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SYMPATRY AMONG THREE SUID SPECIES (FAMILY SUIDAE) ON THE NORTH COAST OF KENYA

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ABSTRACT

Three species of suids occur on the broad coastal plain of Kenya east and north of the Tana River; desert warthog *Phacochoerus aethiopicus*, common warthog *Phacochoerus africanus*, and bushpig *Potamochoerus larvatus*. Systematic camera-trap surveys, comprising 9229 camera-trap days on grids at six study sites, were used to determine the distribution and relative abundance of these three suids in the Boni-Dodori Forest Complex (*ca*. 4000 km²) and in Arabuko-Sokoke Forest Reserve (416 km²) on Kenya's north and central coasts, respectively. In the Boni-Dodori Forest Complex, desert warthog was captured at one camera site, common warthog at four camera sites, and bushpig at 33 camera sites. In Arabuko-Sokoke Forest Reserve, only bushpig was captured (seven camera sites). Sympatry of desert warthog and common warthog seems limited in the Boni-Dodori Forest Complex. Here, desert warthog appears to be narrowly sympatric with bushpig whereas common warthog is broadly sympatric with bushpig. Sympatry of the three suids in this region was not previously reported. This sympatry is absent in Arabuko-Sokoke Forest Reserve.

Keywords: desert warthog, common warthog, bushpig, *Phacochoerus aethiopicus*, *Phacochoerus africanus*, *Potamochoerus larvatus*

INTRODUCTION

Four species of suids occur in Kenya (Stewart & Stewart, 1963; Kingdon, 1979): desert warthog *Phacochoerus aethiopicus* (Pallas, 1766) in grassland, bushland, and woodland in the east (Grubb & d'Huart, 2013); common warthog *Phacochoerus africanus* (Gmelin, 1788) in grassland, bushland, and woodland in the south and west (Cumming, 2013); bushpig *Potamochoerus larvatus* (F. Cuvier, 1822) mainly in forest along the coast and in the central

and southwest regions (Seydack, 2013); and forest hog *Hylochoerus meinertzhageni* Thomas, 1904 in several montane forests (d'Huart & Kingdon, 2013). In Kenya, the two species of warthog are sympatric in at least three regions: Samburu County/Meru National Park; Tsavo West National Park/Tsavo East National Park; and the north coast in the vicinity of Lamu. There is no evidence for hybridization between desert warthog and common warthog (De Jong *et al*., 2016a,b; Butynski & De Jong, 2017; De Jong & Butynski, 2017a,b).

In order to better understand mammalian diversity in the north coast forests of Kenya, systematic camera-trap surveys were used to gather data from the Boni-Dodori Forest Complex (east and north of the Tana River, *i.e.* left bank) and Arabuko-Sokoke Forest Reserve (south of the Tana River and Galana-Sabaki River, *i.e.* right bank; figure 1; Stokes *et al.,* 2016). This paper presents the study's findings on suids.

DESCRIPION OF THE STUDY AREAS

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). They also lie 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 north and central coast (figure 1).

Boni National Reserve (1339 km²), Dodori National Reserve (877 km²), and Boni-Ijara Forest Reserve (*ca.* 1400 km²) are located on the extreme north coast of Kenya (figures 1 & 2). 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; Stokes *et al*., 2016). The 'Boni-Dodori Forest Complex' is, hereafter, referred to as 'Boni-Dodori'.

Boni-Dodori experiences two annual wet seasons with the long wet season in April–June and the short wet season in October–November. Mean annual rainfall ranges from 500 mm in the northeast to 800 mm in the southwest. 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 asl on Sankuri Ridge (Musina *et al.,* 2016).

Human population density is low (< 3 people/km²) in this remote, often insecure, region. Most of the *ca*. 1800 Aweer people in this region live in four villages along a dirt track that is often impassable during the wet seasons (figure 2). These people, traditionally hunter-gatherers, now subsist mainly through small scale agriculture, the primary crop being maize (Musina *et al.,* 2016).

The forest 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. 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).

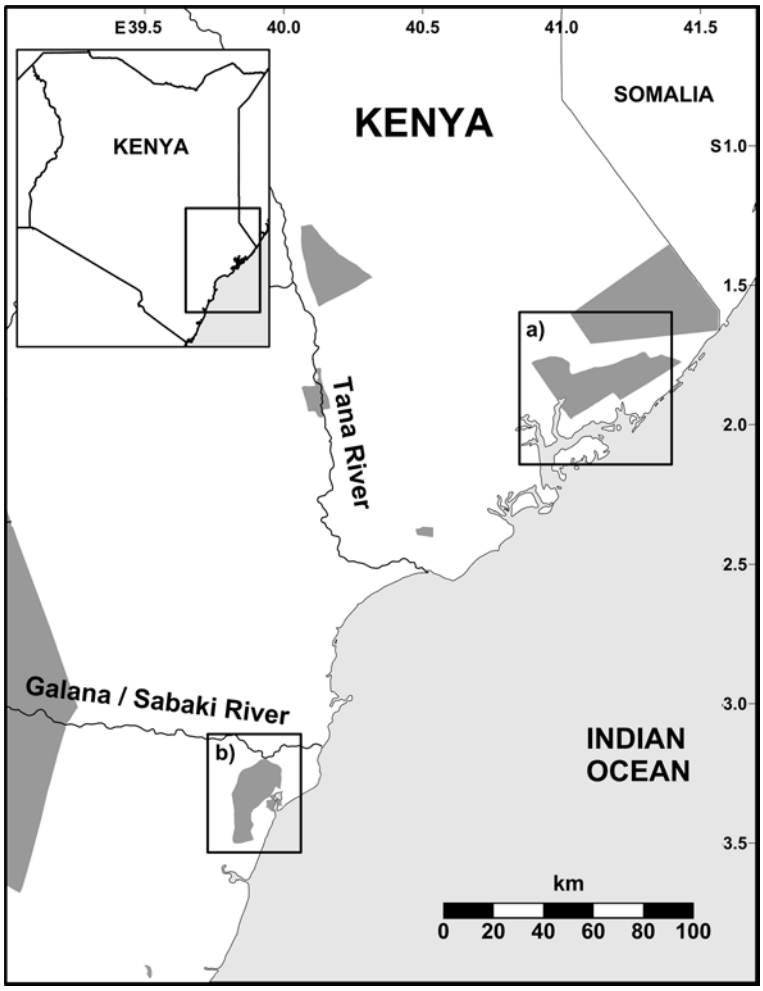

Figure 1. Location of the (a) Boni-Dodori Forest Complex Study Site, north coast of Kenya, and (b) Arabuko-Sokoke Forest Reserve Study Site, central coast of Kenya. Terrestrial protected areas are in grey.

Arabuko-Sokoke FR is the largest remaining forest on the central coast of Kenya (figures 1 & 3; 416 km²; 0–210 m; Bennun & Njoroge, 1999). This forest lies 250 km south of Boni-Dodori. These two forests are separated by two major rivers; Tana and Galana-Sabaki. Arabuko-Sokoke FR is encircled by settlements, agriculture, and a high human population density. As of 2002, about 100 000 people lived in the vicinity of Arabuko-Sokoke FR (ASFMT, 2002). There are two annual wet seasons; April–June and October–November, with April–June being, by far, the wettest period. Mean annual rainfall ranges from 900 mm in the northwest to 1100 mm in the east. Three main vegetation types occur: *Cynometra* forest (dominated by *Cynometra webberi* Bak.f.) and thicket on red sandy soil; *Brachystegia* woodland (dominated by *Brachystegia spiciformis* Benth.) on white sandy soil; and mixed

forest [dominated by *A. quanzensis*, gum copal *Hymenaea verrucosa* Gaertn., *Manilkara sansibarensis* (Engl.) Dubard, *Manilkara sulcata* (Engl.) Dubard, *Combretum schumannii* Engl., and *Drypetes reticulata* Pax] on grey sandy soil. The mixed forest has the highest diversity of trees, containing 67 of the 87 species recorded in Arabuko-Sokoke FR. Here, the abundance of *A. quanzensis*, once the most dominant tree, has been greatly reduced through decades of logging (KIFCON, 1995; Bennun & Njoroge, 1999; ASFMT, 2002).

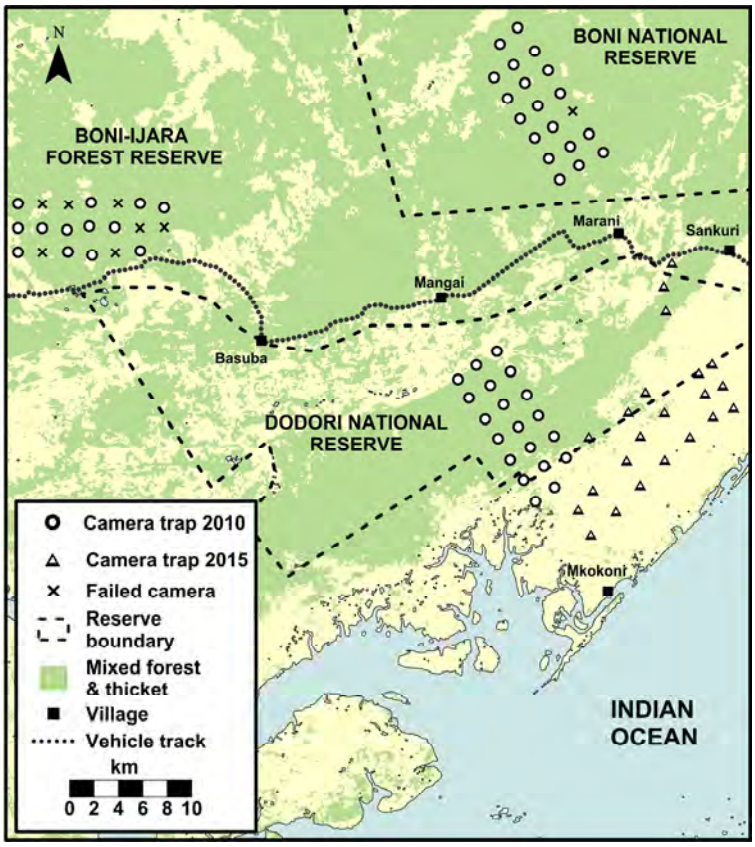

Figure 2. Location of camera-trap grids in the Boni-Dodori Forest Complex.

MATERIALS AND METHODS

Field materials and methods

Cameras were distributed in grids with 2 km between cameras. Cameras were placed in Boni NR (centred on 01°32'13"S, 41°19'32"E during March–June 2010), Dodori NR (01°49'19"S, 41°04'28"E during January–March 2010), Boni-Ijara FR (01°40'34"S, 40°52'32"E during June–September 2010), and in open coastal scrub south of Dodori NR (01°51'11"S, 41°19'09"E during February–July 2015; figure 2). Cameras were placed in Arabuko-Sokoke FR, in *Cynometra* forest (03°21'49"S, 39°50'37"E) and in *Brachystegia* woodland (03°39'14"S, 39°87'19"E) during January–March 2015 (figure 3).

Global Positioning System (GPS) 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. Bushnell Trophy Cam (Bushnell Outdoor Products, Cody, Kansas, USA) and Reconyx RM45 (RECONYX Inc., Holman, Wisconsin, USA) digital cameras were used. Performance of the two camera models was similar. Cameras were programmed to take three photographs per trigger with either no delay (Reconyx) or a 1 second delay (Bushnell). All settings were the default settings. Cameras had a trigger delay of either 0.1 second (Reconyx) or <1 second (Bushnell). Detection range was 25+ m. All cameras used an infrared flash to minimise startling the animals.

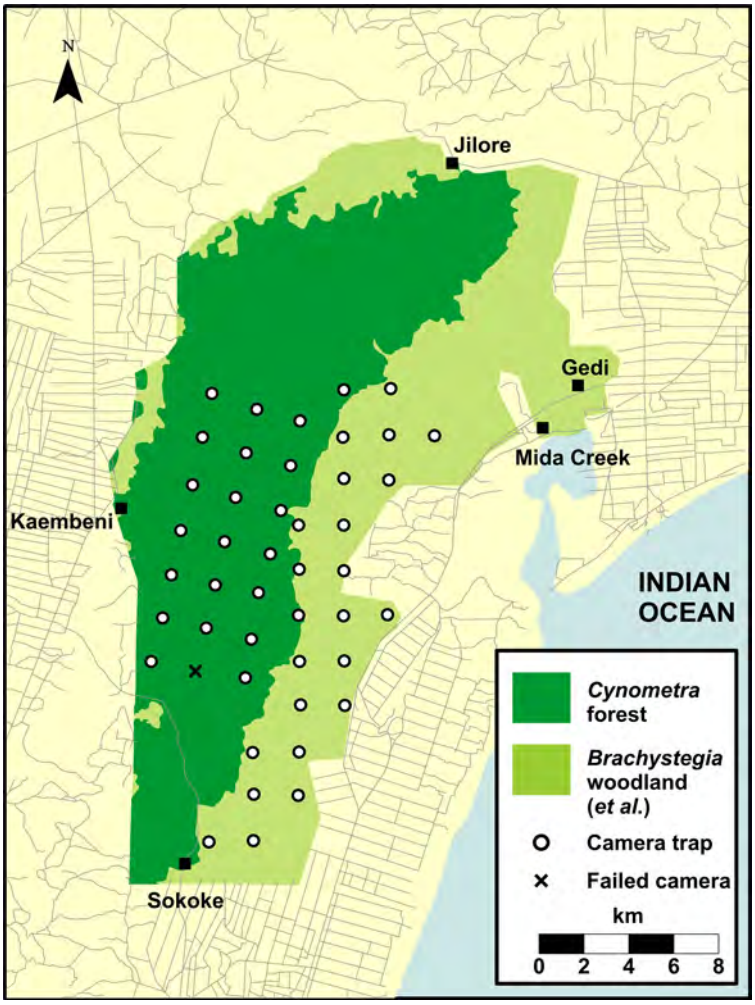

Figure 3. Location of camera-trap grids in the Arabuko-Sokoke Forest Reserve.

Each grid was operated long enough 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.

Data analysis

Exiv2 software (Huggel, 2012) was used to extract information from each photograph (*i.e.* 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).

Identification of desert warthog and common warthog in camera-trap photographs was confirmed by T. Butynski, Y. de Jong and J. P. d'Huart based on criteria described in d'Huart & Grubb (2005), Butynski & De Jong (2010; 2017), Grubb & d'Huart (2013), and De Jong & Butynski (2017a,b). Data were analysed using software developed by Amin *et al.* (2015).

A camera-trap 'independent photographic event' (or 'event') is defined as any sequence of photographs of a given species occurring after an interval of >60 minutes from the previous photograph of that species (Amin *et al.,* 2015). 'Species trap rate' is the mean number of independent photographic events/trap day x 100, for each camera grid. Standard error was calculated from the standard deviation of the daily species trap rate. Species trap rate provides an index of relative abundance with the assumption that species trigger cameras in relation to their density, all other factors being equal. Trap rate provides a comparative index within species when a standardized protocol is used for the surveys, including consistent positioning and management of cameras to help ensure similar detection probabilities.

RESULTS

A minimum effort of 1000 camera-trap days was obtained for each of the six camera grids. Total camera-trap days in Boni-Dodori 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). Total camera-trap days in Arabuko-Sokoke FR was 2209 (mean 49 days/camera).

In Boni-Dodori, this survey resulted in two events of desert warthog at one camera site, six events of common warthog at four camera sites, and 59 events of bushpig at 33 camera sites. In Arabuko-Sokoke FR, only bushpig was camera-trapped (nine events at seven camera sites).

Desert warthog was confirmed at one camera site during two events in Boni-Ijara FR (01°43'12"S, 40°54'55"E; figure 4). One event involved an adult male (figure 5) being closely followed by a sub-adult female. The second event involved an old adult female. These photographs were taken during the middle of the day (11:13 h; 14:37 h). This camera site is 21 km northeast of the nearest locality for which desert warthog is known, *i.e.* Gerille (Obanda *et al.,* 2011) and 22 km east of the second nearest locality for which desert warthog is known, *i.e.* Bodhei (De Jong & Butynski, 2011; 2017).

Common warthog 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 (figures 4 & 5). All common warthog captures were during 08:00–18:00 h.

Bushpig (figure 6) in Boni-Dodori was relatively common and widespread both in thicket and scrub (figure 7). Trap rate was highest in scrub south of Dodori NR (table 1).

Bushpig was the only suid trapped in Arabuko-Sokoke FR (figure 7); five events at four camera sites in *Cynometra* forest and four events at three camera sites in *Brachystegia* woodland (table 1). This species was trapped throughout the day and night, perhaps being most active during late afternoon and early evening (figure 8).

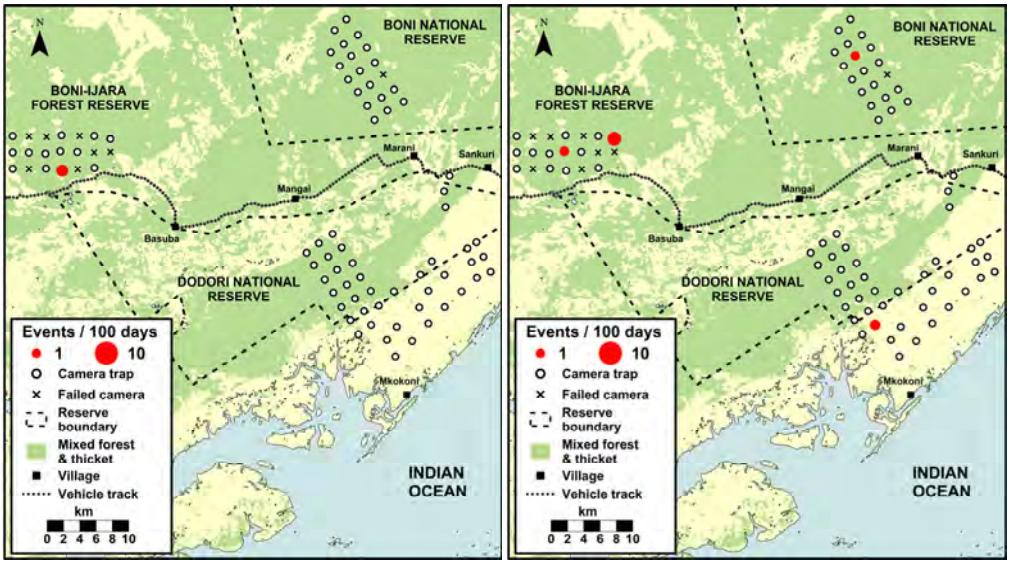

Figure 4. Distribution of desert warthog (left) and common warthog (right) captures by camera-traps in the Boni-Dodori Forest Complex. Size of solid red circle is proportionally weighted by species trap rate. Open circles indicate no warthog captures.

Figure 5. Camera-trap photographs of an adult male desert warthog Phacochoerus aethiopicus *in Boni-Ijara Forest Reserve (left) and an adult male common warthog* Phacochoerus africanus *in Boni National Reserve (right). The adult male desert warthog is most readily distinguished from the adult male common warthog by the hook-shaped infraorbital warts and by ears that fold back at the tip, whereas the common warthog has cone-shaped infraorbital warts and pointed ear tips (d'Huart & Grubb, 2005; Butynski & De Jong, 2017; De Jong & Butynski, 2017a,b). More than 350 photographs of these two species can be viewed on the Warthog Photomap at: www.wildsolutions.nl/photography/photomap/*

Figure 6. Camera-trap photograph of an adult male bushpig Potamochoerus larvatus *in Boni National Reserve.*

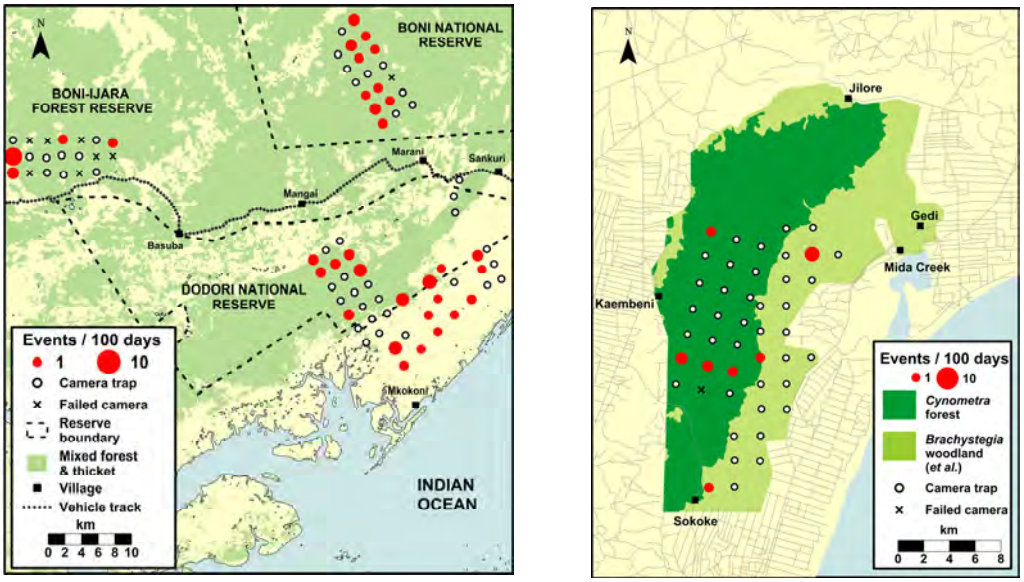

Figure 7. Distribution of bushpig captures by camera-traps in the Boni-Dodori Forest Complex (left) and Arabuko-Sokoke Forest Reserve (right). Size of solid circle is proportionally weighted by species trap rate. Open circles indicated no bushpig captures.

Table 1. Bushpig trap rate, number of photographs of bushpig, and number of independent photographic events in the Boni-Dodori Forest Complex and Arabuko-Sokoke Forest Reserve. Species trap rate = mean number of independent photographic events/trap day x 100.

Site	Trap rate (±SE)	Number of photographs	Number of independent photographic events
Arabuko-Sokoke Forest Reserve *Brachystegia* woodland	0.307 (±0.214)	60	4
Arabuko-Sokoke Forest Reserve *Cynometra* forest	0.508 (±0.245)	216	5
Dodori National Reserve	0.545 (±0.212)	186	7
Boni National Reserve	0.791 (±0.223)	156	13
Boni-Ijara Forest Reserve	0.899 (±0.376)	45	9
Scrub south of Dodori National Reserve	0.935 (±0.187)	433	30

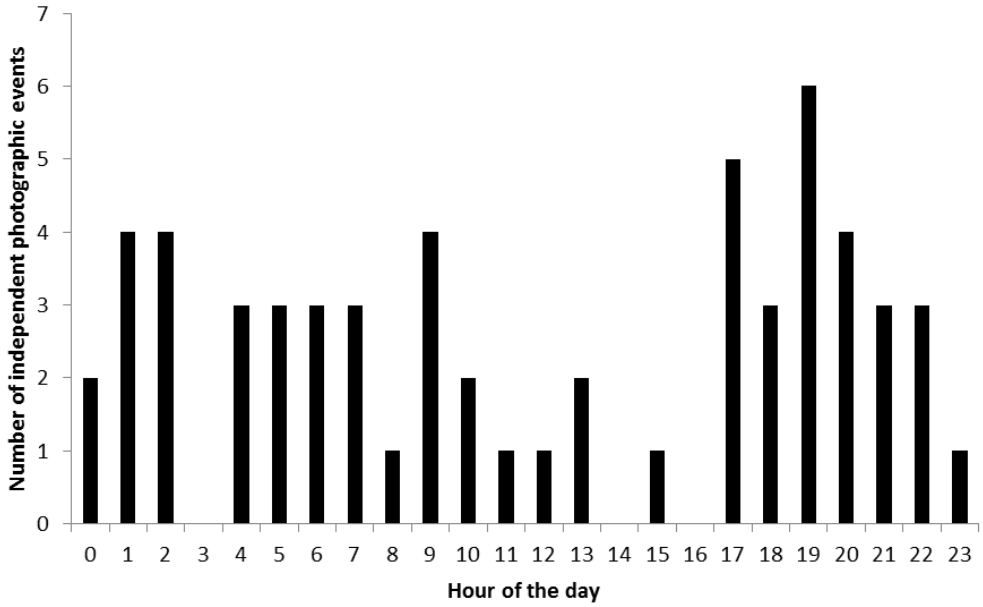

Figure 8. Bushpig 24-hour activity pattern derived from pooled camera-trap independent photographic events (n=59) in the Boni-Dodori Forest Complex.

DISCUSSION

Prior to this study, presence of desert warthog in Boni-Dodori was known on the basis of only two skulls, one from Dodori NR and one from Mkokoni in the Kiunga Marine National Reserve (d'Huart & Grubb, 2001). Occurrence in the thicket of Boni-Ijara FR is unexpected as this species is generally associated with grassland, bushland, and woodland (Grubb &

d'Huart, 2013; De Jong & Butynski, 2017b). The single capture site is, however, close to woodland. It would be useful to survey this woodland more extensively.

The low density of common warthog in Boni-Dodori and its absence in Arabuko-Sokoke FR reflect the species' preference for grasslands, bushlands, and woodlands (Cumming, 2013; Butynski & De Jong, 2017).

The extensive occurrence of bushpig in Boni-Dodori is associated with dense vegetation and scrub; habitats preferred by the species (Seydack, 1990; 2013). Bushpig is at relatively low density in the *Cynometra* forest and *Brachystegia* woodland of Arabuko-Sokoke FR.

Sympatry of desert warthog and common warthog appears to be limited on the north coast of Kenya, where both species are relatively uncommon. This may be because most of the habitats are suboptimal or unsuitable for both species, probably because of the fine scale habitat mosaics in the region. Here, desert warthog 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 not been previously reported, although this is known for other localities in Kenya (*e.g.* Meru National Park, Tsavo East National Park, and mainland Lamu; De Jong & Butynski, 2017a,b). This sympatry is absent in Arabuko-Sokoke FR where only bushpig was recorded.

The ecological and behavioural relationships among the three species of suid on the north coast of Kenya merit further investigation, being of theoretical and applied interest in their own right, as well as for a deeper understanding of the ecological diversity of Boni-Dodori. Although a broad level of niche separation between bush pig and common warthog has long been recognised, the presence of common warthog in Boni-Dodori extends the known zone of sympatry among these three suids. This indicates that they cannot be considered as simply 'allo-species' performing similar ecological roles in geographically separate parts of Africa. There are, therefore, further questions to answer about their comparative ecology and behaviour at a local scale. At the practical level, this also draws attention to the fact that, although the forests are often singled out as the principal habitat of high conservation value on the north coast of Kenya, the reality is that the habitat mosaic characteristic to the region is probably a vital element in the maintenance of these conservation values. As such, conservation planning should aim to maintain continuity among all natural habitats in this region—from the shoreline to the interior bush—not just the forests.

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