ,  $n = 30$ ). We therefore restricted the following analyses to the relative importance of primate visits ( $V$ ), the variable we had directly observed.

#### Statistical analyses

To visualise the complex patterns of similarity among plants (in their visitor spectra) and animals (in their fruit choice) we used non-metric multidimensional scaling (NMDS). This method is an iterative search procedure that places objects from a distance matrix of visitor spectrum (or fruit choice) in a space of minimized dimensionality



We tested for phylogenetic effects in the residuals of all the multiple regressions. We calculated Moran's  $I$  autocorrelation coefficients for all phylogenetic distance classes (Gittleman and Kot 1990). All regressions with significant Moran's  $I$  values were corrected by phylogenetic eigenvector regression (Diniz-Filho et al. 1998), including the phylogenetic eigenvector with the highest eigenvalue in the regression model. Residuals of the regression were again tested for phylogenetic autocorrelation. After including the phylogenetic eigenvector, none of Moran's  $I$  values were significantly different from zero. Including the phylogenetic eigenvector in the regressions did not change any of the results.

All calculations were conducted in R 2.6.0 and 2.10 (R Development Core Team 2005). Packages "vegan" (Oksanen et al. 2008) and "MASS" (Venables and Ripley 2002) were used for NMDS. Package "ape" (Paradis et al. 2004) was used for the calculation of Moran's  $I$  and package "bblme" for the calculation of Akaike weights.

## Results

### Fruits and fruit consumers

In total, 3,375 visits by fruit consumers were observed. We identified 76 bird species, four primate species and one squirrel species (Appendix 1 in Supplementary material). Primates fed on 45% of all plant species totalling 19% of all visits (Table 1; Appendices 1 and 2 in Supplementary material). Birds fed on all but one plant species, *Peponium vogelii*, which was consumed only by primates (Table 1). Frugivorous birds mostly swallowed (50.3%) and pecked (49.9%) at fruits, rarely dropped them (0.04%) or carried them away in their beaks (0.002%; the cumulative percentage is >100% because some individuals behaved in more than one way). Primates mostly swallowed fruits entirely (79%), dropped them (41%) or ate them piecemeal (25%). Birds pecked at large fruits more frequently than at small fruits (linear regression: pecking birds versus FSI:  $\beta = 65.1$ ,  $t = 2.4$ ,  $P = 0.02$ ,  $r^2 = 0.18$ ,  $n = 30$ ). We included in the following analysis all interactions in which animals fed on fruits. However, the results do not change qualitatively if we only include interactions where fruits were swallowed.

Primates fed on fruits of plants with a mean height of 27.7 m, birds fed on fruits of plants with a mean height of 15.7 m. Fruits eaten by primates had a mean length of 21 mm (range 10–75 mm) and a mean weight of 5.8 g (range 0.4–49 g). Fruits eaten by birds were on average 13 mm long (range 4–29 mm) and weighed 1.4 g (range 0.02–8.3 g). Both groups fed on red, violet, dark violet, yellow and orange fruits. Black, white and blue fruits were only consumed by birds, whereas green fruits were only

consumed by primates (Appendix 3 in Supplementary material). Fruit bats of undetermined species were observed feeding on *Ficus sur*, *Ficus exasperata*, *Antiaris toxicaria* (all Moraceae) and *Cyphostema cyphopetalum* (Vitaceae; Table 1).

### Correlation of plant and fruit characteristics

We found multiple correlations among plant and fruit characteristics (all Pearson's correlations). Small fruits stood in larger infructescences than large fruits (FSI vs. infructescence:  $r = -0.63$ ,  $P < 0.001$ ,  $n = 30$  for all correlations), and fewer small fruits had a peduncle (FSI versus peduncle:  $r = 0.52$ ,  $P < 0.01$ ). Plant height correlated with fruit size ( $r = 0.46$ ,  $P < 0.01$ ), fruit number ( $r = 0.60$ ,  $P < 0.001$ ), and inversely with the proportion of simultaneously ripe fruits ( $r = -0.38$ ,  $P = 0.04$ ). Plants with fewer fruits and plants with a lower crop mass produced fruits with a higher chromatic contrast to the background according to a model of avian vision (crop size,  $r = -0.45$ ,  $P = 0.01$ ; crop mass,  $r = -0.39$ ,  $P = 0.03$ ). Plants producing many ripe fruits at the same time produced fruits with higher fructose and glucose contents than plants with a more staggered fruit production (proportion ripeness versus sugar:  $r = 0.42$ ,  $P = 0.02$ ). The contents of glucose and fructose were higher in plants from open habitats compared to those in undisturbed forest ( $r = 0.49$ ,  $P < 0.01$ ).

The phylogenetic eigenvector with the highest eigenvalue (Ev1) correlated negatively with fruit size (FSI vs. Ev1:  $r = -0.37$ ,  $P = 0.045$ ) and plant height (plant height versus Ev1:  $r = -0.64$ ,  $P < 0.001$ ).

### Visitor spectra and fruit choice

The NMDS placed the plants and animals in a two-dimensional space according to their similarity in visitor spectra and fruit choice, respectively. The amount of variance explained by each axis is indicated by the range of values (Fig. 2).

In general, the range of plants was larger than that of animals, which shows that some plants were more specialized on few dispersers than animals on few plants. The fruit choice of primates differed from that of birds. All primate species fed on similar fruit types (*Peponium vogelii*, *Trilepisium madagascariense*, all *Ficus* spp., *Antiaris toxicaria*), all located between 1.1 and 1.7 on NMDS 1 and between -0.2 and 0.2 on NMDS 2. Birds were more catholic in their fruit choice, which ranged from -0.65 on NMDS 1 (Cameroon sombre greenbul, *Andropadus curvirostris*) to 1.1 on NMDS 1 (black and white casqued hornbill, *Bycanistes subcylindricus*). This hornbill, the largest bird species, had the highest score on NMDS 1 and was therefore most similar in fruit choice to the primates. In

general, the body mass of birds was positively correlated with NMDS 1 score ( $r = 0.55$ ,  $P = 0.017$ ,  $n = 18$ ). Birds also covered a wide range of values on NMDS 2, from  $-1.2$  (violet-backed starling, *Cinnyricinclus leucogaster*) to  $0.7$  (yellow-rumped tinkerbird, *Pogoniulus subsulphureus*). NMDS 2 scores of birds correlated negatively with their average group size while visiting a plant ( $r = -0.50$ ,  $P = 0.034$ ,  $n = 18$ ); there was no correlation with body mass.

To illustrate how plant and fruit characteristics influenced the fruit choice of primates and birds, we plotted them as vectors in the NMDS plane. The relative importance of primates as plant visitors increased with increasing values on NMDS 1. Increasing height of a plant, increasing crop mass and increasing fruit size distinguished plants that were visited by primates from those that were not. As such, primates fed on tall plants with large fruits and high crop mass, whereas birds fed primarily on smaller fruits and fruits growing in large infructescences.

Plant height and crop mass also showed a gradient along the second axis that distinguished between different bird species. Fruit colour did not separate primates and birds as fruit consumers but separated different bird species along NMDS 2. Small plants with low fruit production produced fruits with high chromatic contrast for avian vision and were visited by a distinct subset of bird species, in particular the yellow-rumped tinkerbird, yellow-whiskered greenbul (*Oriolus auratus*) and joyful greenbul (*Chlorocichla laetissima*). Red fruits indicated by high values on PC3 were associated with high chromatic contrast against the background. Plants with such highly contrasting fruits had a high proportion of ripe fruits.

Phylogenetic eigenvectors 1 and 13 had a significant influence on the distribution of plant species in the NMDS plane. Eigenvector 1 had a high eigenvalue of 27% and ran in parallel to NMDS 1 separating plants whose fruits were consumed by primates from those consumed only by birds. Primates fed primarily on plants of the subclass Rosidae with one Asteridae, *Manilkara butugii*, as an exception. Eigenvector 13 had a very low eigenvalue of 0.02% and was consequently neglected as an explanatory variable.

#### Model of fruit choice

A multiple regression model of relative primate visitation rates as dependent variable against the plants and fruit characteristics that were significant in the NMDS (plant height, crop mass, ripeness, FSI, infructescence, PC3, chromatic contrast detected by birds) showed that fruit size, plant height, and crop mass were the most important variables explaining fruit choice by primates (global model:  $F_{7,22} = 6.12$ ,  $r^2 = 0.66$ ,  $P < 0.001$ , Akaike's information criterion = 5.22; Table 2). Moran's  $I$  values of the residuals

**Table 2** Global model on plant traits that contribute to differential fruit choice of primates and birds

Plant traits <sup>a</sup>	$\beta$	SE	Akaike weight
Intercept	-0.1134	0.2900	
Fruit size index	0.3577	0.1038	0.9957
Plant height	0.0104	0.0061	0.8165
Crop mass	0.0242	0.0702	0.8162
Fruit colour (PC 3)	-0.0472	0.0510	0.1308
Chroma	-0.0008	0.0041	0.1287
Infructescence	0.0179	0.0403	0.0568
Ripe fruits	0.0026	0.0023	0.0552

PC Principal component

<sup>a</sup> The relative importance of plant traits for explaining the proportion of fruits consumed by primates is indicated by high summed Akaike weights. Large fruit size, tall plants, and large crop mass characterised plants whose fruits were consumed by primates

were not significantly different from zero. Thus, no correction for phylogenetic effects was necessary in this analysis.

#### Discussion

Primates were observed feeding on 45% of all fruiting plant species, whereas birds fed on all species except *Peponium vogelii*. Taken together, the four primate species had a more specialized fruit diet than the frugivorous birds. Moreover, the fruits consumed by primates were more similar to each other than the fruits consumed by birds. This result reflects the fact that the four species of primates were more similar to each other in terms of morphology and size than the 18 species of birds included in the NMDS.

#### Plant and fruit morphology influence fruit choice

Plant height, fruit size, and crop size were all correlated. These correlations complicate causal inferences on the relative importance of each of the factors. Yet, such non-random correlations form the functional basis of the seed dispersal syndrome hypothesis. The interpretation of such syndromes requires care. Although we found overall little evidence for phylogenetic signals in our analyses, the phylogenetic eigenvector with the highest eigenvalue correlated with the relative importance of primates as fruit visitors as well as with plant height and fruit size. As such, our results indicate that primates fed on a phylogenetically restricted subsample of large plants with large fruits of the subclass Rosidae. The primate seed dispersal syndrome that we found can be explained by ecological fitting without evolutionary change, that is that primates consume the fruits of a phylogenetically restricted subsample that they can exploit most efficiently. Alternatively, the pattern could

be explained by one-sided evolution of one of the partners or by mutual coevolution where both partners adapt to each other. We are unable to differentiate between these hypotheses directly. However, the covariance between plant and fruit size likely indicates genetic or developmental constraints. Consequently, this covariance likely restricts the evolutionary potential for plants to respond to selection upon fruit size imposed by seed dispersers.

The novel aspect of our results is that the seed dispersal syndromes were correlated to plant height and therefore likely explicable by functional (morphological and physiological) linkages between complex plant traits. Such linkages are termed phenotypic integration and are explicable by genetic, physiological or developmental constraints. Covariance among reproductive traits and between vegetative and reproductive plant traits have been noted previously and are attributable to phenotypic responses to the environment, genetic responses to natural selection, and the limits of such responses imposed by developmental and genetic linkage such as epistasis and pleiotropy (e.g. Herrera 2002; Peréz et al. 2007). As such the covariance among distinct plant traits that we observed suggests that ecological fitting is the most parsimonious hypothesis to explain trait matching between fruiting plant and fruit-eating primates.

According to our models, fruit size was the most important trait determining the relative importance of primates as fruit consumers. Primates consume only fruits larger than 10 mm (Dew and Wright 1998), whereas few birds consumed large fruits (up to 29 mm). Importantly, the functional overlap between both groups is less than these numbers suggest. Birds peck at large fruits which reduces the likelihood of successful seed dispersal, whereas primates can swallow larger fruits entirely. Our conclusion that body size (and gape width) is the major determinant of fruit choice is corroborated by the observation that the largest frugivorous bird, the black and white casqued hornbill, was more similar to primates in fruit choice than to other birds.

Plant height is another important factor shaping the differential fruit choice of primates and birds. Primates consumed fruits from plants with an average height of 27.7 m; considerably higher than the fruiting plants visited by birds (mean height of 15.7 m). The higher foraging height of primates might, at least partly, be explained by the larger fruits in the canopy rather than by an intrinsic foraging preference for higher trees. This pattern is probably further exacerbated by the fact that larger primates may not be able to climb small bushes with weak branches.

Finally, crop mass was positively correlated to the visitation rate of primates. This result is consistent with the generally high attractiveness of plants with a large fruit crop. Large fruit crops might be especially important for primates owing to their relatively high body mass coupled with their social foraging behaviour (Chapman and Chapman 2000).

Yet, given that birds are likewise attracted by large fruit crops (Ortiz-Pulido and Rico-Gray 2000), our result might rather be explicable by the correlations between fruit crop and fruit size. Similarly, our result that primates feed primarily on single fruits might be explicable by the negative correlation between fruit number within an infructescence and fruit size.

The only fruit consumed exclusively by primates, *Peponium vogelii*, had a very thick husk which birds cannot open with their bills. As such, this plant is specialized for seed dispersal by primates; all birds are excluded from its dispersal, even the large-sized hornbills. The missing interaction between *P. vogelii* and birds is a “forbidden link” (Jordano et al. 2003). This species is thus expected to be most severely affected by the over-hunting of primates.

We emphasise that our observation period was not sufficiently long to account for a full visitor spectrum of most plants. Thus, our analyses capture the relative attractiveness of plants for primates and birds during different days of the 4-month observation period of peak fruit availability but not the full visitor spectrum of each plant. We found no pronounced seasonality in the abundance of frugivores within our observation period making it unlikely that differences in the observed visitor spectrum among plant species are due to changes in consumer abundances rather than differences in fruit traits. However, it is important to note that the patterns of fruit choice are likely to change according to the pronounced seasonality of fruit availability in tropical forests. This is because fruit consumers are more choosy at times of high fruit availability compared to seasons of relative fruit scarcity (Schaefer and Schaefer 2006). Given that our study period covered the peak of fruit availability, the differences in the foraging behaviour of primates and birds might be less pronounced in the Kakamega forest during the rest of the year.

#### Fruit colour and fruit compounds

Given that fruit colour differs in a large sample of 402 plant species whose fruits were either dispersed by primates or by birds (Lomáscolo and Schaefer 2010), it is perhaps surprising that fruit colour had no influence on the relative number of visits by birds and primates. We suggest that this discrepancy is due to the considerably lower sample size of our study. However, fruit colour variation did explain differential fruit choice among bird species. In the NMDS, the vector of increasing chromatic contrasts of fruits against their background (as seen by birds) was parallel to the second axis of the NMDS. In particular, birds such as yellow-rumped tinkerbirds and grey-throated barbets fed primarily on small plants with few, red fruits that contrasted strongly with the background. The negative correlation between scores on NMDS 2 and group size of birds is at least partly

explicable by the social behaviour of violet-backed starlings that occurred mostly in groups of more than 23 individuals and that scored low on NMDS 2.

Plants producing relatively few fruits had relatively high chromatic contrast to the background. We suggest that this pattern is adaptive because increased chromatic contrast facilitates long-distance fruit detection by frugivorous birds (Cazetta et al. 2009). Importantly, fruit detection is particularly critical in plants that produce few fruits. The larger a fruit crop, the easier it is detected by means other than visual contrasts (i.e. by size and by the activity of other frugivorous animals). At the same time plants with few fruits had a large proportion of ripe fruits which may increase fruit detection. On the other hand a large proportion of ripe fruits may simply reflect the low attractiveness of such plants to frugivores leading to the accumulation of ripe, undispersed fruits.

The fruit compounds we measured did not differentiate the fruits consumed primarily by primates and those consumed primarily by birds. Our results show that the content of glucose and fructose depended mainly on light availability in open habitats rather than on disperser identity. We can obviously not exclude the possibility that protein, lipids or secondary compounds other than the indices of phenolic contents that we tested might differentially affect the feeding behaviour of primates and birds. Taken together, the novel contribution of this study is that fruit syndromes in this African rainforest are defined by plant and fruit size and most likely characterised by a process of ecological fitting.

## Conclusion

We found a primate plant-syndrome that was characterised by plant and fruit size as well as crop mass but not by fruit colour or the contents of phenols, tannins, glucose or fructose. Our data suggest that plants' potential to respond to selection imposed by seed dispersers is constrained by covariance between fruit and plant morphology. A bird syndrome was less apparent because birds fed on a larger variety of fruit types. Fruit colour explained differential fruit choice of bird species. Small plants with few fruits produced red fruits that contrasted strongly with the background and were consumed by a distinct set of bird species. Few plant species depended strongly on primates as seed dispersers. It is conceivable that the dispersal of species like *P. vogelii* might diminish if primates are overexploited in this region.

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