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AFRICA'S FORGOTTEN FORESTS: THE CONSERVATION VALUE OF KENYA'S NORTHERN COASTAL FORESTS FOR LARGE MAMMALS

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ABSTRACT

In comparison to other ecosystems in east Africa, the biodiversity of the coastal forests of Kenya's northern coastline is poorly documented, even in the case of large terrestrial mammals. In response to this, we undertook a systematic survey of the Boni-Dodori forests using four camera trap grids with camera spacing of 2 km covering 300 km^2 over 7020 camera trap days. We recorded 37 mammal species and derived camera trap rates and estimated occupancy for 31 medium-to-large terrestrial species, some of which represent range extensions. Remarkably, the critically endangered Aders' duiker was the most frequently recorded species. A distinctive form of giant sengi and the vulnerable Sokoke bushy-tailed mongoose were also widely distributed and relatively abundant. Other significant records of threatened species included African wild dog, African lion and Pousargues's monkey. Species richness and relative abundance of all species were higher than that recorded for

Arabuko-Sokoke Forest, Kenya's only other large coastal forest, using the same camera trap survey protocol.

Keywords: Boni-Dodori forest, coastal forest, camera trapping, mammals, species richness, trap rates, occupancy

INTRODUCTION

The mosaic of grassland, bushland, thicket, woodland, and forest of coastal Kenya lies within the 'Coastal Forest Mosaic Biotic Zone' (figure 3 in Happold & Lock, 2013) and 'Northern Zanzibar-Inhambane Coastal Forest Mosaic Ecoregion' (WWF, 2016). It also lies within the 'Coastal Forests of Eastern Africa Biodiversity Hotspot', known for globally significant levels of species richness and endemism (Burgess & Clarke, 2000). Although natural habitats over much of this Hotspot have been greatly altered by urban development, exploitation of natural products, and agriculture (Mittermeier *et al.*, 2005), several protected areas exist on Kenya's coast.

Boni National Reserve (1339 km²), Dodori National Reserve (NR) (877 km²), and Boni-Ijara Forest Reserve (FR) (*ca.* 1400 km²) are located on the extreme north coast of Kenya (figure 1). These three reserves, and their surroundings, comprise the 'Boni-Dodori Forest Complex' (*ca.* 4000 km²; Oduori, 1990; Amin *et al.*, 2015; Musina *et al.,* 2016). The 'Boni-Dodori Forest Complex' is, hereafter, referred to as 'Boni-Dodori'.

The biodiversity status of Boni-Dodori is poorly known due to political insecurity and difficult logistical problems limiting access to the area. During the April and October–November wet seasons, roads often become impassable. These conditions have contributed to low human population density (<3 people/km²) and minimal development in the region. The Aweer, who had lived throughout the Boni-Dodori forest, were forcibly moved by the state at the time of the Shifta War (1963–1967) to settlements along the Bothei Junction – Kiunga road. An estimated 1,500 Aweer live in the forest today, still located at the settlements of Milimani, Basuba, Mangai and Mararani, and at Kiangwe on the Dodori Creek (Musina *et al.*, 2016). The population living in the forest is likely to have declined over recent decades. The people, traditionally hunter gatherers, have been persuaded to engage in small-scale, largely subsistence agriculture, much of it dominated by maize cultivation. The national hunting ban of 1977 greatly impacted local livelihoods – albeit some small scale hunting may continue – and 'gathering' (*e.g.* wild yams, fruits, honey) from the forests remains an important activity (Morris *et al.*, 2011; p 48). The knowledge systems of the Aweer remain poorly understood, but are inevitably closely linked to the biodiversity and ecosystem functions of the forests.

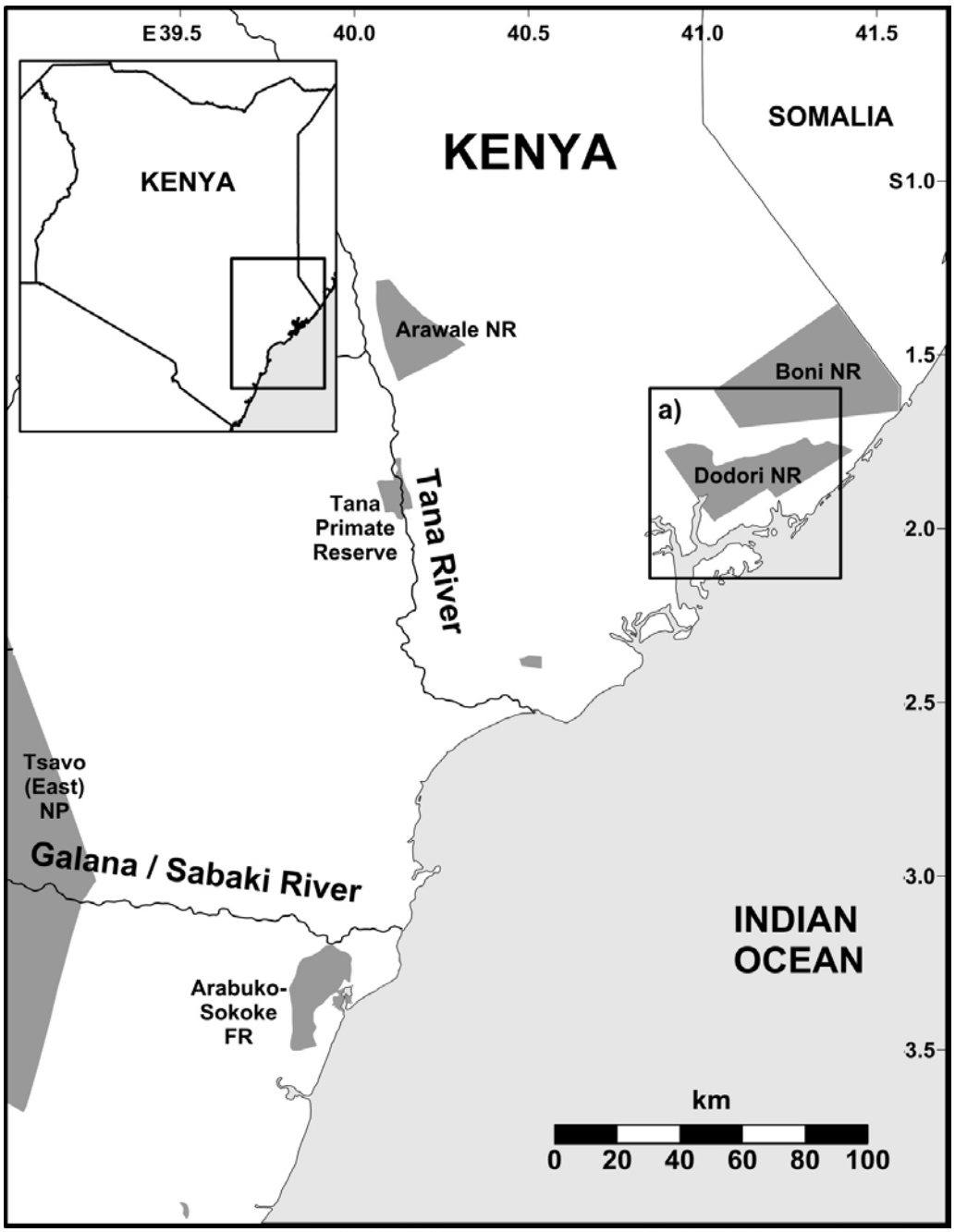

Figure 1. Location of the Boni-Dodori Forest Complex study site, north coast of Kenya. Terrestrial protected areas are in grey.

The use of camera traps to survey medium-to-large size terrestrial mammals has become increasingly common (Ahumada *et al*., 2011; O'Connell *et al*., 2011). It is a particularly suitable technique in forest habitats with advantages over traditional methods (Amin *et al*.,

2016). We based our mammal survey in the Boni-Dodori on a standardized camera trapping approach using a systematic grid layout (Tobler *et al.*, 2008; Ahumada *et al.*, 2011). The main objective of our study was to establish baseline data on the medium-to-large sized mammal communities of the Boni-Dodori as part of developing a longer-term conservation and management plan for the area.

MATERIALS AND METHODS

Study area

Boni–Dodori is mainly located on a flat plain with a braided drainage system separated by marine sands and clay ridges. Towards the coast, several parallel fossilised sand dunes run southwest-northeast, the highest reaching *ca*. 100 m on Sankuri Ridge (Musina *et al.*, 2016). Mean annual rainfall ranges from 500 mm in the north-east to 800 mm in the south-west.

The forests of Boni-Dodori consists of 10–15 m high trees and a dense understory interspersed by grassland, bushland, and thicket. Boni-Ijara FR and Boni NR hold an extensive forest of scattered tall trees and dense understory that is bordered by acacia woodland and scrub towards the coast. Dodori NR features seasonally flooded grassland with doum palm *Hyphaene compressa* H.Wendl. and patches of forest and thicket. Dodori NR also supports a gradation to more open habitats, not found at the other sites, along its southern coastal margin. Forest trees in Boni-Dodori include mbamba-kofi *Afzelia quanzensis* Welw., tamarind *Tamarindus indica* L., *Croton megalocarpoides* Friis & M.G.Gilbert, *Asteranthe asterias* (S.Moore) Engl. & Diels, *Grewia plagiophylla* K.Schum., *Manilkara* spp., *Diospyros* spp., and *Acacia* spp., mainly on white or grey sandy soil. *Ochna* spp. shrubs and *Fernandoa magnifica* Seem. trees occur on the red sandy soil of Sankuri Ridge (Oduori, 1990; Musina *et al.,* 2016).

Field sampling methods

We set up four camera trap grids with camera spacing of two km in the Boni NR (20 cameras covering 44 km^2 centered on 1°32'13''S, 41°19'32''E) between 17 March 2010 and 17 June 2010, Dodori NR (20 cameras covering 44 km^2 1°49'19''S, 41°04'28''E) between 14 January 2010 and 16 March 2010, Boni-Ijara FR (20 cameras covering 44 km^2 1°40'34''S, 40°52'32''E) between 19 June 2010 and 6 September 2010, and in the open coastal scrub habitat south of the Dodori NR (22 cameras covering 36 km^2 1°51'11''S, 41°19'09''E) between 27 February 2015 and 27^{t} July 2015 (figure 2).

Global Positioning System (Garmin GPS c60) receivers were used to place each camera within 100 m of each grid point. Cameras were positioned 30–45 cm above ground and pointed to a target zone 4–8 m away (often perpendicular to a game trail). The intention was to capture full body lateral photographs of mammals. Reconyx RM45 (RECONYX Inc., Holman, Wisconsin, USA) digital cameras were used. Cameras were programmed to take three photographs per trigger with no delay. All cameras used an infrared flash night (or at low light levels in the day time) to minimise startling the animals.

Each grid was operated for a sufficient duration to achieve at least 1000 camera trap days of sampling effort (O'Brien *et al.*, 2003). Field personnel were trained and tested in their ability to deploy camera traps to obtain a well-defined and consistent camera field of view. Upon camera set-up, they triggered each camera while holding a white board on which was written the location ID, date and time. This was repeated upon camera recovery.

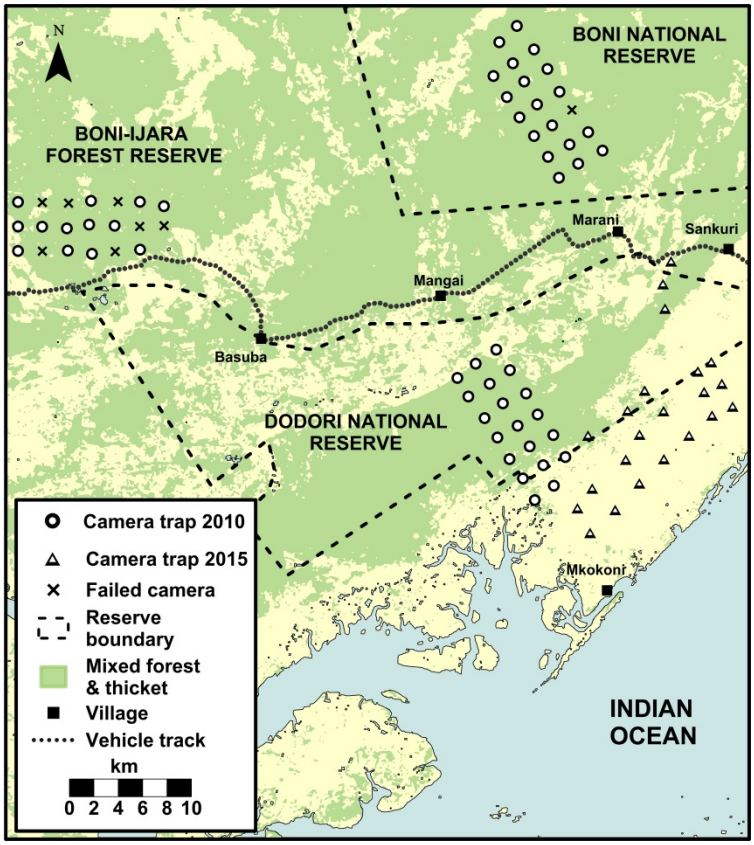

Figure 2. Location of camera trap grids in Boni-Dodori Forest Complex, Kenya.

Data analysis

Exiv2 software (Huggel, 2012) was used to extract EXIF information from each photograph (image name, date and time). Species of animals in the photographs were identified (when possible). These data were compiled in an Excel spreadsheet (Microsoft Office Professional Plus 2010) and analysed with software developed specifically for camera trap data analysis (Amin & Wacher, 2017).

Only terrestrial mammal species that have an estimated average mass greater than 0.5 kg (medium-to-large mammals) were considered for the analyses as they are the main target group for camera traps placed at ground level. Smaller mammals induce sampling error through reduced likelihood of detection by the camera trap thermal sensor and accurate identification of small mammals to species level is often not possible from camera traps set up for medium-to-large mammals (Tobler *et al.*, 2008).

We calculated species sample-based rarefaction curves and estimated the medium-to-large ($>$0.5 kg) terrestrial mammal species richness for each area using the non-parametric incidence-based estimator Jackknife with order one (Bunge & Fitzpatrick, 1993).

We calculated Simpson's diversity index and Shannon-Wiener diversity index for each area from species daily trap rates using package *vegan* in *R statistical software* (Oksanen *et al.*, 2017). Simpson's diversity index is most sensitive to changes in more common highly

abundant species while Shannon-Wiener diversity index is most sensitive to changes in rare less abundant species (Magurran, 2004). To allow for ease of interpretation, Shannon-Wiener diversity index was converted to the Effective Number of Species, *i.e.* the number of equally-common species required to give a particular value of an index (Jost, 2006).

We calculated the trap rate for each species as the mean number of independent photographic "events" per trap day x 100. We defined an "event" as any sequence for a given species occurring after an interval of $=>60$ min from the previous three-image sequence of that species (Amin *et al.*, 2015).

We used single season occupancy analysis (MacKenzie *et al.*, 2006) to estimate proportion of area occupied for those species whose home ranges are less than the camera spacing of 2 km. Modelled occupancy can therefore be used as an index of abundance for these species under assumption of constant home range (Efford & Dawson, 2012). For species with home range greater than camera spacing, modelled occupancy can be interpreted as extent of area use across the surveyed area. We constructed a detection / non-detection history, using a ten-day period as the sampling occasion, for each species and camera per survey grid. We tested for significant differences in species occupancy between sites using the "Wald" parametric statistical test with $P< 0.05$ considered to be significant (Amin *et al.*, 2015).

RESULTS

A minimum effort of 1000 camera trap days was obtained for each of the four camera grids. Total camera trap days was 7020 (mean 95 days/camera). Due to political insecurity, the retrieval of cameras south of Dodori NR was delayed. Here, cameras were retrieved after 3240 camera trap days (mean 147 days/camera).

A total of 31 medium-to-large terrestrial mammal species were photographed in Boni-Dodori (22 species in Boni NR; 26 species in Dodori NR; 20 species in Boni-Ijara FR and 24 species in the open coastal scrub habitat south of the Dodori NR) (table 1). We also recorded small soft-furred sengi but we were unable to distinguish in the images possible two species: rufous sengi *Elephantulus rufescens* and four-toed sengi *Petrodromus tetradactylus* that are known to co-occur in coastal forests in Kenya. We have therefore included both species. In addition, the survey recorded four medium-to-large arboreal species; Pousargues's Sykes' monkey *Cercopithecus mitis albotorquatus*, vervet monkey *Chlorocebus pygerythrus*, red bush squirrel *Paraxerus palliatus* and at least one unidentified galago species (table 1).

Seven medium-to-large terrestrial mammal species expected in the surveyed habitats according to IUCN (2017) distribution maps and literature were not detected by the camera trap surveys (table 2). Also, no images of people were recorded.

The species accumulation curves for medium-to-large terrestrial mammal species in Boni-Dodori are shown in figure 3. Dodori NR had much higher estimated species richness (31) and Boni-Ijara forest the lowest with 22 species (table 3). Aders' duiker *Cephalophus adersi* and suni *Nesotragus moschatus* were the most frequently encountered species accounting for 86.6%, 79%, 84.9% and 65.9% of the total medium-to-large terrestrial species trap rates in Boni NR, Boni-Ijara FR, Dodori NR and south of Dodori NR respectively. This dominance by Aders'duiker and suni is reflected in the low Shannon-Wiener and Simpson diversity indices (table 3).

Table 1. Mammal species recorded in Boni-Dodori Forest Complex, Kenya.DNR: Dodori National Reserve; BNR: Boni National Reserve; BIF: Boni-Ijara forest; DNR-S: Dodori National Reserve—mainly south of the reserve. IUCN status: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC).

Species	Trophic leve	Habit	Habitat	Body weight (k	IUCN status	DNR	BNR	BIF	DNR-S
African civet *Civettictis civetta* (Schreber, 1776)	Carnivore	Terrestrial	Savanna / woodland	12	LC	Y	N	N	Y
African lion *Panthera leo* (Linnaeus, 1758)	Carnivore	Terrestrial	Savanna / woodland	133.25	VU	N	N	Y	N
African wild dog *Lycaon pictus* (Temminck, 1820)	Carnivore	Terrestrial	Savanna / woodland	22.7	EN	N	Y	N	Y
Caracal *Caracal caracal* (Schreber, 1776)	Carnivore	Terrestrial	Savanna / woodland	11.45*	LC	Y	Y	N	Y
Common dwarf mongoose *Helogale parvula* (Sundevall, 1847)	Carnivore	Terrestrial	Savanna / woodland	0.267	LC	Y	Y	Y	Y
Honey badger *Mellivora capensis* (Schreber, 1776)	Carnivore	Terrestrial	Mixed habitat	10.6*	LC	Y	Y	Y	Y
Large-spotted genet *Genetta maculata* (Gray 1830)	Carnivore	Terrestrial	Forest	1.75	LC	Y	Y	Y	Y
Leopard *Panthera pardus* (Linnaeus, 1758)	Carnivore	Terrestrial	Mixed habitat	49.75	NT	Y	Y	Y	Y
Marsh mongoose *Atilax paludinosus* (G.[Baron] Cuvier, 1829)	Carnivore	Terrestrial	Mixed riverin	3.4	LC	Y	N	N	N
Slender mongoose *Herpestes sanguineus* (Rüppell, 1835)	Carnivore	Terrestrial	Savanna	0.548	LC	Y	N	Y	Y
Sokoke bushy-tailed mongoose *Bdeogale omnivora* Heller, 1913	Carnivore	Terrestrial	Forest	1.15	VU	Y	Y	Y	Y
Spotted hyaena *Crocuta crocuta* (Erxleben, 1777)	Carnivore	Terrestrial	Savanna / woodland	52	LC	Y	Y	Y	Y
White-tailed mongoose *Ichneumia albicauda* (G.[Baron] Cuvier, 1829)	Carnivore	Terrestrial	Savanna / woodland	4.315	LC	N	Y	N	Y
Aders' duiker *Cephalophus adersi* Thomas, 1918	Herbivore	Terrestrial	Forest	9.15	CR	Y	Y	Y	Y

Species	Trophic level	Habit	Habitat	Body weight (kg)	IUCN status	DNR	BNR	BIF	DNR-S
African buffalo *Syncerus caffer* (Sparrman, 1779)	Herbivore	Terrestrial	Savanna / woodland	598.7	LC	Y	Y	Y	Y
African elephant *Loxodonta africana* (Blumenbach, 1797)	Herbivore	Terrestrial	Mixed habitats	4640	VU	Y	Y	Y	Y
Blue duiker *Philantomba monticola* (Thunberg, 1789)	Herbivore	Terrestrial	Forest	5.05	LC	N	Y	N	N
Bushbuck *Tragelaphus scriptus* (Pallas, 1766)	Herbivore	Terrestrial	Woodland	35	LC	Y	Y	Y	Y
Common hippopotamus *Hippopotamus amphibius* Linnaeus, 1758	Herbivore	Semi-aquatic	Riverine savanna	1465.5	VU	Y	N	N	N
Harvey's duiker *Cephalophus harveyi* (Thomas, 1893)	Herbivore	Terrestrial	Forest	11.4	LC	Y	Y	Y	Y
Kirk's dik-dik *Madoqua kirkii* (Günther, 1880)	Herbivore	Terrestrial	Savanna / woodland	4.88	LC	Y	N	N	Y
Lesser kudu *Tragelaphus imberbis* (Blyth, 1869)	Herbivore	Terrestrial	Savanna / woodland	93.75	NT	Y	N	N	Y
Suni *Nesotragus moschatus* Von Dueben, 1846	Herbivore	Terrestrial	Forest	5.2*	LC	Y	Y	Y	Y
Waterbuck *Kobus ellipsiprymnus* (Ogilby, 1833)	Herbivore	Terrestrial	Savanna / woodland	211	LC	Y	N	N	N
Aardvark *Orycteropus afer* (Pallas, 1766)	Insectivore	Terrestrial	Mixed habitats	52.35	LC	Y	Y	Y	Y
Boni giant sengi *Rhynchocyon* sp.	Insectivore	Terrestrial	Forest	0.6		Y	Y	Y	Y
Four-toed sengi *Petrodromus tetradactylus* Peters, 1846	Insectivore	Terrestrial	Forest	0.2	LC	Y	Y	Y	Y
Rufous sengi *Elephantulus rufescens* (Peters, 1878)	Insectivore	Terrestrial	Forest	0.2	LC	Y	Y	Y	Y
Bushpig *Potamochoerus larvatus* (F. Cuvier, 1822)	Omnivore	Terrestrial	Savanna / woodland	70.6*	LC	Y	Y	Y	Y
Common warthog *Phacochoerus africanus* (Gmelin, 1788)	Omnivore	Terrestrial	Savanna woodland	68.05	LC	Y	Y	Y	N
Desert warthog *Phacochoerus aethiopicus* (Pallas, 1766)	Omnivore	Terrestrial	Savanna / woodland	72.5	LC	N	N	Y	N

Table 2. Medium-to-large terrestrial mammal species expected in Boni-Dodori Forest Complex, Kenya according to IUCN species distribution maps and literature, but not detected in the camera trap surveys. IUCN status: Vulnerable (VU), Least Concern (LC).

Species	Habitat	IUCN Status
African hedgehog *Atelerix albiventris* (Wagner, 1841)	Savanna / Woodland	LC
Wild cat *Felis silvestris lybica* Schreber, 1777	Mixed habitats	LC
Serval *Leptailurus serval* (Schreber, 1776)	Savanna / Woodland	LC
Egyptian mongoose *Herpestes ichneumon* (Linnaeus, 1758)	Savanna / Woodland	LC
Zorilla *Ictonyx striatus* (Perry, 1810)	Savanna / Woodland	LC
Guenther's dik-dik *Madoqua guentheri* Thomas, 1894	Savanna / Woodland	LC
Haggard's oribi *Ourebia ourebi haggard* (Thomas, 1895)	Savanna / Woodland	VU
Common duiker *Sylvicapra grimmia* (Linnaeus, 1758)	Savanna / Woodland	LC

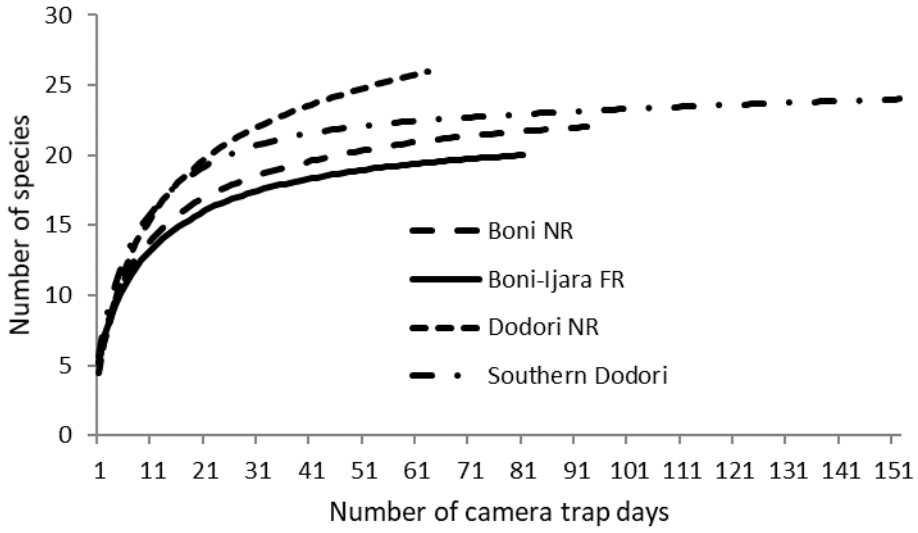

Figure 3. Rarefied species accumulation curves for medium-to-large terrestrial mammals in Boni-Dodori Forest Complex, Kenya.

Forest antelopes

We recorded 5449 independent photographic events of four species of forest antelopes. Aders' duiker, Harvey's duiker *Cephalophus harveyi* and suni were photographed in all four sampling sites. Blue duiker *Philantomba monticola* was recorded only in the Boni NR at one site with two events. The common duiker *Sylvicapra grimmia*, documented to occur in the region (Wilson 2013; IUCN, 2017) and known to prefer more open habitats, was not recorded, probably reflecting the deliberate selection of more forested habitat for the camera trap arrays. Overall, the

Table 3. Medium-to-large terrestrial mammal species richness and diversity estimates for Boni-Dodori Forest Complex, Kenya. The effect number of species is calculated as the exponential of the Shannon-Wiener diversity index.

Species	Trophic Level	*Cynometra* forest		*Brachystegia* and mixed forest	
		Trap rate	Occupancy (SE)	Trap rate	Occupancy (SE)
African civet, *Civettictis civetta*	Carnivore	0.29	0.279 (0.184)	0.92	0.885 (0.449)
Caracal, *Caracal caracal*	Carnivore	0.59	0.351 (0.223)	0.43	0.410 (0.286)
Honey badger, *Mellivora capensis*	Carnivore	0.61	0.351 (0.154)	1.54	0.715 (0.248)
Large-spotted genet, *Genetta maculata*	Carnivore	15.93	1 (0)	9.37	0.891 (0.079)
Slender mongoose, *Herpestes sanguineus**	Carnivore	0.13	0.043	0	0
Sokoke bushy-tailed mongoose, *Bdeogale omnivora**	Carnivore	1.11	0.225 (0.089)	4.98	0.527 (0.136)
Spotted hyaena, *Crocuta crocuta*	Carnivore	0	0	0.12	0.059
White-tailed mongoose, *Ichneumia albicauda**	Carnivore	0.16	0.082 (0.087)	1.04	0.484 (0.3)
Aders' duiker, *Cephalophus adersi**	Herbivore	0.08	0.043	0	0
African buffalo, *Syncerus caffer*	Herbivore	0	0	0.12	0.118
African elephant, *Loxodonta africana*	Herbivore	0.65	0.336 (0.163)	0	0
Blue duiker, *Philantomba monticola**	Herbivore	4.51	0.588 (0.108)	0.84	0.064 (0.062)
Bushbuck, *Tragelaphus scriptus**	Herbivore	0.21	0.224 (0.140)	0.99	0.432 (0.233)
Common duiker, *Sylvicapra grimmia**	Herbivore	0	0	0.48	0.118
Harvey's duiker, *Cephalophus harveyi**	Herbivore	0.53	0.999 (0.095)	0.13	0.249 (0.254)
Suni, *Nesotragus moschatus**	Herbivore	29.66	1 (0)	25.06	0.961 (0.059)
Aardvark, *Orycteropus afer+*	Insectivore	0.39	0.174	0	0
Golden-rumped sengi, *Rhynchocyon chrysopygus**	Insectivore	13.17	0.998 (0.028)	13	0.718 (0.112)
Bushpig, *Potamochoerus larvatus+*	Omnivore	0.44	0.999 (0.033)	0.45	0.701 (0.543)
Crested porcupine, *Hystrix cristata+*	Omnivore	0.16	0.043	0.15	0.059
Northern giant pouched rat, *Cricetomys gambianus**	Omnivore	3.8	0.435 (0.104)	11.82	0.721 (0.113)
Yellow baboon, *Papio cynocephalus*	Omnivore	0.12	0.092 (0.062)	6.02	0.786 (0.124)

two more inland forests had much higher and similar trapping rates for the three forest antelope species (figure 4).

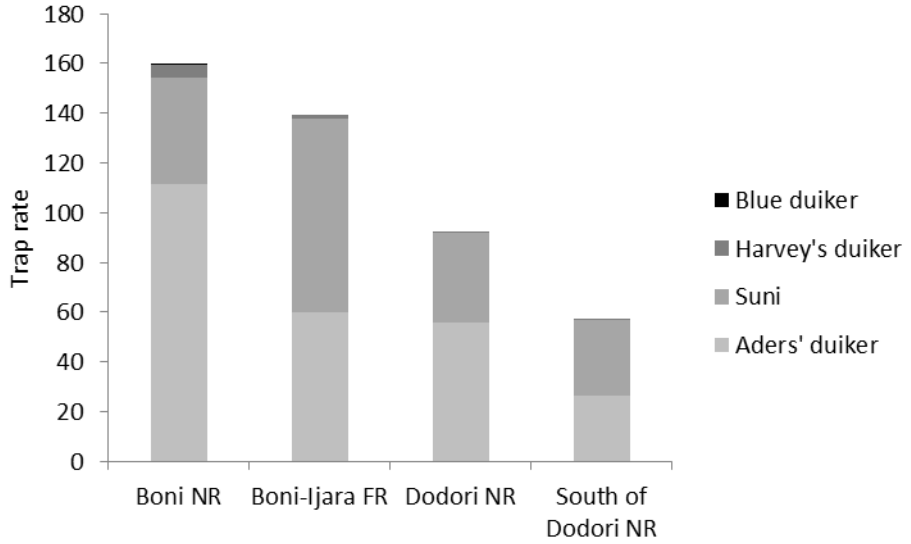

Figure 4. Trap rate (mean camera trap events/day x 100) for forest antelope species recorded at each of the four Boni-Dodori Forest Complex sites, Kenya.

The Critically Endangered Aders' duiker was detected at all operational camera sites in Boni NR and Boni-Ijara FR, resulting in modelled occupancy estimates ( ) of 1, with = 0.95 (SE = 0.05) in the Dodori NR and = 0.86 (SE = 0.073) in the habitat south of Dodori NR (table 4).

Occupancy estimates indicate Harvey's duiker is more widely distributed in the two more inland forests at Boni (> 0.7) than nearer the coast in Dodori (< 0.2, P < 0.005) (table 4). Suni were widely distributed in all four forests with no significant difference in occupancy estimates between the four sites (>= 0.95; P > 0.3) (table 4).

Carnivores

Thirteen species of carnivore were recorded. The Endangered African wild dog *Lycaon pictus* (IUCN, 2017) was recorded on three occasions in Boni NR in 2010 and on one occasion in the coastal strip south of Dodori NR in 2015. At least three individuals were observed. The African lion *Panthera leo* (Vulnerable; IUCN, 2017) was only recorded once in the Boni-Ijara FR. The leopard *Panthera pardus* (Near-Threatened; IUCN, 2017) was the most frequently recorded large carnivore in Boni-Dodori and more widely encountered in the Boni forests (>= 0.8) than in the Dodori forest (< 0.3) (table 4). Photograph sequences showing pairs of leopards, including a mother resting and playing with a well grown cub, and several instances of leopards inspecting and marking cameras suggest a well-established population and confident, curious behaviour of this species in front of camera traps.

Caracal *Caracal caracal* were recorded at moderate levels in Boni NR and both Dodori grids, particularly in the more open habitats of the southern Dodori grid, where an adult walking with a juvenile was recorded in April 2015.

The Sokoke bushy-tailed mongoose *Bdeogale omnivora* (Vulnerable; IUCN, 2017) was found to be widely distributed with occupancy ranging from 0.49 to 0.71 across the four sampling sites (table 4). There was no significant difference in occupancy ($P > 0.3$).

Afrotheria

The African elephant *Loxodonta africana* (Vulnerable; IUCN, 2017) was infrequently detected at 13 of the 81 sampling sites in all four areas (table 4). A herd of 26 with at least five young were recorded passing a camera in the Boni-Ijara FR. The aardvark *Orycteropus afer* was recorded in all four areas at 17 out of the 81 sites and 28 events, all at night.

All the giant sengis photographed in Boni-Dodori lacked the golden rump typical of *Rhynchocyon chrysopygus* (Günther, 1881) found in the Arabuko-Sokoke forest (Amin *et al.*, 2017). They were also more abundant in Boni NR and Boni-Ijara NR camera trap grids (> = 0.8) than in the Dodori grids (< 0.2), with a significant difference in occupancy ($P < 0.001$) (table 4). The surveys also generated over 32 000 camera trap images of soft-furred sengi (possibly of two species, see above) mostly recorded at night in contrast to the strictly diurnal behaviour of the giant sengi. The study provided the first detailed 24-hour behaviour data comparing giant and soft-furred sengis simultaneously (Amin *et al.*, 2017).

Suids

Desert warthog *Phacochoerus aethiopicus* was captured at one camera site during two events in Boni-Ijara FR (Amin *et al.*, 2017). One event involved an adult male being closely followed by a sub-adult female. The second event involved an old adult female. These records represent a minor east and northeast range extension of some 20–25 km (Obanda *et al.* 2011, De Jong & Butynski 2011, 2017).

Common warthog *Phacochoerus africanus* was recorded at two camera sites (four events) in Boni-Ijara FR, at one camera site in Boni NR (one event), and at one camera site (one event) in Dodori NR.

Bushpig *Potamochoerus larvatus* was captured at 33 camera sites (59 events) in Boni-Dodori, being widespread both in thicket and scrub. Trap rate was highest in scrub south of Dodori NR (table 4).

DISCUSSION

The study has confirmed that the Boni-Dodori is of major importance to mammal conservation within the eastern Africa coastal biodiversity hotspot, with indications that it remains relatively undisturbed, holding complete communities of predators and herbivores. Thirty-seven mammal species were recorded in Boni-Dodori with 31 forest and mixed habitat terrestrial medium-to-large mammal species. In comparison, in Arabuko-Sokoke forest, the only other large coastal forest reserve south of the Tana River, our comparative camera trap survey using identical field protocols and analysis, recorded 28 mammal species of which 22 were forest and mixed habitat terrestrial medium-to-large mammal species (table 5). Community structure of mammals differed substantially between Boni-Dodori and Araboko-Sokoke forests (figure 5 and 6). The results indicate reduction (or elimination) of larger carnivores in Arabuko-Sokoke forest compared to Boni-Dodori, where their absence may relate to the evident relative increase in small carnivores, particularly the large-spotted genet. The results also show much higher occurrence of smaller forest antelopes in Boni-Dodori

Table 4. Medium-to-large terrestrial mammal species recorded in Boni-Dodori Forest Complex, Kenya. For each site and species, we present the mean number of independent photographic events per trap day times 100 and the modelled occupancy estimates (□) with standard error (in brackets). Where data is insufficient for occupancy modelling, naïve occupancy is presented in square brackets. Species indicated with '' have home ranges < camera spacing of 2 km and species indicated with '+' have no documented home ranges in forest systems. DNR: Dodori National Reserve; BNR: Boni National Reserve; BIF: Boni-Ijara forest; DNR-S: Dodori National Reserve - mainly south of reserve*

Species	DNR		BNR		BIF		DNR-S	
	Trap rate	□□□SE)	Trap rate	□□□SE)	Trap rate	□□□SE)	Trap rate	□□□SE)
African civet *Civettictis civetta*	0.36	[0.15]	0	0	0	0	0.09	[0.09]
African lion *Panthera leo*	0	0	0	0	0.10	[0.08]	0	0
African wild dog *Lycaon pictus*	0	0	0.18	[0.16]	0	0	0.03	[0.05]
Caracal *Caracal caracal*	0.36	[0.15]	0.37	0.12 (0.09)	0	0	0.75	0.62 (0.21)
Honey badger *Mellivora capensis*	0.18	[0.10]	0.24	[0.21]	0.10	[0.08]	0.38	0.25 (0.10)
Large-spotted genet *Genetta maculata*	2.91	0.75 (0.14)	0.48	[0.37]	0.90	0.64 (0.24)	3.40	0.87 (0.07)
Leopard *Panthera pardus*	0.36	[0.20]	1.22	0.81 (0.24)	4.20	0.99 (0)	0.31	[0.27]
Marsh mongoose *Atilax paludinosus**	0.09	[0.05]	0	0	0	0	0	0
Slender mongoose *Herpestes sanguineus**	0.09	[0.05]	0	0	0.20	[0.08]	0.03	[0.05]
Sokoke bushy-tailed mongoose *Bdeogale omnivora**	1.55	0.56 (0.19)	3.27	0.71 (0.11)	4.30	0.63 (0.14)	0.41	0.49 (0.20)
Spotted hyaena *Crocuta crocuta*	0.82	0.27 (0.14)	0.48	[0.26]	0.80	0.40 (0.19)	0.31	[0.32]
White-tailed mongoose *Ichneumia albicauda**	0	0	0.06	[0.05]	0	0	0.75	0.34 (0.11)
Aders' duiker *Cephalophus adersi**	56.07	0.95 (0.05)	111.55	1 (0)	60.14	1 (0)	26.48	0.86 (0.07)
African buffalo *Syncerus caffer*	1.48	0.35 (0.13)	1.24	0.11 (0.07)	0.49	0.39 (0.14)	0.41	0.34 (0.13)

Species	DNR		BNR		BIF		DNR-S	
	Trap rate	□□□SE)	Trap rate	□□□SE)	Trap rate	□□□SE)	Trap rate	□□□SE)
African elephant *Loxodonta africana*	0.27	[0.10]	0.12	[0.11]	1.20	0.24 (0.12)	0.22	[0.23]
Blue duiker *Philantomba monticola**	0	0	0.12	[0.05]	0	0	0	0
Bushbuck *Tragelaphus scriptus**	3.36	0.51 (0.12)	1.09	0.17 (0.09)	0.40	[0.08]	1.53	0.65 (0.12)
Common hippopotamus *Hippopotamus amphibius*	0.09	[0.05]	0	0	0	0	0	0
Harvey's duiker *Cephalophus harveyi**	0.27	0.16 (0.14)	5.34	0.71 (0.11)	1.40	0.79 (0.28)	0.13	[0.09]
Kirk's dik-dik *Madoqua kirkii**	0.09	[0.05]	0	0	0	0	6.35	0.23 (0.09)
Lesser kudu *Tragelaphus imberbis**	0.36	0.16 (0.14)	0	0	0	0	8.63	0.78 (0.09)
Suni *Nesotragus moschatus**	35.66	1 (0)	42.71	0.95 (0.05)	77.72	1 (0)	30.29	0.96 (0.04)
Waterbuck *Kobus ellipsiprymnus*	0.09	[0.05]	0	0	0	0	0	0
Aardvark *Orycteropus afer*+	0.36	[0.15]	0.42	[0.32]	0.50	[0.31]	0.37	0.20 (0.10)
Boni giant sengi *Rhynchocyon* sp.*	1.46	0.15 (0.08)	5.38	0.80 (0.10)	7.89	0.85 (0.10)	0.72	0.18 (0.08)
Bushpig *Potamochoerus larvatus*+	0.55	[0.25]	0.79	[0.53]	0.90	0.40 (0.19)	0.94	0.85 (0.21)
Common warthog *Phacochoerus africanus**	0.09	[0.05]	0.06	[0.05]	0.40	[0.15]	0	0
Desert warthog *Phacochoerus aethiopicus*+	0	0	0	0	0.20	[0.08]	0	0
Northern giant pouched rat *Cricetomys gambianus**	0.55	[0.20]	2.25	0.58 (0.13)	2.20	0.40 (0.14)	0.50	0.19 (0.08)
Porcupine *Hystrix* sp.+	0.93	[0.25]	0.42	0.11 (0.07)	0.60	0.48 (0.27)	0.50	0.42 (0.15)
Yellow baboon *Papio cynocephalus*	0.82	[0.25]	0.12	[0.11]	0	0	1.49	0.46 (0.11)

Table 5. Medium-to-large terrestrial mammal species recorded in Arabuko-Sokoke Forest, Kenya. For each site and species, we present the mean number of independent photographic events per trap day times 100 and the modelled occupancy estimates (□) with standard error (in brackets). Where data is insufficient for occupancy modelling, naïve occupancy is presented in square brackets.

Species	Trophic Level	Cynometra forest		Brachystegia and mixed forest	
		Trap rate	Occupancy (SE)	Trap rate	Occupancy (SE)
African civet, *Civettictis civetta*	Carnivore	0.29	0.279 (0.184)	0.92	0.885 (0.449)
Caracal, *Caracal caracal*	Carnivore	0.59	0.351 (0.223)	0.43	0.410 (0.286)
Honey badger, *Mellivora capensis*	Carnivore	0.61	0.351 (0.154)	1.54	0.715 (0.248)
Large-spotted genet, *Genetta maculata*	Carnivore	15.93	1 (0)	9.37	0.891 (0.079)
Slender mongoose, *Herpestes sanguineus**	Carnivore	0.13	0.043	0	0
Sokoke bushy-tailed mongoose, *Bdeogale omnivora**	Carnivore	1.11	0.225 (0.089)	4.98	0.527 (0.136)
Spotted hyaena, *Crocuta crocuta*	Carnivore	0	0	0.12	0.059
White-tailed mongoose, *Ichneumia albicauda**	Carnivore	0.16	0.082 (0.087)	1.04	0.484 (0.3)
Aders' duiker, *Cephalophus adersi**	Herbivore	0.08	0.043	0	0
African buffalo, *Syncerus caffer*	Herbivore	0	0	0.12	0.118
African elephant, *Loxodonta africana*	Herbivore	0.65	0.336 (0.163)	0	0
Blue duiker, *Philantomba monticola**	Herbivore	4.51	0.588 (0.108)	0.84	0.064 (0.062)
Bushbuck, *Tragelaphus scriptus**	Herbivore	0.21	0.224 (0.140)	0.99	0.432 (0.233)
Common duiker, *Sylvicapra grimmia**	Herbivore	0	0	0.48	0.118
Harvey's duiker, *Cephalophus harveyi**	Herbivore	0.53	0.999 (0.095)	0.13	0.249 (0.254)
Suni, *Nesotragus moschatus**	Herbivore	29.66	1 (0)	25.06	0.961 (0.059)
Aardvark, *Orycteropus afer+*	Insectivore	0.39	0.174	0	0
Golden-rumped sengi, *Rhynchocyon chrysopygus**	Insectivore	13.17	0.998 (0.028)	13	0.718 (0.112)
Bushpig, *Potamochoerus larvatus+*	Omnivore	0.44	0.999 (0.033)	0.45	0.701 (0.543)
Crested porcupine, *Hystrix cristata+*	Omnivore	0.16	0.043	0.15	0.059
Northern giant pouched rat, *Cricetomys gambianus**	Omnivore	3.8	0.435 (0.104)	11.82	0.721 (0.113)
Yellow baboon, *Papio cynocephalus*	Omnivore	0.12	0.092 (0.062)	6.02	0.786 (0.124)

'' home ranges < camera spacing of 2 km ; '+' no documented home ranges in forest systems*

compared to Arabuko-Sokoke, further emphasising the high conservation value of the northern coastal forests.

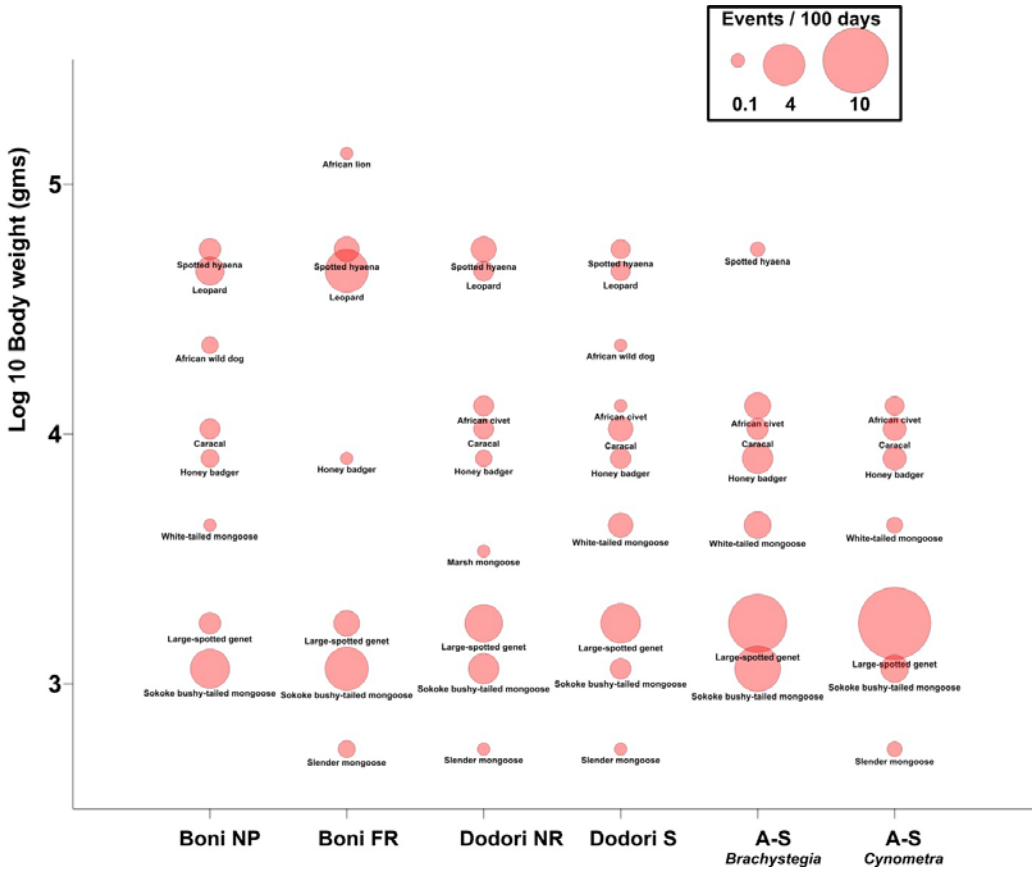

Figure 5. Representation of medium-to-large carnivore species in Boni-Dodori and Arabuko-Sokoke Forests, Kenya, on the basis of body size; each circle represents a species in functional space; size of the circle proportional to the trap rate for that species.

An outstanding result of our study has been a major revision of the status of the Critically Endangered Aders' duiker. Arabuko-Sokoke has long been considered the major site for this species nationally and internationally, but two metrics (trap rate and occupancy), were both one to two orders of magnitude greater in Boni-Dodori, compared to equivalent measures at the Arabuko-Sokoke forest (Amin *et al.*, 2015). The very high levels of occupancy in the Boni-Dodori camera trap grids, close to or at 100%, suggest that this species is consistently distributed through this habitat. Population density estimates (Amin *et al.*, 2015) strongly indicate that the Boni–Dodori is the most important known population centre for this critically endangered coastal forest endemic. The detection of blue duiker in Boni NR resulted in a 200 km northward extension of its previously recorded range (Andanje *et al.* 2011; Kingdon & Hoffman, 2013; IUCN, 2017).

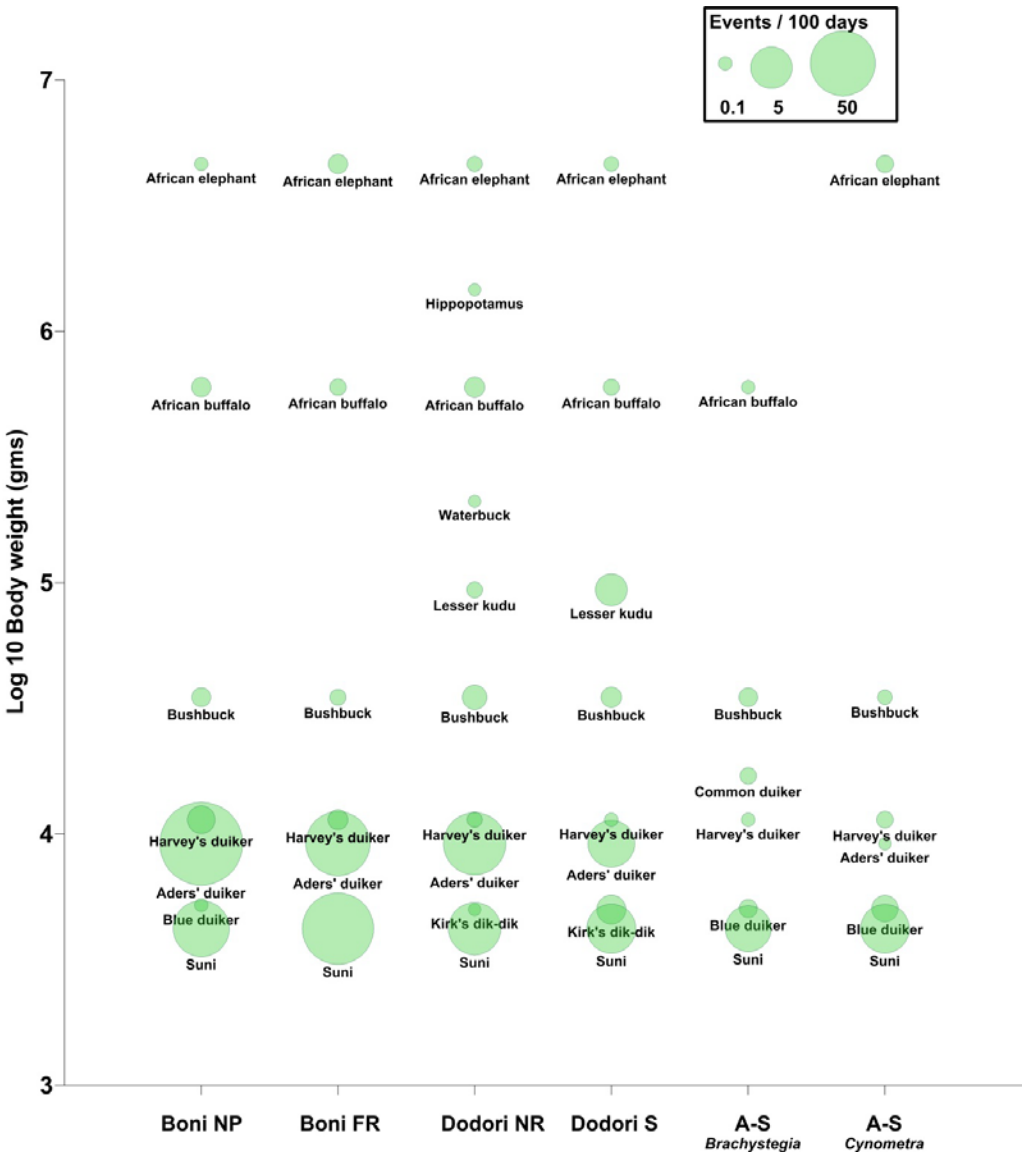

Figure 6. Representation of medium-to-large herbivore species in Boni-Dodori and Arabuko-Sokoke Forests, Kenya, on the basis of body size; each circle represents a species in functional space; size of the circle proportional to the trap rate for that species.

Another important finding of the study was a significant population of a very distinctive form of the giant sengi in Boni-Dodori, with the corollary that the range of the better known golden-rumped sengi in Arabuko-Sokoke forest could now be even smaller than previously understood (manuscript under preparation).

This study has also confirmed the range extension of soft-furred sengi. Our pilot study in 2008 had captured a four-toed sengi and a rufous sengi in a capture net and a Sherman folding trap respectively along with 31 images of the four-toed sengi from opportunistically placed cameras (Andanje *et al.*, 2010). Range extension for the Sokoke bushy-tailed mongoose to the

Boni-Dodori was also confirmed. The species was first reported from Milimani in Boni in 1995 (Engel & Van Rompaey, 1995 quoted in Mammals of Africa, 2013). Our records also show a range extension of the porcupine compared to IUCN Red List (2017) and Mammals of Africa (Happold, 2013) distribution maps that show no porcupine presence along the Kenya coast. Available distribution data places two species, crested porcupine *Hystrix cristata* (Linnaeus, 1758) and Cape porcupine *H. africaeaustralis* (Peters, 1852) living sympatrically in adjacent coastal areas of Tanzania; they were not distinguishable in the available images and it remains unresolved from this study which species occurs along the Kenya coast.

Prior to this study, presence of desert warthog in Boni-Dodori was known on the basis of only two skulls (d'Huart & Grubb 2001; Amin *et al.*, 2017). The species appears to be narrowly sympatric with bushpig whereas common warthog appears to be broadly sympatric with bushpig. The sympatry of three suids in this region has been reported in detail separately (Amin *et al.*, 2017).

The study also recorded presence of an important population of African wild dog (Endangered; IUCN, 2017) confirmed alongside a suite of large carnivores (African lion, leopard, spotted hyaena *Crocuta crocuta*).

Besides revealing a greater number of species in Boni-Dodori compared to the Arabuko-Sokoke forest, camera trap rates were higher (often much higher) at Boni-Dodori for every one of the 20 medium-to-large mammal species shared between the two sites (Amin *et al.*, 2018). There were only four taxa unique to the Arabuko-Sokoke forest. Two of these, the golden-rumped sengi and Zanzibar Sykes's monkey *C. mitis albogularis* (Sykes, 1831), have close ecological and phylogenetic equivalents in Boni-Dodori, the plain-coloured giant sengi (which remains of uncertain taxonomic status) and Pousargues's Sykes's monkey. The remaining two medium-to-large mammal species unique to the Arabuko-Sokoke forest dataset were a hare *(Lepus* sp.*)* and common duiker, both recorded at very low frequencies and are not closely associated with coastal forest.

The forest thicket map (figure 2) also highlights the potentially isolated status of the forest and thicket habitat of Dodori NR. This habitat is separated from Boni forests over much of its length by a wide belt of grassland, through which the major vehicle access route runs linking the four main villages of the area. The grassland mosaic distributed through the coastal forests is of biodiversity importance in its own right, inhabited by species such as Haggard's oribi (*Ourebia ourebi haggardi*), a distinctive form classified as Vulnerable by IUCN (IUCN, 2017). The drier bush habitat of Dodori is also an important area for the Near Threatened lesser kudu *Tragelaphus imberbis* (IUCN, 2017). This study emphasises the need for conservation management and planning to retain the habitat mosaic and simultaneously prevent isolation of the forest habitats of Dodori NR.

The Boni-Dodori forest complex represents the only remaining section of the Kenyan coastline retaining a significant frontage of undisturbed natural habitats, transitioning from coral reef to lagoons, mangroves, coastal forest and grasslands, through to the interior bush, all supporting threatened biodiversity. Its protection and conservation is all the more urgent given the land-grabs, land conversion, and felling of indigenous hardwoods associated with, and driven by, the planned development of a major seaport at Lamu and cross-country pipeline development (Morris & Amin, 2012).

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