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Reliance on Exotic Plants by Two Groups of Threatened Samango Monkeys, *Cercopithecus albogularis labiatus*, at Their Southern Range Limit

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Abstract Understanding how threatened species adapt their behavior to landscapes shaped by humans is increasingly important to ensuring they persist in a changing world. Matrix habitats can be shared spaces where human and nonhuman primates coexist. We set out to determine how an endemic, threatened forest specialist, the frugivorous, arboreal samango monkey (*Cercopithecus albogularis labiatus*), has responded to a matrix habitat made up of residential gardens and commercial plantations in Eastern Cape province, South Africa. We followed two groups from dawn to dusk for a mean of 3 days/mo for 12 mo (February 1, 2011 to January 31, 2012) using scan sampling to collect data on their diet, activity, and ranging patterns. We used resource abundance transects to describe the groups' home ranges and monitored tree phenology to calculate fruit and seed availability indices. Monkeys from both groups consumed large quantities of exotic plant species, accounting for >50% of their overall annual diet, with seeds of the invasive black wattle (*Acacia mearnsii*) the most commonly consumed exotic species followed by acorns of two oak species (*Quercus robur* and *Q. palustris*.). However, monkeys responded to the availability of indigenous rather than exotic fruits and seeds and increased their

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consumption of exotics when indigenous fruits were less available. Although monkeys spent less time moving when feeding on exotic species compared to indigenous species, eating exotics did not free up monkeys' time to rest or socialize, as additional time was required to process exotic foods. To offset the possible negative consequences of the monkeys' reliance on exotic seeds, including escalating conflict between monkeys and people in gardens, we suggest gradual removal of exotic plant species in the habitat and replacement with indigenous species as one mitigation strategy.

Introduction

Wild animals are increasingly compressed within small patches of native vegetation surrounded by matrices of human-modified land (Chapman *et al*. 2007; Estrada 2009; Estrada *et al*. 2012; Fischer and Lindenmayer 2007). Some of these matrices consist of exotic plants (nonnative species found outside their normal distributional range: van Wilgen 2011), which may provide an additional resource for native wildlife (Vitule *et al*. 2012), including threatened species (Schlaepfer *et al*. 2011). Exotic plants, because they lack natural predators and disease risks (Iponga 2011; van Wilgen and Impson 2011), can alter the quality and quantity of nutrients available to local wildlife by, for example, yielding an increased availability and abundance of certain plant parts such as seeds (Richardson and van Wilgen 2004; van Wilgen 2011; Vitousek 1990) or fruit (Davis 2011).

Opportunistic taxa such as some primates can thrive on exotic vegetation given their dietary flexibility and ability to exploit newly available resources (McKinney *et al*. 2015). The incorporation of exotic species into the diet can influence primates' patterns of activity. For example, vervets (*Chlorocebus pygerythrus*: Saj *et al*. 1999) and baboons (*Papio* spp.: Strum 2010; van Doorn *et al*. 2010) that consume cultivated plant parts (crops) and human food waste spent less time foraging and traveling and more time resting and socializing because metabolic demands were easily and quickly satisfied. Ring-tailed lemurs (*Lemur catta*) that ate white cedar (*Melia azedarach*) and cattley guava (*Psidium cattleianum*) devoted less time to moving and feeding than a group without access to such exotics (Gabriel 2013). In contrast, chacma baboons (*Papio ursinus*) living in exotic pine (*Pinus* spp.) plantations had similar annual activity budgets to those living in natural habitats, although their relatively smaller home ranges suggested that pine nuts are spatially clumped but require similar processing times to native foods (Hoffman and O'Riain 2011).

According to optimal foraging theory, primates should choose to eat a specific food item that maximizes their energy returns, by weighing up the benefits, e.g., high energy food source, and the costs/constraints, e.g., high secondary compounds, increased visibility to predators (Krebs and Davies 1993). Fruits, which are easily processed and are a high-energy resource (Hemingway and Bynum 2005; Kaplin and Moermond 2000; Wilson and Downs 2012), are a classic preferred food of frugivorous primates, constituting the majority of the diet, and are eaten when available (Marshall and Wrangham 2007). Leaves are a common fallback food for frugivorous primates, e.g., blue monkeys

(*Cercopithecus mitis*: Foerster *et al.* 2012), and are eaten when preferred species and parts are seasonally unavailable (Marshall and Wrangham 2007). Fallback foods are usually abundant and easily located but hard to process because of high fiber and plant secondary compounds (Hemingway and Bynum 2005; Lambert 2002; Rosenberger 2013). An important question in matrix habitats is therefore whether primate species targeting exotic plant species consume them as preferred or fallback foods.

Exotic fruits and crops are often targeted by primates (Strum 2010). These plant parts are generally more abundant and have higher sugar content than indigenous fruit (Mokotjomela *et al.* 2013), and/or they are more available during seasonal shortages of endemic fruits. For instance, a population of howlers (*Aloutta caraya*) targeted exotic orange trees (*Citrus sinensis*), where >60% (and as much as 97%) of fruits eaten were oranges (Bicca-Marques and Calegaro-Marques 1994). A group of chimpanzees (*Pan troglodytes verus*) increased their reliance on cultivated plants when experiencing a dearth in the availability of wild fruits (Hockings *et al.* 2009). Primate populations may even come to depend on or develop preferences for exotic plant species, which help them achieve higher population densities and improved survival probabilities in fragmented habitats (Pozo-Montuy *et al.* 2013; Singh *et al.* 2001). For example, Zanzibar red colobus monkeys (*Procolobus kirkii*) that rely heavily on exotic Indian almond (*Terminalia catappa*) outside of Jozani National Park exist at the highest population densities recorded for any nonhuman primate (Siex and Struhsaker 1999).

The samango monkey (*Cercopithecus albogularis*, subspp. *labiatus*, *erythrarchus*, and *schwarzi*: Dalton *et al.* 2015), a forest specialist, is threatened in South Africa (Linden *et al.* 2016), where it is becoming increasingly isolated and detrimentally affected by forest fragmentation and deforestation from historic logging and ongoing forestry plantations (Friedman and Daly 2004; Kingdon *et al.* 2008; Lawes 1992). Groups are reluctant to disperse between forest patches or to inhabit small and isolated forest fragments (Friedman and Daly 2004; Lawes 1992, 2002; Lawes *et al.* 2000). Matrix habitat planted with exotic species might help to increase connectivity and encourage movement between fragments, as it does for the Angola black-and-white colobus (*Colobus angolensis palliates*: Anderson *et al.* 2007). Some samango monkey populations have been observed to occupy matrix habitat and eat plant parts from exotic species including loquat (*Eriobotrya japonica*), pine (*Pinus* spp.), oak (e.g., *Quercus robur*), black wattle (*Acacia mearnsii*), and bugweed (*Solanum mauritanum*) (Breytenbach 1988; Lawes *et al.* 1990; Linden *et al.* 2015; McMahon 1977; von dem Bussche and van der Zee 1985).

Samango monkeys are arboreal and frugivorous, with 50% of their diet consisting of fruit (range: 52–92%); followed by leaves (range: 2–44%), with flowers, insects, seeds, and fungi eaten in smaller quantities (reviewed in Coleman and Hill 2015). During seasonal fruit scarcity, these monkeys consume more mature leaves, flowers, and unripe fruits (Lawes 1991; Lawes *et al.* 1990). Samango monkeys are able to subsist on a folivorous diet when fruit is scarce largely as a consequence of being hindgut fermentors, such that they are able to extract protein from the usually nondigestible cellulose in plant cell walls (Bruorton and Perrin 1988).

We studied two groups of samango monkeys in and around the village of Hogsback, Amathole Mountains, Eastern Cape, South Africa, where both groups had access to a matrix of exotic plants as well as indigenous forest. One group's home range included the village, and thus had more people, dogs, shops, houses, roads, and electrical lines

compared to the other group's range. Both groups' ranges included people's small holdings that had been planted with exotic ornamental plant species, e.g., *Azalea*, and supplementary food for the growers such as vegetables, e.g., maize (*Zea mays*); nut and fruit trees, e.g., cherry plum (*Prunus cerasifera*); and pecan trees (*Carya illinoinensis*) (http://hogsbackgardens.blogspot.co.za/). These food items provide an incentive for monkeys to enter residential properties and have possibly resulted in the monkeys' home ranges increasingly overlapping with people's gardens. Starting about 10 yr ago, human–monkey conflict escalated in Hogsback, with people complaining that monkeys did not previously occur outside of the adjoining indigenous forest, that they are wasteful with food obtained from planted fruit and nut trees, are becoming bold and aggressive, are targeting rubbish bins and houses for food, and are also increasing in numbers (Nowak et al. 2014, 2017, this issue; Wimberger and Bidner 2012).

We predicted that samango monkeys would target the abundant exotic species, particularly black wattle and oak trees. These species occur in large stands in Hogsback and the seeds are consumed readily by nonhuman and human primates where they are native, as they are a good source of oils and protein (Guo *et al.* 2007; Seigler 2003). We set out to understand the extent of monkeys' reliance on exotic plants and the seasonal and habitat drivers of this consumption. Hogsback is a highly seasonal site at the most southerly extent of this taxon's range, with seasonal variation in day length representing an important ecological constraint, as short winter days restrict the length of time available for foraging and other activities (Hill *et al.* 2003). We use multiple linear regression models to determine the factors that best account for the consumption of indigenous and exotic species by samango monkeys at Hogsback, exploring the role of seasonal variations in day length, rainfall, group ID, and indices of indigenous fruit and seeds and exotic fruit and seed availability. As consumption of exotic fruit and seeds would provide monkeys with high protein and fat content, we examine if time feeding on indigenous fruits and exotic seeds was associated with activity patterns and day journey lengths. Finally, we expected that the group with greater access to the village and gardens would exploit exotic species relatively more and so incorporate group size into all of our analyses.

Methods

Study Site and Study Groups

The study site lies within the Amathole mountain range in the Eastern Cape province of South Africa, at an altitude of *ca.* 1270 m and includes the village of Hogsback (32°35′ S, 26°56′E). Our behavioral study ran from February 1, 2011 to January 31, 2012, where we define seasons as autumn (March–May), winter (June–August), spring (September–November), and summer (December–February). Although typically a summer rainfall area (mean annual rainfall = 1029 mm), during the study period there was high winter rainfall (measured daily on site by a resident using a rain gauge; Webster *unpubl. data*). Temperatures ranged from a mean minimum of 5.7 (±1.2)°C in winter (June–August), when it often snows, to a maximum of 29.6 (±2.2)°C in summer (December–February) (South African Weather Service: SAWS *unpubl data*). Day length ranges from 10.0 h in winter to 14.3 h in summer, which we derived based on

the time difference between the sunrise and sunset times provided by a hand-held Global Positioning System (GPS, Garmin Dakota 20, Garmin Ltd., Olathe, KS, USA) for our specific location.

The natural vegetation (indigenous forests) at the site is characterized as southern mistbelt forest, typically found between 1000 and 1400 m (Afromontane) and dominated by large trees including yellowwood (*Podocarpus*/*Afrocarpus* spp., white stinkwood (*Celtis africana*), cape chestnut (*Calodendrum capense*), and forest knobwood (*Zanthozylum davyi*: Mucina and Geldenhuys 2006). However, these indigenous forests are degraded as a result of the historical harvesting of large yellowwood trees, the introduction of exotic pine (*Pinus* spp.) within commercial plantations and the invasion of exotic species, particularly Australian black wattle (Webster 2009).

We selected two samango monkey groups that use indigenous forest and a matrix of residential gardens. The range of G1 (*ca.* 27 individuals) overlapped with Hogsback village, while we chose G2 (*ca.* 18 individuals) on the basis of its range being 1.5 km outside the center of the village and ≥1 km from the other study group. G2's home range contained a very small portion (<1%) of commercially planted exotic pine. Both groups' home ranges were outside any formally protected area.

We followed each group from dawn to dusk (summer *ca.* 05:00–19:00 h, winter *ca.* 07:00–17:00 h) for a mean of 3 days/mo for 12 mo to collect data on diet, activity, and ranging patterns. We followed G1 for 356 days (6 summer, 9 autumn, 11 winter, 9 spring) and G2 for 34 days (6 summer, 10 autumn, 10 winter, 8 spring). Our locating of groups was facilitated with the use of VHF (Telenax, Mexico) radio collars, fitted by a veterinarian in September 2010 on the group male, and two (G2) or three (G1) adult females in each group. Before data collection we habituated both groups to close observation (*ca.* 5 m) over a period of 6 mo.

Diet and Activity Budgets

We conducted instantaneous scans sampling every 15 min (four samples per hour), with each scan lasting 5 min (Guo *et al.* 2007; Kaplin and Moermond 2000). Although there is some debate on the accuracy of scan sampling methods for examining foraging and food intake rates (Amato *et al.* 2013; Harcourt and Stewart 1984; Reynoso-Cruz *et al.* 2016; Zinner 1999), it was the most appropriate method for this study given relatively large group sizes and difficulty identifying individuals. We collected data on adult females (physically large, long nipples), subadults (physically smaller, females have short nipples; males have visible testes) and juveniles (physically smaller, females have no visible nipples; males have hardly visible testes) but not on infants (physically small, not independent, suckle) or adult males (one male per group, large testes, physically larger than adult females). We estimated that both groups had a similar ratio of individuals within each age class (roughly 5% adult male, 30% adult females, 65% subadults and juveniles), but cannot rule out some small variation that may influence our results. In total, we collected 387 observation hours for G1 [13,132 individual scan samples; mean = 25.0 (±17.3 SD) individuals/h], and 374 observation hours for G2 [12,027 individual scan samples; mean = 23.5 (±15.2 SD) individuals/h].

We classified activity into five broad categories: 1) feeding (including eating, i.e., ingesting food, and foraging, i.e., searching for and processing food); 2) moving, e.g., walking, running; 3) socializing (affiliative interactions such as grooming); 4) resting,

e.g. sitting, lying; and 5) other (Kaplin and Moermond 2000; van Doorn *et al.* 2010). We categorized all plant parts consumed as either indigenous or exotic, and grouped them into types: fruit (including unripe, ripe), seed pod/nut (hereafter termed seed, including unripe, ripe), leaves (including young, mature), stems, buds (including buds, shoots), exudate, invertebrates, human food waste, and other (including fungus, lichen, and clay). We combined unripe and ripe fruit and seed and also young and mature leaves for some species, e.g., fruit of *Celtis africana*, vine leaves, when it was difficult for us to distinguish visually between different stages that were eaten by monkeys in the tall canopy, as was done by Tesfaye *et al.* (2013), who studied Boutourlini's blue monkeys (*Cercopithecus mitis boutourlini*). We combined plant parts eaten from the two most common oak species (*Quercus robur* and *Q. palustris*) in Hogsback and in the groups' diet, as species distinction was not important in determining the role of this exotic food in the diet of these monkeys.

We derived a measure of consumption of each food item by summing the number of individuals observed to be eating a particular food item during each of the four 5-min scans within each hour of observation, then dividing by the total number of individuals observed in that hour. Similarly, we quantified activity budgets by summing the number of individuals observed to be engaged in a particular behavior during each of the four scans within each hour of observation, then dividing by the total number of individuals observed in that hour. To control for seasonal differences in day length, we calculated mean dietary and activity proportions for each day and multiplied by the day length to determine hours per day devoted to feeding on a specific item or devoted to an activity (following Hill *et al.* 2003, 2004; Hoffman and O'Riain 2011). We then excluded the "other" activity category from further analysis. To allow for dietary comparisons with other studies, we also present mean annual percentages of each dietary item consumed out of total eaten.

Home Range Characteristics

We recorded the location of the approximate group center every 30 min during group follows with a hand-held GPS (Dakota 20, Garmin Inc., Olathe, KS, USA). We imported GPS data points (G1, $N = 954$, G2 $N = 947$) into ESRI® ArcMap^{TM} 9.3.1 (ESRI 2009) and projected them in UTM Zone 35S, spheroid WGS 1984, central meridian 27. We calculated annual home ranges using 90% fixed kernel density estimator, a common method for calculating home range (Gabriel 2013) from Hawth's Analysis Tools 3.27 (Beyer 2004) extension with a smoothing factor (H) of 50 and raster cell size of 10. We used Hawth's Analysis Tools to overlay a grid on the GPS data points, with a grid cell size of 50×50 m chosen based on an estimate of group spread (similar to that reported for blue monkey; Kaplin 2001).

We labeled each grid cell as either indigenous or matrix by visually assessing whether native or exotic plants were dominant (>50%) in each cell of the grid, placed over a recent (2010) aerial photograph of the area (Department of Rural Development and Land Reform, South Africa: Cape Town). We visually estimated boundaries between habitat types by on-the-ground observations. Within each of these two types of habitats, and for each group, we placed three fixed strip-width transects (100×10 m, 0.1 ha; modified from Boyes and Perrin 2010). The size of the sampled area should capture the diversity of the habitat within the home range and cover the key habitat,

with adequate sample size considered to be between <1% (Chaves *et al.* 2012) and 10% (Snaith and Chapman 2008). We sampled 0.6 ha of each group's home range, which constituted *ca*. 3% of each group's home range (*ca*. 12% of the groups' core home ranges), and due to homogeneity of indigenous habitat, we deemed this adequately sampled. Not all species consumed by the monkeys were detected along our matrix habitat transects because of the clumping of exotic species, but we did not want to bias our sampling by specifically targeting certain patches. We recorded the species, height, and diameter at breast height (DBH) of all trees with >5 cm DBH along each transect and with a width of 5 m on either side (following Boyes and Perrin 2010; Renton 2001). DBH has been established as a good proxy of fruit abundance (Boyes and Perrin 2010; Chapman *et al.* 1992; Renton 2001). We calculated tree densities (no./ha) and tree species richness for each habitat type within each group's home range by dividing the total number of trees or species by 0.3 ha. We also calculated the percentage of large trees (>40 cm; Lee *et al.* 2014) for each habitat.

As the samango monkey is largely frugivorous (Coleman and Hill 2015), we focused on fleshy fruit availability, but also monitored the availability of black wattle seed pods and oak acorns given their consumption observed during the habituation phase (*ca*. 6 mo). We calculated a fruit and seed availability index (FSAI) by combining stand basal areas of trees used by the monkeys with their fruit and seed phenology (adapted from Agostini *et al.* 2010). We measured the fruiting and seed phenology at the end of each month (April 2011–February 2012), calculating separate FSAI measures for indigenous (I-FSAI) and exotic plant species (E-FSAI) for each group. We monitored between one and seven individual trees from most of the fruiting species targeted by the monkeys including 9 indigenous and 13 exotic species (see species in bold in Electronic Supplementary Material [ESM] Table SI). These species were within the groups' ranges (not limited to those encountered on transects) and we visually scored the fruits and seed (ripe or unripe) between 0 (none present) to 1 (full canopy) in increments of 0.1. We included measures of seeds contained in dry pods/nuts still in the tree and not measures of dry fruit. We did not measure fallen fruit and seeds. For each month, we calculated a fruiting and seed phenology score for each species weighted by the number of individuals of that species that were monitored (using the total number of individual trees monitored that month, range 25–40). We multiplied this weighted score by the stand basal areas for the species, calculated from the sum of the basal areas of individuals encountered on transects divided by the total area sampled for each group (0.6 ha). To estimate fruit and seed availability for March, during a hiatus in data collection, we calculated the mean for February and April; the results from the analyses reported here are unaffected if these data are excluded.

Statistical Analyses

We conducted all statistical analyses in SPSS v. 22.0.0.1 (IBM, New York). We set out to understand the extent of monkeys' reliance on exotic plants and the seasonal and habitat drivers of this consumption using multiple linear regression models with backward removal of nonsignificant terms. As dependent variables, we used hours per day spent feeding (incorporating eating and foraging) on indigenous species, exotic species, indigenous fruit, exotic seeds, indigenous leaves, black wattle seeds, and oak seeds. Although stepwise multiple regression may inflate the probability of type I errors

(false positive results) (Wilkinson 1979), particularly where there are large numbers of correlated parameters, we restricted the variables incorporated in the full model to analyze the relative effects of a small realistic set of candidate predictors. We used the following factors in the initial models: day length, group ID, index of indigenous fruit and seed availability (I-FSAI), and index of exotic fruit and seed availability (E-FSAI). We also included rainfall (cumulative monthly values), as it is an important correlate of plant flushing and flowering (van Schaik *et al.* 1993), and because rainfall patterns were atypical in this study year. We did not include ambient temperature, as it linearly correlated with day length. We checked various diagnostics of model validity and stability and none indicated obvious influential cases, nor significant deviations from the assumptions of normality and homogeneity of residuals (Field 2005; Quinn and Keough 2002). Using partial correlations, we examined the similarity in the IFSAI and EFSAI profiles for both groups. Controlling for day length and group, we used Pearson's correlations to examine if feeding (h/day) on indigenous fruits and exotic seeds was associated with activity patterns and day journey lengths. We incorporated group effects into all of our analyses to explore or account for differences between groups.

Ethical Note

The project was approved by the National Zoological Gardens of South Africa's Research and Ethics Committee and the University of Fort Hare. We obtained permits from the Department of Economic Development and Environmental Affairs, and Department of Agriculture, Forestry and Fisheries, Eastern Cape Province. A registered veterinarian, A. T. Tordiffe, led the capture of monkeys for placement of radio-collars, and we obtained a National Threatened or Protected Species (TOPS) permit. Our research did not involve direct contact with monkeys during observational follows. The monkeys were habituated to the presence of one observer (K. Wimberger). Because the monkeys were already entering gardens when we commenced this study, the process of habituation did not encourage this behavior, although we note that habituation can have implications for human–monkey conflict and monkey risk-taking behavior (Nowak *et al.* 2014; Williamson and Feistner 2011).

Results

Determining the Extent of Seasonal Variation in Exotic Species Consumption

More than 50% of the total diets of both groups were exotic species (G1: 58.7 ± 27.5% SD, G2: 52.1 ± 32.0% SD), followed by indigenous species (G1: 26.6 ± 23.2%, G2: 38.6 ± 29.5). Other items, e.g., invertebrates, food waste, each contributed <5% to the monkeys' diets (Table I). The most consumed dietary item out of the annual total was exotic seeds, followed by indigenous fruits and leaves (Table I).

G1 ate fruit and seeds from 29 species, 19 of which were exotic, while G2 ate fruit and seeds from 27 species, 12 of which were exotic (ESM Table SI). The top species targeted for fruits and seeds were exotic black wattle (G1: annual mean 22.3 ± 26.3%;

Table I Contribution of each food item to the diet (mean% eating scans) of two samango groups (G1, G2) in Hogsback, South Africa (February 2011–January 2012) with plant parts split into exotic, indigenous, and unknown categories (mean ± SD%)

Dietary item	Plant parts	G1	G2
Exotic plant species	Fruit	4.3 ± 5.1	2.2 ± 4.2
	Seed	37.4 ± 24.2	35.0 ± 25.3
	Leaf	6.5 ± 8.4	4.6 ± 7.4
	Stem	1.6 ± 2.0	1.3 ± 2.5
	Bud	3.9 ± 7.4	2.9 ± 8.3
	Flower	4.9 ± 11.7	5.8 ± 15.4
	Exudate	0.2 ± 0.6	0.5 ± 0.7
Indigenous plant species	Fruit	12.5 ± 18.7	18.1 ± 20.8
	Seed	3.4 ± 7.7	2.3 ± 4.2
	Leaf	5.7 ± 7.5	11.0 ± 12.7
	Stem	1.2 ± 1.9	1.1 ± 2.01
	Bud	2.6 ± 7.7	4.3 ± 9.4
	Flower	1.1 ± 2.4	1.8 ± 3.1
Unknown plant species	Total	<0.1	<0.1
Invertebrates		4.8 ± 6.9	2.8 ± 2.7
Other: clay, fungus, lichen		–	0.7 ± 2.8
Human food waste		1.5 ± 3.0	<0.1
Unidentified items		4.7 ± 4.6	3.7 ± 4.5

G2: 27.6 ± 25.8%), exotic oak (combination of *Quercus robur* and *Q. palustris*, G1: 13.6 ± 27.0%; G2: 5.4 ± 19.3%), and indigenous red currant (*Searsia chirindensis*) (G1: 8.4 ± 13.7%; G2: 13.0 ± 17.4%). The monkeys processed the fruits and seeds of each of those species differently (described in ESM Table SI). The other dietary items each contributed <5% to the diet (ESM Table SI).

The two groups were comparable in their seasonal food choices, eating exotic seeds year-round with peaks in indigenous fruit consumption in autumn (February – May) (Fig. 1). However, in winter, G2, unlike G1, had a pronounced peak in feeding on indigenous leaves.

Determining the Extent of Seasonal Changes in Exotic Plant Availability

Each group's home range contained more than two-thirds matrix habitat (Table II). The areas of indigenous habitat in both groups' home ranges had similar tree densities and species richness, but G2 had larger trees (>40cm DBH) and more red currant trees (Table II) than G1. Meanwhile, the matrix component was markedly different for the two groups. In G1's home range, the matrix had a low tree density and species richness, and many large trees compared with the matrix available to G2 (Table II). The gardens within Hogsback generally had large, open grassy areas and stands of old, emergent exotic trees to which only G1 had access. Both groups had large stands of black wattle in their home ranges, but G2 had a relatively higher density of wattle. Meanwhile, G2 had relatively few oaks in its home range compared with G1.
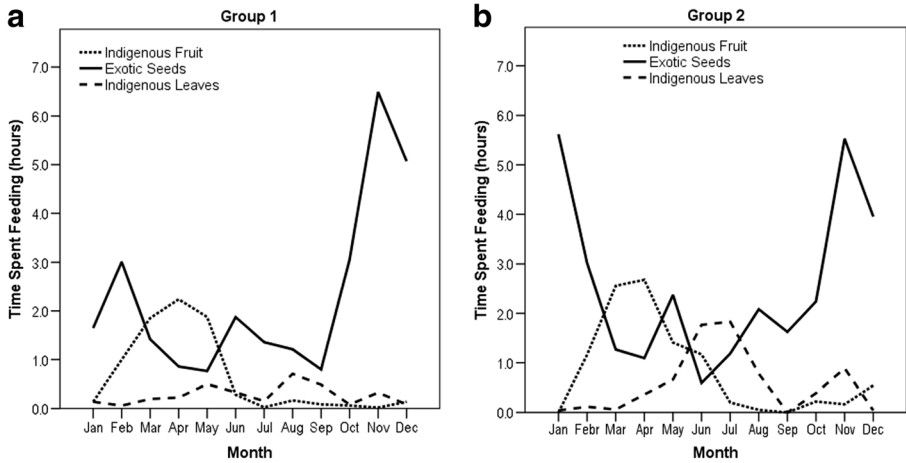
Fig. 1 Monthly variation in time spent feeding (eating and foraging) on indigenous fruit, exotic seeds, and indigenous leaves by two groups of samango monkeys in Hogsback, South Africa: **a** G1 and **b** G2 (February 2011–January 2012).

The seasonal pattern of availability was similar for both indigenous and exotic plant species, but exotics tended to have lower availability year round (Fig. 2). Both groups experienced similar extreme seasonal changes in food availability (Fig. 2) with highly correlated I-FSAI profiles for the two groups ($r = 0.86$, $N = 12$, $P < 0.001$). I-FSAI peaked in summer–autumn (January–April), with a trough in indigenous fruit over winter (June–August). E-FSAI also peaked in late summer (February–March), and declined during winter (June–August) (Fig. 2). However,

Table II Home range size and environmental characteristics of indigenous and matrix habitat types for two groups of samango monkeys (G1, G2) in Hogsback, South Africa (February 2011–January 2012) including densities of important indigenous (red currant) and exotic (black wattle and oak) food species

Home range characteristics	G1	G2
Home range size	27.9ha	22.0ha
Percentage matrix habitat	67%	73%
Indigenous habitat		
Tree density	1593 trees/ha	1467 trees/ha
Species richness	34 species	26 species
% trees of >40cm DBH	7.3	10.0%
Red currant	33 trees/ha	50 trees/ha
Matrix habitat		
Tree density	480 trees/ha	1053 trees/ha
Species richness	23 species	32 species
% trees of >40cm DBH	29.2%	9.2
Black wattle tree density	30 trees/ha	283 trees/ha
Oak tree density	53 trees/ha	0 trees/ha[a]

[a] No oak trees were encountered along transects, as there was only one small grove of oaks planted within this group's home range
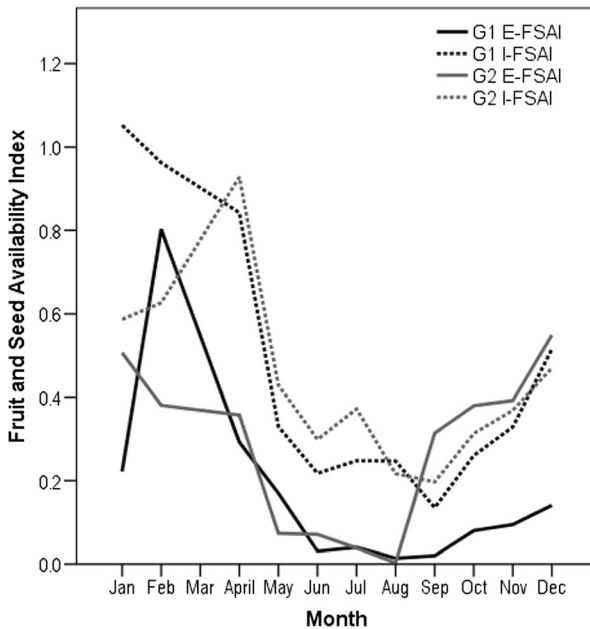
Fig. 2 Monthly variation in the fruit and seed availability index for indigenous (I-FSAI; *dotted*) and exotic (E-FSAI; *solid*) plant species for two groups of samango monkeys in Hogsback, South Africa, G1 (*black*) and G2 (*gray*), from February 2011 to January 2012.

from September to December, E-FSAI in G2 habitat increased more than in G1 habitat, such that the E-FSAI profiles for the two groups did not correlate ($r = 0.38$, $N = 12$, $P = 0.23$). These results reflect the differences in tree density and species richness between the groups' ranges (particularly black wattle and oak).

Determining the Drivers of Exotic Plant Consumption

Despite the prevalence of exotic species in the diet, indigenous food availability was the primary determinant of feeding (Table III). Both groups spent more time feeding on indigenous plant species, as more indigenous fruit and seeds were available. As fewer indigenous fruits and seeds became available and days became longer, monkeys switched to exotic species (Table III), but exotic food availability did not drive overall food choices (ESM Table SII). G2 fed significantly more on indigenous species than did G1. Rainfall was not significant in either model.

Time spent feeding on indigenous fruit increased with I-FSAI, even as day length decreased (in autumn and winter) (Table IV). Indigenous leaves were eaten when exotic fruit and seed availability was low and when days were shorter in winter (Table IV). However, G2 ate more indigenous leaves than G1 (Table IV, Fig. 1). Monkeys from both groups ate more exotic seeds when days were longer (in summer), independent of when exotic or indigenous fruits and seeds were most available.

When we considered black wattle and oak seed consumption separately, different patterns emerged for exotic seeds. Monkeys' diets consisted of >95% black

Table III Linear regression models of time spent feeding (eating and foraging) on indigenous and exotic species each day by samango monkeys in Hogsback, South Africa (February 2011–January 2012), with day length, indigenous fruit, and seed availability (I-FSAI) and group as variables

Indigenous species feeding (h/day)			
r^2	df	F	P
0.42	3,65	15.69	<0.001
Model	B	T	P
Constant	6.02	4.76	<0.001
Day length	−0.54	−5.32	<0.001
I-FSAI	2.33	4.31	<0.001
Group	0.77	2.76	0.008
Exotic species feeding (h/day)			
r^2	df	F	P
0.57	2,66	43.05	<0.001
Model	B	T	P
Constant	−6.72	−4.74	<0.001
Day length	1.01	8.18	<0.001
I-FSAI	−4.19	−6.42	<0.001

Only variables that contributed significantly to the model are shown, with the full model provided in ESM Table SII

wattle seeds on some days (mostly during November–December), while oak acorns accounted for >50% of the diet on some days in winter. The time that monkeys devoted to feeding on black wattle seeds increased with day length but declined with increasing I-FSAI (Table V), suggesting consumption increased when preferred natural fruits were unavailable. In contrast, consumption of oak acorns (especially by G1) increased as day lengths became shorter. Oak seed consumption was not influenced by I-FSAI but increased with E-FSAI (Table V). Interestingly, this result appears to be driven by G2 that had only one small stand of oak trees in its range and acorn availability was thus not reflected in the E-FSAI estimate for this group.

Effects of Exotic Plant Consumption on Activity Budgets

The time monkeys spent both eating and foraging increased with exotic seed consumption, such that feeding overall also increased significantly (Table VI). In contrast, monkeys spent less time moving when feeding on exotic seeds, and this was also reflected in a reduction in their day journey lengths. There was no relationship between feeding on exotics and resting time but increased time spent feeding on exotic seeds significantly decreased the time monkeys had for socializing.

Monkeys' feeding time was unaffected by indigenous fruit consumption but both groups spent more time moving and had longer day journeys the more they fed on indigenous fruits (Table VI). Resting time decreased significantly as a result, but had no effect on social time.

Table IV Linear regression models of time spent feeding (eating and foraging) on indigenous fruit, exotic seed, and indigenous leaves by samango monkeys in Hogsback, South Africa (February 2011–January 2012) with day length, indigenous fruit, and seed availability (I-FSAI); exotic fruit and seed availability (E-FSAI); and group as variables

Indigenous fruit feeding (h/day)			
r^2	df	F	P
0.76	2,66	46.11	<0.001
Model	B	T	P
Constant	1.67	3.04	0.003
I-FSAI	2.40	9.51	<0.001
Day length	−0.18	−3.87	<0.001
Exotic seed feeding (h/day)			
r^2	df	F	P
0.70	1,67	64.75	<0.001
Model	B	T	P
Constant	−7.52	−6.58	<0.001
Day length	0.77	8.05	<0.001
Indigenous leaf feeding (h/day)			
r^2	df	F	P
0.32	3,65	10.24	<0.001
Model	B	T	P
Constant	1.28	1.99	0.051
Day length	−0.11	−2.04	0.046
Group	0.30	3.43	0.001
E-FSAI	−0.88	−2.31	0.024

Only variables that contributed significantly to the model are shown, with full models in ESM Table SIII

Discussion

Two groups of samango monkeys in Hogsback consumed large amounts of exotic plant species. Contrary to an expectation that consumption of exotic fruit and seeds would vary according to exotic fruit and seed availability, the availability of native foods inside indigenous forest and not availability of exotic foods was selected as the primary driver of samango monkeys' foraging decisions in our models. The monkeys ate indigenous species as they became seasonally available, while they targeted exotic plant species when indigenous food availability declined. Day length was a significant factor influencing exotic fruit and seed consumption. Furthermore, the group with greater access to the village (G1) also had greater access and made more use of exotic species. Although previous studies have suggested that monkeys spend less time foraging and moving and more time resting and socializing the more they fed on exotic fruits and seeds, this was not the case in our analysis. Instead, the more the monkeys fed on exotic seeds, the more time they spent feeding and the less time socializing; therefore, a reliance on exotic plants does not appear to free up monkeys' time. While the drivers

Table V Linear regression models of time spent feeding (eating and foraging) on exotic black wattle (*Acacia mearnsii*) and oak (*Quercus robur* and *palustris*) seeds by samango monkeys in Hogsback, South Africa (February 2011–January 2012) with day length, indigenous fruit, and seed availability (I-FSAI); exotic fruit and seed availability (E-FSAI); and group as variables

Black wattle seed feeding (h/day)

r^2	df	F	P
0.50	2,66	33.47	<0.001
Model	B	T	P
Constant	−9.25	−6.49	<0.001
Day length	1.00	8.09	<0.001
I-FSAI	−2.19	−3.34	0.001

Oak seed feeding (h/day)

r^2	df	F	P
0.28	3,65	8.39	<0.001
Model	B	T	P
Constant	3.19	5.30	<0.001
Group	−0.48	−3.96	<0.001
Day length	−0.18	−3.74	<0.001
E-FSAI	0.95	2.69	0.009

Only variables that contributed significantly to the model are shown, with full models in ESM Table SIV

Table VI Partial correlations (controlling for day length and group; $N = 65$ days) of time in activity (feeding is a combination of eating and foraging) and day journey length (DJL) and time spent feeding on indigenous and exotic plant species by samango monkeys in Hogsback, South Africa (February 2011–January 2012)

Activity		Time feeding on indigenous fruit (h/day)	Time feeding on exotic seeds (h/day)
Feeding (h)	Correlation	−0.19	0.63
	P	0.129	**<0.001**
Eating (h)	Correlation	0.23	0.38
	P	0.061	**0.002**
Forage (h)	Correlation	−0.59	0.39
	P	**<0.001**	**0.001**
Move (h)	Correlation	0.75	−0.34
	P	**<0.001**	**0.005**
Rest (h)	Correlation	−0.57	−0.23
	P	**<0.001**	0.061
Social (h)	Correlation	0.04	−0.35
	P	0.754	**0.004**
DJL (m)	Correlation	0.53	−0.26
	P	**<0.001**	**0.031**

Significant relationships are highlighted in bold

of the monkeys' use of the matrix are complex, our analysis suggests that exotic plants represent potential fallback foods in this human-modified and seasonal environment.

The availability of native foods inside indigenous forest was the primary driver of samango monkeys' foraging decisions in Hogsback. Interestingly, however, indigenous fruits contributed a small proportion to the groups' diets (max 18% of total diet), which is at the lower spectrum of what has been observed in other samango and blue monkey populations (17.0–54.6%: Tesfaye *et al.* 2013; 26.3–91.1%: Coleman and Hill 2015). However, because native fruits were targeted as soon as they became available, they appeared to be the monkeys' preferred food item. When indigenous fruit availability declined in winter, both Hogsback groups ate indigenous leaves to extents similar to those of other populations of samango monkeys in South Africa (Coleman and Hill 2015; Lawes 1991). The annual mean amount of leaves eaten by Hogsback monkeys (*ca*. 5–11% of total diet) was again at the lower spectrum of the wide range reported for other populations, e.g., 1.6–51.6% (Coleman and Hill 2015) and 6.7–51.3% (Tesfaye *et al*. 2013). This low to moderate reliance on leaves may be explained by the access that these monkeys have to a matrix planted with exotic species including ones with high-quality (high protein and calorie) seeds.

Compared with other populations, the Hogsback groups have a much higher intake of seeds (*ca*. 40% of total diet) relative to a previously observed range of 0.6–16.5% (Tesfaye *et al*. 2013) and can be described as granivorous. Seed predation by frugivorous primates is viewed as uncommon and possibly a last resort fallback food item (Gautier-Hion *et al*. 1993; Kaplin *et al*. 1998). In fact, indigenous seed consumption by the Hogsback samango monkeys was low (*ca*. 3% of total diet). Given that consumption of exotic seeds did not increase with decreasing availability of indigenous fruits, their role as potential fallback foods is more complicated and best deciphered by examining monkeys' consumption of oak and black wattle seeds separately.

Black wattle seeds appear to be an important fallback food, with both groups eating more of these seeds with decreasing availability of indigenous fruit. These seeds seem to fulfill the description of staple fallback foods, defined by Marshall and Wrangham (2007) as foods available year round, usually eaten throughout the entire year, and in some seasons, constituting the whole diet. Although *Acacia* sp. can have high protein (20%) and fat content, e.g., 68% linoleic oil, black wattle in particular has high tannin content (*ca*. 28.8%: Seigler 2003) and was planted in South Africa for its high total phenolics content for the tannin industry (de Beer 1986). These tannins likely impede the digestive process, and their consumption may explain why Hogsback monkeys exhibit geophagy, which counteracts possible ill effects on digestion, as seen in chacma baboons (Pebsworth *et al*. 2012). Black colobus (*Colobus satanas*: McKey 1978) and Wolf's mona monkey (*Cercopithecus wolfi*: Gautier-Hion *et al*. 1993) have also been observed to eat seeds with high levels of secondary chemicals instead of mature leaves with the same chemicals because of the much higher nutritional value of seeds (more digestible, higher in fats, higher in protein). In line with Lambert's (2007) definition of two types of fallback strategies, Hogsback samango monkeys are thus choosing a high-quality fallback food (seeds) that is less abundant but mechanically protected (hard covering) rather than low-quality (nutrient-poor) fallback foods (mature leaves) that are abundant, but that sometimes require anatomical adaptations; e.g., samango monkeys have hindgut fermentation (Bruorton and Perrin 1988).

As the short winter days coincide with the lowest mean monthly temperatures, and lowest indigenous and exotic fruit–seed availability in Hogsback, this energetic bottleneck places a greater premium on fallback acorns at this time. In fact, day length was an important determinant of diet and behavior in virtually all analyses, confirming its importance as an ecological constraint (Hill 2005; Hill *et al.* 2003, 2004; van Doorn *et al.* 2010). During winter, the two groups appear to use different strategies to survive this period, with G1 relying heavily on acorns (fat and protein rich: Shimada and Saitoh 2006), and G2 relying more on leaves (generally low levels of soluble carbohydrate energy: Hemingway and Bynum 2005; Lambert 2002; Rosenberger 2013). G1 did not increase their consumption of acorns with decreasing availability of indigenous fruit but day length was the key determinant of acorn foraging, with consumption greatest in mid-winter when there was little other food around. Without a measure of fallen food availability, we are unable to state whether the relationship with E-FSAI, largely driven by G2, suggests there could be a preference for acorns in certain situations. As it stands, therefore, consumption of acorns is only partially consistent with Marshall and Wrangham's (2007) definition of fallback food and a more detailed analysis of seasonal acorn availability should be explored further.

Monkeys in G1 significantly increased their time foraging on the ground in gardens in winter as they were eating fallen acorns, despite increased risks from humans and domestic dogs, suggesting these seeds are high-quality food items (energetic gains outweigh risks; see Nowak et al. 2014, 2017, this issue). G1 thus seems to employ a risk-prone strategy (Krebs and Davies 1993; Nowak et al. 2014, 2017, this issue) by searching for patchily distributed clumps of high-quality foods (acorns), which are nutritionally dense but require increased handling time (Lambert 2007). G2 also ate fallen acorns but not to the extent that G1 did, and so seemed to employ a relatively risk-averse strategy, switching to leaves, which are more abundant and evenly distributed (compared to oak trees) and are generally less protein rich and higher in secondary compounds than acorns (Lawes *et al.* 1990; van Schaik *et al.* 1993). The differences in strategy employed by the two groups may be a consequence of the differences in the availability of oak trees (G2 had relatively few oaks in its home range: only one small grove) and possibly vine leaves (G2 had a higher density of large exotic trees) in the two home ranges. More ecological work, including measuring fallen fruit, would be needed to understand better the role of species availability and distribution within these two areas and how it relates to possible behavioral differences between the groups. A further possible explanation of our observed differences in groups' strategies is that G1, whose home range encompasses the village, has learned how to manage anthropogenic risk to a better extent than G2 (no village access) and as a result, exploits exotics in people's gardens in winter while G2 falls back on leaves.

Animals are expected to invest more time in foraging and eating during periods of low food diversity and availability, to feed at the expense of rest time and thus to trade off between energy acquisition and rest (Lawes 1991; Lawes *et al.* 1990; van Schaik *et al.* 1993). Having to spend less time feeding is often associated with increased availability of nutrient dense food sources (Guo *et al.* 2007; Riley 2007). We expected that monkeys would spend less time foraging and moving and more time resting and socializing the more they fed on exotic fruit and seeds. Both indigenous and exotic fruiting species are patchily distributed throughout the

habitat, but exotic tree species (esp. black wattle, oak) occur in large clumps that provide monkeys with high food biomass that can support a group for long periods. Monkeys spent less time moving when consuming exotics compared to indigenous species. However, the time required to extract seeds from the wattle pods and oak acorns meant more overall time spent foraging. Similar patterns have been observed in vervets eating indigenous umbrella thorn tree (*Acacia tortillas*) pods (Isbell and Young 1993) and chacma baboons eating exotic pine nuts (Hoffman and O'Riain 2011). The large amount of time spent foraging could also be due to time spent having to search for the seeds in the leaf litter if they have fallen to the ground. We thus found that monkeys did not have extra time for resting and actually decreased their social time when concentrating their feeding on exotics.

Despite several limitations in our study design, namely 1) our vegetation sampling missing clumps of some exotic species used by monkeys; 2) our lack of foresight to measure availability of fallen fruits (mostly acorns); 3) our lack of precise data on group demography; and 4) our lumping of different stages of plant parts, which may have different nutritional values and digestibility (Lambert and Rothman 2015), as well as the relatively short (1yr) duration of our study, our data strongly suggest that these samango monkeys have become well adapted to a human-modified habitat through their use of exotic plant species. We suggest that people's gradual removal of exotic plant species in the areas of monkeys' known home ranges may facilitate their return to a greater relative use of native fallback foods, as in other groups in the Amathole region that have no access to exotic plant species and still survive the winter.

One consequence of samango monkeys using matrix habitats is that they are brought into closer contact with potential risks from humans and human infrastructure. These monkeys suffer from unquantified morbidity and mortality from electrocutions, cars, pellet-gun wounds, snares, and domestic dogs. Besides the known negative health consequences of living commensally with humans (Estrada *et al.* 2012) and eating food waste (Kemnitz *et al.* 2002), consumption of exotics may have detrimental effects on their health, such as increased wear on teeth, and thus affect longevity (Tordiffe *et al. unpubl. data*). Another further possible consequence of matrix use is a compromise of monkeys' role as seed dispersers in indigenous forests (Linden *et al.* 2015) if they are predominately eating and dispersing exotics. Reproductive rates might become artificially high as a result of exotic species intake, as found elsewhere (Siex and Struhsaker 1999; Singh *et al.* 2001), possibly increasing human–primate conflict.

To manage these matrix-using samango monkey groups, we recommend 1) phasing out the planting of exotic species, 2) active planting of indigenous species in gardens, and 3) removal of fallen black wattle and oak seeds where and when possible before and during the winter season. We also recommend that groups without access to exotic plant species be studied to enable comparisons with the groups we studied to help inform management of this southernmost, behaviorally distinct and seasonally limited population of African guenons.

Compliance with Ethical Standards

Conflicts of interest   The authors have no conflict of interest and no competing financial interests.

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