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The northern coastal forests of Kenya are nationally and globally important for the conservation of Aders' duiker *Cephalophus adersi* and other antelope species

Rajan Amin · Samuel A. Andanje · Bernard Ogwonka · Abdullahi H. Ali · Andrew E. Bowkett · Mohamed Omar · Tim Wacher

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Abstract Aders' duiker *Cephalophus adersi* is a critically endangered small antelope endemic to the coastal forests of east Africa. Threatened by habitat loss and hunting, the species was until recently known to persist only on Zanzibar, Tanzania, and in the Arabuko-Sokoke National Reserve, Kenya. However, more recent observations, have confirmed the occurrence of Aders' duiker in Kenyan coastal forests north of the Tana River. This paper reports systematic camera trapping results for three sites in the Boni–Dodori

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R. Amin (✉) · T. Wacher
Conservation Programmes, Zoological Society of London, Regent's Park, London NW1 4RY, UK
e-mail: raj.amin@ioz.ac.uk

T. Wacher
e-mail: tim.wacher@zsl.org.uk

S. A. Andanje · B. Ogwonka
Ecosystem and Landscape Conservation Department, Kenya Wildlife Service,
P.O. Box 40241–00100, Nairobi, Kenya
e-mail: sandanje@kws.go.ke

B. Ogwonka
e-mail: bogwonka@kws.go.ke

A. H. Ali
Department of Conservation Biology, National Museums of Kenya, P. O. Box 24481Marula Lane, Nairobi, Kenya
e-mail: a.hussein.ali@gmail.com

A. E. Bowkett
Field Conservation and Research Department, Whitley Wildlife Conservation Trust, Paignton Zoo, Totnes Road, Paignton TQ4 7EU, UK
e-mail: andrew.bowkett@paigntonzoo.org.uk

M. Omar
Wildlife Conservation Division, Kenya Wildlife Service, P.O. Box 40241–00100 Nairobi, Kenya
e-mail: msaid@kws.go.ke

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coastal forest system north of the Tana and the only other known mainland site for Aders' duiker, the Arabuko-Sokoke forest. From a total survey effort of 5,723 camera trap days, we demonstrated that the known area of occurrence for Aders' duiker has more than doubled with occupancy values at or close to 100 % for all three northern sites. An index of relative abundance for Aders' duiker was also one to two orders of magnitude greater at these sites compared to Arabuko-Sokoke. Application of a replicate count N-mixture model to camera trap data from Boni National Reserve resulted in an estimate of 7.3 Aders' duikers/km^2 (95 % CI 4.5–10.1/km^2). The results also indicate higher densities of suni *Nesotragus moschatus* and Harvey's duiker *Cephalophus harveyi* in the northern forests relative to Arabuko-Sokoke. Blue duiker *Philantomba monticola* was recorded at low density in Arabuko-Sokoke forest but not detected at the northern sites. These findings significantly improve the conservation prospects for Aders' duiker and highlight the global importance of the northern coastal forests of Kenya.

Keywords Aders' duiker · Arabuko-Sokoke National Reserve · Boni–Dodori forest · Camera-trap · Harvey's duiker · Suni

Introduction

The identification of priority sites for protection and management of fauna and flora is common practice in conservation both locally and globally (Bibby 1998; Brooks et al. 2006; Dinesen et al. 2001). Priorities can be based on indicators representing changes in biodiversity and severity of threat (Mittermeier et al. 2005; Myers et al. 2000) or on particular taxonomic groups of conservation concern (e.g. Anderson 2002; Bennun and Fishpool 2000). However, prioritization exercises rely on knowledge at the time and new information about a region can drive the need for reassessment of conservation importance (e.g. Doggart et al. 2006). Here we present new data on forest antelopes that provide a significant reassessment of the conservation importance of a hitherto poorly studied region within the 'coastal forests of Eastern Africa biodiversity hotspot' (Burgess et al. 1992).

Antelopes and other artiodactyl species are important to African forest and woodland ecosystems for their biomass (White 1994) and role in ecological process (Feer 1995). Many of these species are increasingly threatened by habitat loss and hunting (East 1999). Forest antelope are often targets for the bushmeat trade (Fa et al. 2005; Wilkie and Carpenter 1999) and as a result have locally and regionally declined (e.g. van Vliet et al. 2007). The Boni and Dodori National Reserves and surrounding areas have previously been identified as key locations for antelope conservation. The threatened Haggard's oribi *Ourebia ourebi haggardi* is present in the grassland habitats (East 1999), and the area ranked highly in a site selection analysis based on Afro-tropical antelopes even before the presence of Aders' duiker *Cephalophus adersi* was taken into account (Kershaw et al. 1994). Harvey's duiker *C. harveyi* was previously considered 'well-represented' in the Boni–Dodori forests (East 1999) but population data on other antelope species is limited.

Aders' duiker was assumed to be restricted to one site on the African mainland, Arabuko-Sokoke forest, as well as several fragmented forests on Unguja Island, Zanzibar (Finnie 2008). Recent sightings of Aders' duiker in the Boni–Dodori forests (Andanje and Wacher 2004; Andanje et al. 2011) confirmed a previously overlooked report of this species in the Boni forests from the early 1970s (Gwynne and Smith 1974). Aders' duiker is attributed 'critically endangered' conservation status (Finnie 2008). Its sympatry with Harvey's duiker, blue duiker *Philantomba monticola* and suni *Nesotragus moschatus*

(Andanje et al. 2011) further supports the high conservation value of Kenya's northern coast for antelope species. The presence of Aders' duiker, the additional recent discovery of an unknown form of giant elephant-shrew *Rhynchocyon* sp. (Andanje et al. 2010) and presence of other species of high conservation interest, such as African wild dog *Lycaon pictus* (Githiru et al. 2008), prompted the need for a systematic baseline study of mammal species richness and status for the Boni–Dodori forests using camera traps. The original sampling protocol was therefore designed to establish a baseline for the entire larger mammal community and was not focused purely on antelopes.

Quantitative data on Aders' duiker and other small forest adapted antelopes are generally scarce. The aim of this study was to use data from the large mammal camera trap grid to compare the presence and relative abundance of Aders' duiker with the three similar sized and potentially competitor forest antelope species found in these surveys. Four other antelope species recorded in the camera arrays have been excluded on ecological grounds; lesser kudu *Tragelaphus imberbis*, dik–dik *Madoqua* sp. and waterbuck *Kobus ellipsiprymnus* were infrequently recorded and mainly associated with cameras at a habitat transition on the periphery of the Dodori forest. Bushbuck *T. scriptus* were more generally distributed in the sample cameras but have been excluded from the comparisons because they are physically larger than the duikers and Suni, and are not associated with closed canopy forest (Plumptre and Wronski 2013).

Use of camera-trapping 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 the dense habitats of coastal forest and thicket with advantages over alternative methods based on sign recognition (Bowkett et al. 2009, 2013). We based the camera trap survey design on a standardized approachs using a systematic grid layout (Tobler et al. 2008; Ahum ada et al. 2011).

Materials and methods

Study area

The wooded habitats of coastal Kenya form part of the Coastal Forests of Eastern Africa biodiversity hotspot, an area known for globally significant levels of species richness and endemism (Burgess and Clarke 2000; Mittermeier et al. 2005). Much of this habitat in Kenya has been cleared for coastal development and agriculture (Mittermeier et al. 2005), however, several protected areas exist along the northern Kenyan coast (Table 1). Boni and Dodori National Reserves, in Lamu East and Ijara Districts respectively, were gazetted in 1976. They lie adjacent to the Boni forest and these three areas, referred to henceforth as the 'Boni–Dodori forest system', form a cluster on the northern Kenyan coast (Fig. 1). The remote location and history of insecurity have resulted in a comparatively low human population density and minimal development. Four principal villages, occupied by the Awer people, are located along a bush track running between the Boni and Dodori National Reserves, although the exact location of the gazetted boundaries remains uncertain.

The Arabuko-Sokoke National Reserve (NR), established in 1932, is 250 km to the south in Kilifi County. It is separated from the northern Kenyan coastal forests by two major intervening rivers, the Tana and Galana/Sabaki. It is completely encircled by un-clustered village settlements with an estimated human population greater than 100,000 (ASFMT 2002). Both study areas experience illegal hunting and timber extraction, with impact of poaching likely to be much higher in the smaller but much more heavily populated Arabuko-Sokoke NR.

Table 1 Summary data on legal status, size, location and sampling period for the four camera trapping grids

Sample area status	Size (km^2)	Established	Camera trap grid central point	Camera trap sampling period
Dodori National Reserve	877	1976	1°49.31′S, 41°04.47′E	14 Jan. 2010 to 16 Mar. 2010
Boni National Reserve	1,339	1976	1°32.22′S, 41°19.53′E	17 Mar. 2010 to 16 Jun. 2010
Boni forest	450[a]	Not applicable	1°40.57′S, 40°52.53′E	19 Jun. 2010 to 06 Sep. 2010
Arabuko-Sokoke National Reserve	420	1932	3°21.34′S, 39°50.35′E	01 Oct. 2010 to 21 Jan. 2011

[a] Area approximated as no formal boundary has been established

Habitat in the Boni–Dodori forest system consists of a mosaic of forest, thicket and savannah (Kuchar and Mwendwa 1982). Arabuko-Sokoke is mostly forested with three main vegetation types: *Cynometra* forest and thicket, *Brachystegia* woodland and mixed forest (ASFMT 2002).

Field sampling methods

Survey design at each site consisted of cameras systematically spaced at 2 km intervals on a regular 3 × 7 square grid, oriented to the available habitat patches (Ahumada et al. 2011), (Fig. 1). Two cameras at Dodori forest fell marginally outside the gazetted boundary line. The grid spacing resulted in cameras at a density of one per 4,000 ha. Range sizes of the target species investigated in this study are known or believed to be small relative to this sampling regime. Documented range sizes are between 0.5 and 4 ha for the 5–5.4 kg suni (Kingdon and Hoffman 2013a) and 2.6–11.9 ha for the 4.8–5.3 kg blue duiker (Hart and Kingdon 2013). Home range sizes have not been reported for Aders' duiker or the slightly larger Harvey's duiker, although the Natal red duiker (often considered a very close relative or sub-species of Harvey's duiker, van Vuuren and Robinson 2001) is reported to use home ranges of 2–15 ha (Hoffmann and Rowland 2013). The largest average home range size for any duiker for which radio-tracking data is available is 63 ha for white-bellied duiker *Cephalophus leucogaster*, which at 15.5–17 kg (Hart 2013a) is heavier than either Aders' duiker (9–9.2 kg, Williams 2013) or Harvey's duiker (11–12 kg, Kingdon and Rovero 2013). We consider it reasonable to infer that camera sites in this study are independent of each other with respect to the expected movement patterns of all four antelope species being investigated and it can be assumed that the probability of the same individuals being detected at more than one camera location is correspondingly low.

We positioned the sampling grids of cameras in extensive areas of forest and thicket based on habitat and accessibility. ArcGIS 9.3 (ESRI, Redlands, CA USA) software and GPS receivers were used to locate camera sampling unit centre points. A single camera trap was placed within 100 m of each centroid under closed canopy forest or thickets. We set the cameras at a height of 30–45 cm, positioned perpendicular to game trails at a distance of c. 4–8 m with the aim of obtaining full body lateral images of small antelopes and other mammal species. We used Reconyx RM45 (RECONYX, Inc., Holman, WI, USA) digital cameras, programmed to take three pictures per trigger with no delay. All other default settings were used. RM45 cameras have a trigger time of 0.1 s with a detection range of 25+ m. All images were in black and white (Fig. 2). These cameras use an infrared flash at night (or at low light levels in the day time), intended to minimise risk

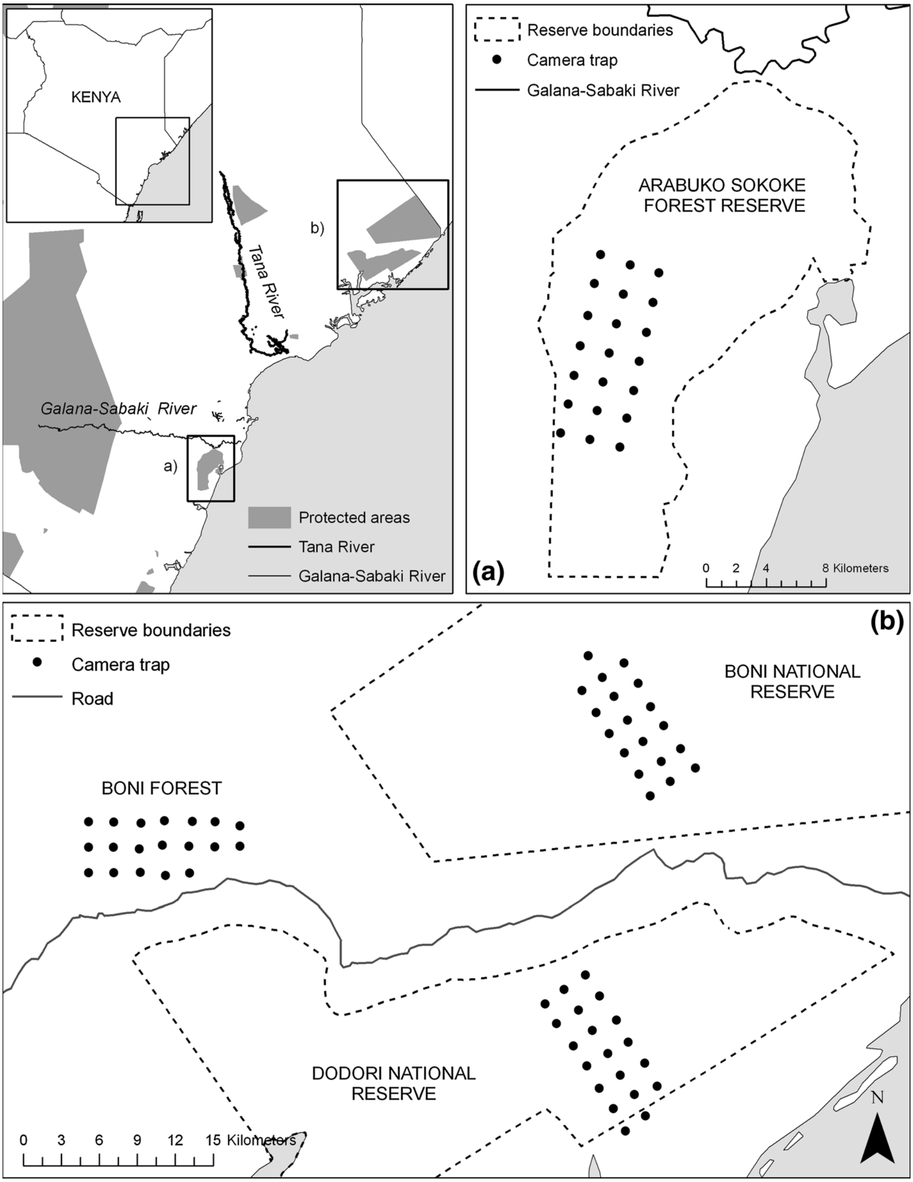

Fig. 1 Location of four study areas in central and northern coastal Kenya; *insets* show location of camera trap arrays relative to protected area boundaries at Arabuko-Sokoke National Reserve (**a**) and Boni–Dodori forest system (**b**)

of startling animals when they enter the camera view. Each survey was conducted for a minimum of 50 days in order to achieve 1,000 camera trap days of sampling effort (O'Brien et al. 2003) with 20 fully functioning cameras. The camera installation protocol called for survey teams to trigger photographs of themselves as the last action at the end of camera set up operations and as the first action on arrival to recover cameras, as a means to help verify camera function.

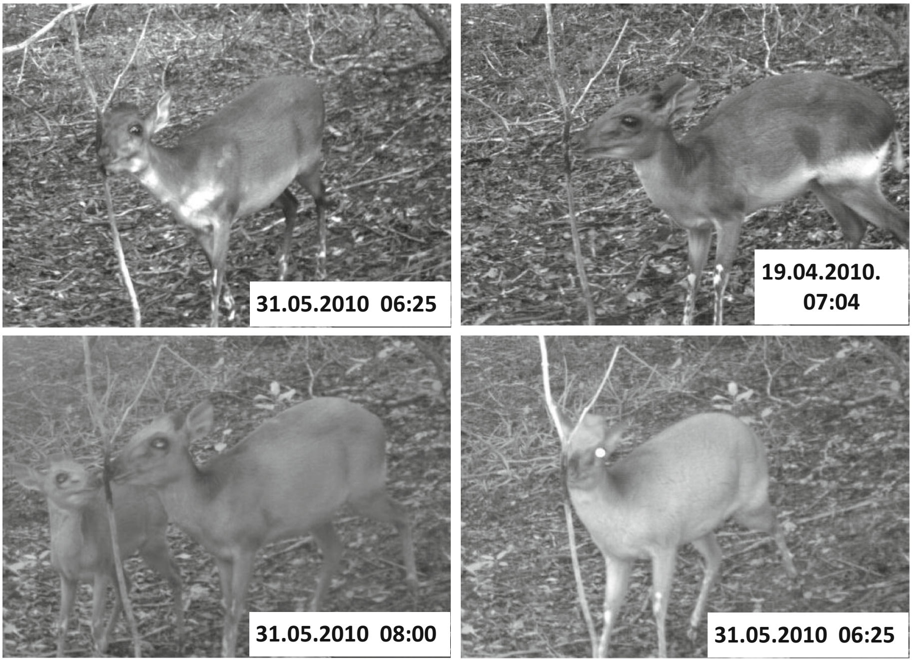

Fig. 2 Camera trap images of Aders' duiker at one location in Boni National Reserve labelled by date and time. Adult female and calf (*left*) and adult male (*right*). Note established scent mark (dark patch just below the fork on the sapling), effect of infrared illumination on duiker appearance (lower images) and role of spot pattern on legs for individual recognition

Data compilation and processing

We used Exiv2 software tool (Huggel 2012) to extract image metadata. The camera trap label, date, time and temperature record were compiled for each image in an excel sheet (Microsoft Office Professional Plus 2010). All photographs were classified to species, and grouped into independent photographic events. For this study an 'event' was defined as any sequence of photos from a given species occurring after an interval of $\geq$60 min from the previous images of that species (Bowkett et al. 2008; Tobler et al. 2008). Identification of our target species mostly presented few problems. Distinguishing species under infrared illumination was sometimes unclear, especially suni from blue duiker. Behavioral features such as differences in tail movement (e.g. flicked laterally in suni, vertically in blue duiker, Foley 2008) were sometimes useful in such cases. The white rump-band and leg-spots of Aders' duiker, key distinguishing features, were sometimes partially or strongly obscured in infra-red illuminated black and white images (Fig. 2). Multiple images at each trigger were helpful in minimising these effects. However a small number of cases (3.5 % of all images attributed to duikers or suni) had to be excluded from our analysis because positive identification was not possible.

Species distribution

We used single season occupancy analysis (MacKenzie et al. 2006) to estimate the probability that a sample unit is occupied by a species (ψ), within each of the four forest sites for each species. Occupancy of each species was analyzed separately with package *unmarked* in

R statistical software (Fiske and Chandler 2011; R Development Core Team 2008). We grouped samples (days) into ten-day sampling occasions to improve detection probability of the rarer species and constructed detection (1), non-detection (0) history for each species per study site. We also calculated naïve occupancy which is defined as the number of cameras at which a species is detected divided by the total number of operational cameras.

We tested for statistically significant differences in occupancy between the four study sites using 95 % confidence intervals. Confidence intervals (CIs) for modelled occupancy estimates were derived from the *unmarked R* software program and we used a jack-knife procedure to compute standard error and CIs of naïve occupancy. Non-overlapping 95 % CIs indicated a significant difference in occupancy. However, CIs that overlap slightly may also imply a significant difference. Consequently, we performed a Wald test to provide an independent and robust measure of difference, with $p < 0.05$ considered to be significant.

To assess potential area of duiker habitat in the northern forest zone we obtained two Landsat images (30 m resolution) for the scene, Path 165, Row 061 (March 2009 and March 2010), covering the northern coastal forests. We selected the most cloud free images during the dry season to classify the habitat into grassland and forest cover. For each image, we used knowledge based methods (Meng et al. 2009) to classify cloud cover and shadows as "NoData" in IDRISI Kilimanjaro software (Eastman 2004). We then used the spatial analyst extension in ArcGIS version 10.1 and performed unsupervised classification using a cluster algorithm, generating 20 spectral clusters. These data were stratified into 'zones', where land cover types within a zone have similar spectral properties collapsing the 20 spectral classes identified in the cluster analysis into a raster image with the three classes (forest and thickets, non-forest and water) (Kuemmerle et al. 2009; Baumann et al. 2012).

The resulting classified images were interpreted visually using the Landsat images, and, where available, high-resolution QuickBird imagery from Google Earth™ (Kuemmerle et al. 2009; Baumann et al. 2012). Using the boundary clean tool in ArcGIS Spatial Analyst, we removed the remaining correction errors and converted the raster images into vector datasets (polygon). We further simplified the polygon dataset using the dissolve tool in ArcGIS data management tool. Using the mosaic tool in ArcGIS data management tool, we combined the two images into one new image resulting in a complete current vegetation map of the area. We overlaid all confirmed Aders' duiker locations from camera trap surveys and field observations to validate the association between duiker locations and the forest patch and thicket imagery. The area of potential Aders' duiker habitat was measured using ArcGIS software.

Species abundance

We used the mean number of independent photographic events per trap day $\times$ 100 (trapping rate) as a relative abundance index (RAI). RAI is primarily useful for within species comparisons under standardised conditions, but differences in species biology and detectability mean that its use in between species comparisons is limited. We computed the standard error of RAI as the standard deviation of the trapping rate divided by the square root of the number of trap days and applied the Wald test to test for significant difference. To obtain an estimate of the population density of the focal study species, Aders' duiker, across all sampling units we applied an N-mixture model (developed for estimating population size from spatially replicated counts, Royle 2004), available in the software Presence 3.1 (Hines 2006). The camera trap data were adapted to mimic a set of replicated counts by selecting a 1-h period of maximum activity from the derived 24 h activity pattern and dividing this into six 10-min occasions. We created a count matrix of the number of individuals detected in the camera trap images within each 10 min occasion at each sampling unit of Boni NR camera trap grid for Aders' duiker. We could not apply the method to Arabuko-Sokoke NR camera trap data for comparative analysis as the number of Aders' duiker encounters was very low. We obtained a density estimate by dividing the estimated number of adult individuals by the number of sampling units multiplied by the estimated average home range.

Evidence for interference competition affecting Aders' duiker

To further understand processes affecting the status of Aders' duiker, we used the camera trap data to look for evidence of temporal or spatial competition avoidance between the four small forest antelopes sharing the habitat. To compare temporal interactions between the critically endangered Aders' duiker and the three other small forest antelopes sharing its range, we used the number of independent photographic events per hour. As forest antelopes are mainly diurnal/crepuscular (Kingdon and Hoffman 2013b) we compiled photographic events into four six-hourly time periods; 3 am–9 am, 9 am–3 pm, 3 pm–9 pm and 9 pm–3 am. We also compared day (4 am–8 pm) and night (8 pm–4 am) activity patterns. Between site comparisons were limited as only suni produced sufficient data in both study areas to compare activity between Arabuko-Sokoke NR and the Boni–Dodori forest system. We analysed the activity patterns using *Oriana* circular statistics program (Kovach 2011) using pair-wise Chi squared test to test for significance.

To compare spatial interactions between Aders' duiker and the three other species sharing its range, we hypothesised that species pairs showing strong competitive exclusion or intolerance should be characterised by a negative association in RAI at the small spatial scale of the field of view in front of individual cameras. We tested this by Pearson's product-moment correlation of RAI across camera sampling units; since activity patterns are shown to be broadly similar, competitive exclusion should produce a negative correlation. Limited sample size at Arabuko-Sokoke NR meant that these comparisons were only made across the camera grids in the northern forests.

Results

Sampling effort

The four surveys were phased consecutively over 1 year and each camera trap grid was left in the field for 60–111 days with a mean sampling effort of 1,430 camera-trap days per survey (range 1,026–1,940). Camera-trap days were calculated as the total number of 24 h periods each camera was operating normally. Camera attrition and failures resulted in 13–20 usable locations across the four sites (Table 2).

Forest antelope species composition

We recorded 5,449 independent photographic events of four species of forest antelopes. Aders' duiker, Harvey's duiker and suni were photographed in all four sampling sites. Blue duiker was recorded only in Arabuko-Sokoke NR in this data set, although it had also been detected in the Boni–Dodori forest system during a much smaller pilot study in 2008 (Andanje et al. 2011). The common duiker *Sylvicapra grimmia*, documented to occur in the region (IUCN 2012; Wilson 2013) and known to prefer more open habitats, was not recorded, probably reflecting the deliberate selection of more forested habitat for the camera trap arrays.

Species distribution

Aders' duiker was detected at all fully operational camera sites in Boni NR and Boni forest, resulting in modelled occupancy estimates (ψ) of 1, with $\psi = 0.95$ (SE = 0.05) in the Dodori NR. Occupancy could not be reliably modelled for Arabuko-Sokoke NR due to the low detection probability ($p < 0.1$) but naïve occupancy was 0.1. Occupancy estimates for Aders' duiker were at least eight times higher in the northern coastal forests than in Arabuko-Sokoke NR ($p < 0.001$). There was no significant difference in occupancy estimates between the three northern coastal forest sites (Table 2).

Occupancy estimates indicate Harvey's duiker is more widely distributed in the two more inland forests at Boni ($\psi > 0.5$) than nearer the coast in Dodori and Arabuko-Sokoke NRs ($\psi < 0.25$, $p < 0.001$). Although Harvey's duiker was recorded at 27 % of camera stations in Arabuko-Sokoke NR, the uneven frequency of these observations with detection probability less than 0.1 prevented reliable modelling of occupancy. Suni were widely distributed in all four forests with no significant difference in occupancy estimates between the four sites ($\psi > 0.9$; $p > 0.3$) and with higher detectability in the northern coast forests ($p < 0.01$). Blue duiker was only recorded in Arabuko-Sokoke *Cynometra* forest with low detection probability ($p = 0.11$; $\psi = 0.61$, SE = 0.05) (Table 2).

Species abundance

Aders' duiker was the most frequently recorded of the forest antelope species in the camera sampling grids in the three northern coastal forests with the trapping rate in Boni NR (RAI = 106.16, SE = 3.91) almost twice that of Boni forest (RAI = 60.65, SE = 2.11) and Dodori NR (RAI = 56.79, SE = 2.34). By contrast, Aders' duiker was only recorded on two occasions at separate camera sampling sites in Arabuko-Sokoke NR (RAI = 0.11, SE = 0.08), despite an even greater sampling effort (Table 2). In pairwise comparisons there were significant differences ($p < 0.001$) in Aders' duiker RAI between all sites except Boni forest and Dodori NR ($p = 0.22$), where they were photographed at similar rates.

Suni was the second-most frequent forest antelope species recorded. They were most frequently encountered in Boni forest (RAI = 78.94, SE = 3.60). Boni (RAI = 40.39, SE = 1.85) and Dodori (RAI = 35.87, SE = 2.27) NRs had similar trapping rates ($p = 0.12$). Suni differed from Aders' duiker in maintaining a moderately high representation at Arabuko-Sokoke NR. At Arabuko-Sokoke NR, suni were the most frequently recorded antelope species, though at average RAI 23.37 (SE = 1.26), they were still encountered at a lower rate than in any of the three northern forests.

Harvey's duiker was the least commonly recorded forest antelope species. The species was most frequently encountered in Boni NR (RAI = 4.70, SE = 0.55) and the trapping rates were not significantly different between Dodori NR (RAI = 0.28, SE = 0.16) and Arabuko-Sokoke NR (RAI = 0.23, SE = 0.11, $p = 0.25$).

Blue duiker was only recorded in Arabuko-Sokoke NR in this study. Although the trapping rate was very low (RAI = 1.16, SE = 0.24), it was the second most frequently recorded forest antelope after suni at this site.

Overall, the two more inland forests had much higher and similar trapping rates for the three forest antelope species (combined species at Boni NR RAI = 151.26, Boni forest RAI = 141.02). In comparison, the combined trapping rate for Arabuko-Sokoke NR was significantly lower by a magnitude of more than five (RAI = 24.9) and compared to Dodori NR (RAI = 92.94) by a magnitude of more than three (Fig. 3).

Table 2 Sampling effort, occupancy and trapping rate results for four forest antelope species in four Kenyan coastal forests

Grid	No. of deployed cameras (No. of functioning cameras)	No. of camera trap days	Aders' duiker			Harvey's duiker			Blue duiker			Suni		
			RAI (SE)	Ψ (SE)	p (SE)	RAI (SE)	Ψ (SE)	p (SE)	RAI (SE)	Ψ (SE)	p (SE)	RAI (SE)	Ψ (SE)	p (SE)
Boni National Reserve	21 (19)	1,670	106.16 (3.91)	1	1	4.70 (0.55)	0.74 (0.19)	0.32 (0.05)	0	N/A	N/A	40.39 (1.85)	0.95 (0.05)	0.79 (0.04)
Boni forest	21 (13)	1,026	60.65 (2.10)	1	1	1.43 (0.40)	[0.53] (0.03)	N/A	0	N/A	N/A	78.94 (3.60)	1	0.90 (0.03)
Dodori National Reserve	21 (20)	1,087	56.79 (2.34)	0.95 (0.05)	0.85 (0.03)	0.28 (0.16)	0.15 (0.12)	0.17 (0.14)	0	N/A	N/A	35.87 (2.27)	1	0.86 (0.03)
Arabuko-Sokoke National Reserve	21 (18)	1,940	0.11 (0.08)	[0.11] (0.22)	N/A	0.23 (0.11)	[0.23] (0.04)	N/A	1.16 (0.24)	[0.61] (0.05)	N/A	23.37 (1.26)	0.94 (0.05)	0.55 (0.04)

For each site and species, we present total number of camera trap days, mean and standard error of the number of independent photographic events per trap day times 100 (RAI), modelled occupancy estimates (Ψ) with standard error and detection probability (p) estimates with standard error. Where data insufficient for occupancy modelling naïve occupancy is presented in square brackets with standard error (N/A = not applicable for naïve occupancy)

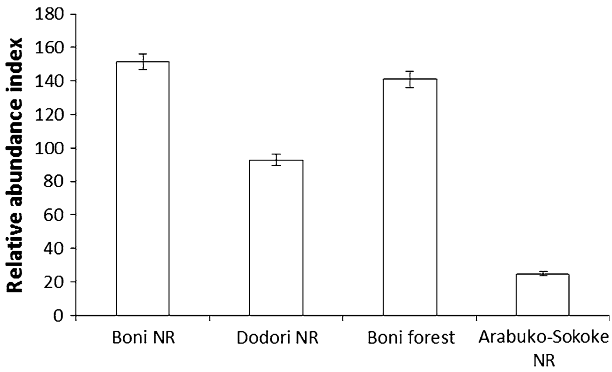

Fig. 3 Relative abundance index (camera trap events/day × 100) combined for the forest antelope species recorded at each of the four Kenyan coastal forest study sites. Standard *error bars* are also shown

The replicate count N-mixture model gave an estimate of 27 Aders' duikers (SE = 5.2, 95 % CI 16.74–37.13) across 19 camera sampling units in Boni NR. We used an average home range of 19.2 ha for Aders' duiker. We derived this estimate from regression analysis of independently published home range against body weight data using the most complete home range estimates available from radio telemetry studies of four other forest duiker species, blue duiker (Hart and Kingdon 2013), white-bellied duiker (Hart 2013a), Ogilby's duiker (Kingdon 2013) and Weyns' duiker (Hart 2013b). Using the information that occupancy was effectively 1 and an assumption that each camera sampling unit was located within a separate home range we thus obtained a density estimate of 7.3 duikers/km^2 (95 % CI 4.5–10.1 duikers/km^2).

Species behaviour

All four forest antelope species showed crepuscular peaks around sunrise and sunset (Fig. 4). Harvey's duiker was found to be strictly diurnal with activity peaks between 0600–0900 and 1500–1800. Blue duiker was also mainly diurnal although two events were recorded at night between 0200 and 0400.

Suni showed a higher level of nocturnal activity than Aders' duiker ($\chi^2 = 34$, $p < 0.001$). We also found a significant difference in suni activity patterns with greater activity at night in the Arabuko-Sokoke forest site compared to the northern coastal forests ($\chi^2 = 15$, $p < 0.001$). There was insufficient trap data for the other forest antelope species to perform a site comparative analysis.

Comparison of RAI across camera sampling units failed to produce any negative correlations in forest antelope presence. All species pairs were significantly positively correlated indicating some degree of spatial association (Aders' duiker—suni, $\rho = 0.56$, $p < 0.001$; Aders' duiker—Harvey's duiker, $\rho = 0.53$, $p < 0.001$; suni—Harvey's duiker, $\rho = 0.321$, $p < 0.02$).

Discussion

Prior to this study the only available estimate for Aders' duiker density, 2.8 individuals/km^2, comes from a drive count at Arabuko-Sokoke NR (Kanga 2003). A pilot camera trapping study for Aders' duiker in the same forest in 2006, using ten film cameras

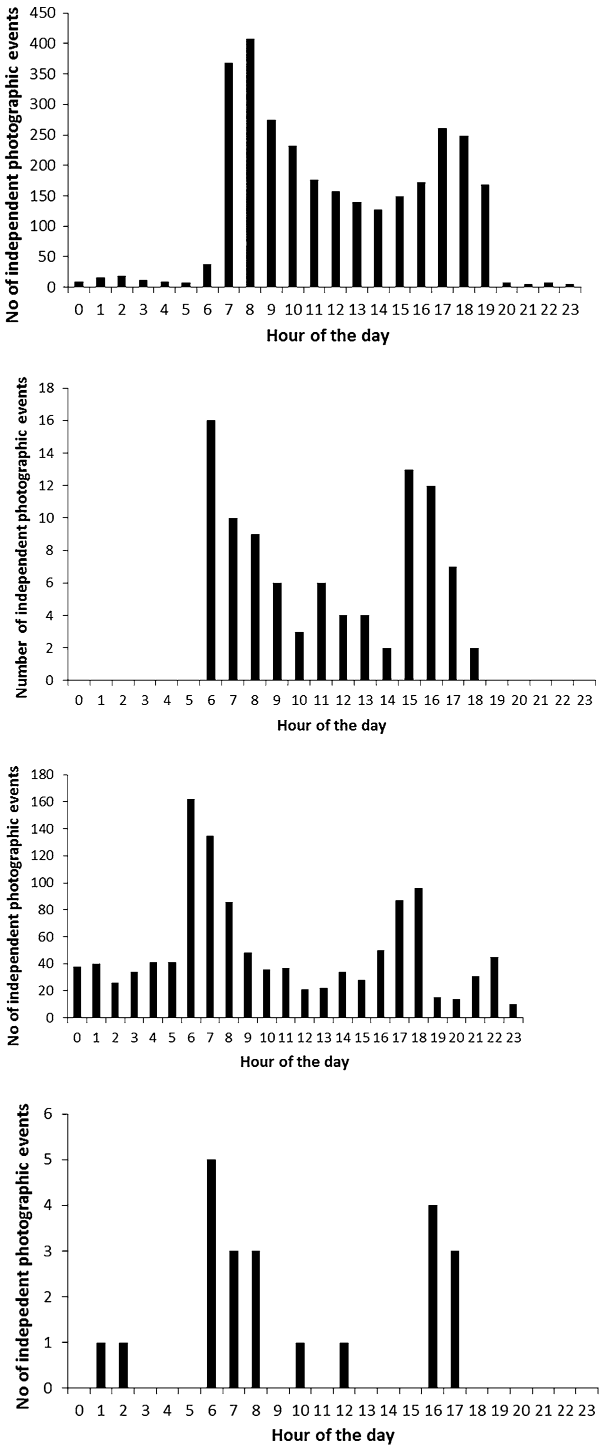

Fig. 4 24-h activity patterns from top to bottom Aders' duiker, Harvey's duiker and suni in the northern coastal forests and blue duiker in the Arabuko-Sokoke National Reserve

deployed opportunistically with a sampling effort of 626 days, reported nine events at one location (Neelakantan and Jackson 2007).

In this study, sampling effort (camera trap days) achieved the recommended level of 1,000 trap days per grid (O'Brien et al. 2003), although total effort varied between the four grids, an unavoidable outcome of difficult logistic and security conditions. Although a longer camera trapping period might increase the chance of recording species at more camera stations across a grid, the grid installed for the longest time (Arabuko-Sokoke NR) reported the lowest occupancy for Aders' duiker by a large margin (Table 2). Rarefaction curves modelling species discovery rates indicate asymptotes effectively reached after 60 days in these grids (unpublished data). Hence we believe that any bias introduced by uneven sampling effort is not significantly affecting the major conclusions regarding relative abundance of Aders' duiker.

The primary result has been that the population state variables (RAI and occupancy), enabling comparison of the status of Aders' duiker between Arabuko-Sokoke and the northern coastal forests, were both one to two orders of magnitude greater at all three sites north of the Tana River. Simple camera trapping rate alone lacks any correction for detectability, and is thus considered unreliable as an RAI (Sollman et al. 2013). We suggest that the fact that these comparisons are made using both occupancy and RAI, comparing results for the same species in similar habitats using a standard protocol, makes these very large and consistent differences meaningful.

The data also provided new insights on the activity patterns and spatial associations of small forest antelopes in this system which indicate potential competitive effects influencing critically endangered Aders' duiker. Suni, the only forest antelope species to maintain a consistent level of nocturnal activity, showed a significantly higher proportion of nocturnal activity at Arabuko-Sokoke NR than in the northern coastal forests. It would be useful to test if levels of disturbance and hunting are correlated with RAI. Otherwise, suni showed a very similar pattern of day time activity to Aders' duiker and Harvey's duiker. No evidence of spatially-based competitive exclusion between these three species was detected from camera trapping rates across individual camera stations. Instead, significant positive correlations in camera trapping rate across stations for the three main species pairings suggest an underlying, positive spatial association between forest antelopes at the scale measured. Similar observations have been made comparing spatial behaviour of blue and Natal duikers in southern Africa (Perrin et al. 2003). Analysis of temporal association/avoidance at each individual camera site might yet reveal some level of ecological separation.

Logistics and resources prevented simultaneous operation of camera grids in the four forest sites. Consequently results at each site were obtained at different periods of the year. The region typically receives bi-modal annual rainfall (April to June and November to December, ASFMT 2002). Our camera grids were active in both seasons in northern forests and Arabuko-Sokoke. Because of this and the relative stable forest interior of the sites, we consider that the large differences between the camera trapping rate and occupancy observed for Aders' duiker between Arabuko-Sokoke NR and the northern coastal forest system are unlikely to be the result of a seasonal effect.

Direct estimation of density from camera trap data using individual identification for capture-recapture or sight-resight approaches (Foster and Harmsen 2011) was considered for Aders' duiker since leg pattern appears to permit identification of individuals (Fig. 2). However, this method was not appropriate for this study because reliable individual recognition rates were very low (no more than 23 % of Aders' duiker images at one of the most favourably placed cameras offered sufficient image quality for leg spot recognition) and also because camera spacing was very much greater than individual home range size in this study. This violates the basic assumption of mark-recapture methods that all individuals in the study population have an equal chance of ‘capture’, managed in practice by placing cameras at > 1 per home range (Foster and Harmsen 2011).

For Aders’ duiker the very high levels of occupancy in the camera trap grids in the Boni–Dodori forest system, very close to or at 100 %, suggest that this species is consistently distributed through this habitat. Applying the density estimate of 7.3 duikers/km^2 to the 84 km^2 for the Boni NR survey grid, we estimate approximately 600 Aders’ duikers in this sample area. The potential forest and thicket area measured from the classified map (Fig. 5) is at least 3,000 km^2. This more than triples the combined previously known range of Aders’ duiker; 420 km^2 Arabuko-Sokoke NR and less than 500 km^2 of scattered duiker

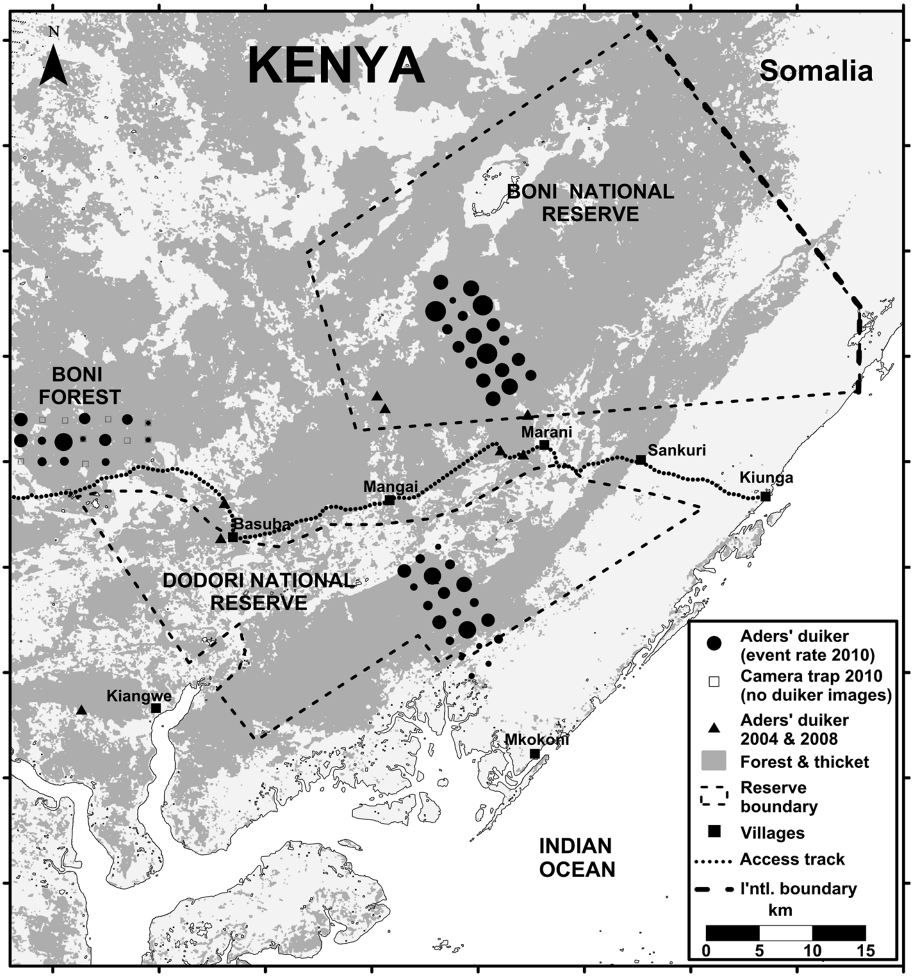

Fig. 5 Distribution of potential duiker habitat in relation to all Aders’ duiker observations in the northern coastal forests of Kenya showing confirmed presence in pilot surveys 2004–2008 as triangles and presence as circle weighted by RAI in three systematic camera trap grids set out in 2010. *Note* Additional coastal villages not shown

habitat across five isolated forests on Unguja Island in Zanzibar (Finnie 2002). These new data strongly indicate that the Boni–Dodori forest system is the most important known population centre for the species.

The forest thicket map (Fig. 5) also helps identify future camera trap study areas to verify the extent of Aders' duiker distribution and occupancy, and shows the potentially isolated status of the forest and thicket habitat of Dodori NR. This sector is separated 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. Whilst this situation is likely to have been stable as part of the forest grassland mosaic, this geography emphasises the need for conservation management and planning to retain the current connectivity of the forest system. The area represents the only remaining sector of the Kenya coastline retaining a significant frontage of undisturbed natural habitat sequences, transitioning from coral reef, lagoons, mangrove, coastal forest and grasslands, and the interior bush, all supporting endangered biodiversity. Besides Aders' duiker, the system contains other unique and critically endangered species, notably the potentially new giant elephant shrew (Rhynchocyoninae) (Andanje et al. 2010) in the forests, hirola *Beatragus hunteri* in the interior and African wild dog ranging throughout. The broader camera trap results (Wacher and Amin 2014) emphasise the high level of diversity and currently undisturbed nature of the mammal community in this zone underscoring the extremely high conservation value of the region. This is all the more urgent given the land-grabs, land conversion, and the felling of indigenous hardwoods associated with and driven by the planned development of a major seaport at Lamu and cross country pipeline development to the same place (Morris and Amin 2012).

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