Zanzibar's endemic red colobus *Piliocolobus kirkii*: first systematic and total assessment of population, demography and distribution

Tim R.B. Davenport, Said A. Fakih, Sylvanos P. Kimiti, Lydia U. Kleine Lara S. Foley and Daniela W. De Luca

Abstract We present the first systematic assessment of the population, demography and distribution of the Endangered Zanzibar red colobus *Piliocolobus kirkii*, in Unguja in the Zanzibar archipelago, based on a survey effort of 4,725 hours. We estimate the total population comprises 5,862 individuals in 342 groups (mean group size 17.12); 3.4 times the mean of all previous estimates. We calculated a total area of occupancy of 376 km², with 4,042 individuals living within protected areas. Mean group sizes were significantly higher within protected areas (20.57) than outside (12.80). The number of adult females was 3,179 (54.21%), with a mean of 9.29 per group, and the number of adult males was 932 (15.89%), with a mean of 2.71 per group, giving a ratio of 3.31 adult females to adult males. This ratio was significantly lower outside protected areas. The total number of infants was 958 (16.34%), with a mean of 2.80 per group, and the number of subadults/juveniles was 793 (13.52%), with a mean of 2.32 per group, giving ratios of 0.30 infants to adult females, and 0.25 subadults/juveniles to adult females. The results indicate that *P. kirkii* is resilient and thriving far better than assumed. However, recruitment is low and the population may be in decline, with individuals outside protected areas most at risk. We tentatively support the categorization of *P. kirkii* as Endangered on the IUCN Red List, argue for greater protected area status for southern Uzi, Vundwe and Mchamgamle, and discuss conservation implications for this charismatic flagship species.

Keywords Census, distribution, Endangered, *Piliocolobus kirkii*, primates, red colobus, Tanzania, Zanzibar

Introduction

In 1868 the botanist, physician, abolitionist and General-Consul of Zanzibar Sir John Kirk spoke of a rare monkey occurring in the island's forests (Forbes, 1894). The species was named that year in his honour; Kirk's or Zanzibar red colobus *Piliocolobus kirkii*, yet 150 years later this endemic species remains poorly known, with no systematic assessment of its population and distribution having been attempted prior to this study. Nonetheless, *P. kirkii* is considered to be one of the rarest primates in Africa, and is categorized as Endangered on the IUCN Red List (Struhsaker & Siex, 2016).

The smallest of the three *Piliocolobus* species occurring in Tanzania (Davenport et al., 2014), and the one with the slowest reproductive rate (Siex & Struhsaker, 1999), the Zanzibar red colobus is a charismatic, group-living, arboreal monkey, restricted to Unguja, the principal island of the archipelago of Zanzibar (Struhsaker, 2010). Suggestions that the species occurred on mainland Tanzania (Rodgers, 1981) have not been substantiated, although there is a small introduced population in Ngezi Forest Reserve on Pemba Island. It has been speculated that the monkeys were formerly distributed throughout Unguja, with higher densities in the west and central areas where deeper, more fertile soils supported higher forests, and lower densities in the coral thickets of the east coast (Pakenham, 1984). A number of population estimates have been made (Table 1), from detailed density calculations in and around Jozani–Chwaka Bay National Park (Struhsaker & Siex, 1998a,b; Siex & Struhsaker, 1999), in Kiwengwa Forest Reserve (Nowak & Lee, 2013; Johansen, 2016) and in Uzi/Vundwe (Nowak & Lee, 2013) and Masingini Forest Reserves (Khamis, 2010), to island-wide approximations of 1,469–2,400 individuals ($\mu = 1{,}774 \pm$ SE 201).

With Unguja's forests disappearing at a rate of 19.4 km² net loss per year (Kukkonen & Käyhkö, 2014), ongoing increases in human population, tourism and residential development, and agricultural expansion, Zanzibar's biodiversity is threatened. To implement appropriate conservation measures for *P. kirkii* we needed to carry out an accurate and complete evaluation of the species' distribution and abundance, and therefore we carried out systematic surveys to collect data for the first empirical assessment of the species' conservation status. Forest primates are challenging to survey accurately, and various techniques have been suggested (Brockelman & Ali, 1987; Whitesides et al., 1988; Plumptre & Cox, 2006; Rovero et al., 2006). However, based on our experience in Tanzanian forests with the kipunji *Rungwecebus kipunji* (Davenport et al., 2006) and the ashy red colobus *P. tephrosceles* we were able to

Tim R.B. Davenport (Corresponding author) Said A. Fakih, Lara S. Foley and Daniela W. De Luca Wildlife Conservation Society, PO Box 922, Zanzibar, Tanzania. E-mail tdavenport@wcs.org

Sylvanos P. Kimiti Wildlife Conservation Society, Mbeya, Tanzania

Lydia U. Kleine Homer, Arkansas, USA

Received 25 May 2017. Revision requested 26 July 2017.
Accepted 11 September 2017. First published online 7 December 2017.

TABLE 1 Total population estimates for the Zanzibar red colobus *Piliocolobus kirkii* on Unguja Island, Zanzibar (Fig. 1), and population/density estimates for individual sites.

Date	Population/density estimates	Area	Source
Total population			
1868	'Rare, but (in) many wooded districts'	Zanzibar	Sir John Kirk (Forbes, 1894)
1884	'If not extinct, so rare as to be not procurable- . . .exists in one spot. . .looks as if it will be lost to science'	Zanzibar	Sir John Kirk (Forbes, 1894)
1886	'Disappeared from nearly every part of the island. . .linger(s) on in (one) clump of forest'	Zanzibar	H.H. Johnston (Forbes, 1894)
1919	'Almost extinct'	Zanzibar	Mansfield-Aders (1919)
1940	'Uncommon. . .(the) forest is reduced to a few fragments'	Zanzibar	Moreau & Pakenham (1940)
1981	1,469 individuals	Zanzibar	Silkiluwasha (1981)
1992	1,000–1,500 individuals	Zanzibar	Struhsaker (1992)
1996	1,500–2,000 individuals	Zanzibar	Struhsaker & Siex (1996)
1997	c. 2,400 individuals	Zanzibar	Othman & Rijali (1997)
1998–2016	< 2,000 individuals	Zanzibar	Struhsaker & Siex (1998a, b, 2016); Siex & Struhsaker (1999, 2013)
Population by site			
1966	200 individuals	Jozani–Chwaka Bay National Park	Hedberg & Hedberg (1966)
1973	15 individuals	Ngezi Forest Reserve (Pemba)	Silkiluwasha (1981)
1974	23 individuals	Masingini Forest Reserve	Silkiluwasha (1981)
1981	350 individuals	Mchangamle	Silkiluwasha (1981)
1981	200 individuals	Nungwi*	Silkiluwasha (1981)
1981	300 individuals	Uzi Island	Silkiluwasha (1981)
1981	235 individuals	Jozani–Chwaka Bay National Park	Silkiluwasha (1981)
1981	13 individuals	Kichwele Forest Reserve*	Silkiluwasha (1981)
1981	50 individuals	Jendele Forest Reserve*	Silkiluwasha (1981)
1991	1,500 individuals	Jozani–Chwaka Bay National Park	Mturi (1991)
1996	183–191 individuals	Uzi Island	Snyder (1996)
1997	c. 200 individuals	Uzi Island	Othman & Rijali (1997)
1998	56–64 individuals	Masingini Forest Reserve	Struhsaker & Siex (1998b)
1998	550 individuals per km^2	*Shambas*	Struhsaker & Siex (1998a)
1999	235 ± SE 23 individuals per km^2	Southern Jozani–Chwaka Bay National Park	Siex & Struhsaker (1999)
1999	<50 individuals per km^2	Coral rag, Jozani–Chwaka Bay National Park	Siex & Struhsaker (1999)
2000	15–30 individuals	Ngezi Forest Reserve (Pemba)	Camperio-Ciani et al. (2001)
2001	95 individuals	Uzi Island	Aylward (2001)
2005	49.72 ± SE 20.4 individuals per km^2	Kiwengwa Forest Reserve	Nowak & Lee (2013)
2005	196.32 ± SE 17.7 individuals per km^2	Uzi Island	Nowak & Lee (2013)
2010	248 individuals	Masingini Forest Reserve	Khamis (2010)
2011	35–40 individuals	Ngezi Forest Reserve (Pemba)	Butynski & De Jong (2011)
2016	87.66 individuals per km^2 (526 ± SE 227.3 individuals)	Kiwengwa Forest Reserve	Johansen (2016)

* *P. kirkii* now extinct

adapt the methods we had designed and employed successfully (Davenport et al., 2007, 2008), to Zanzibar. These are the most precise and comprehensive methods to (a) determine the full distribution of *P. kirkii*, (b) census the total population of the species, and (c) provide the first comprehensive assessment of the species' conservation status.

Study area

The study was carried out across the island of Unguja (1,529 km^2) in the archipelago of Zanzibar in the United Republic of Tanzania. Much of Unguja is coral rag (Fig. 1), characterized by rocky outcrops and less fertile, shallow

soils, providing little benefit to permanent agriculture (Hettige, 1990). This landscape is dominated by shifting cultivation and more natural vegetation. Protected areas and other sites surveyed are listed in Table 2 and included Jozani–Chwaka Bay National Park, Masingini and Kiwengwa Forest Reserves, Jambiani–Muyuni Proposed Forest Reserve, Kichwele, Dunga and Kibele Forest Reserve Plantations, as well as all other sites where *P. kirkii* has been recorded, suggested or was a possible inhabitant. Bungi Usalaama is an army barracks and was included as a proxy protected area for the purposes of this study, as no civilians are allowed within its boundaries. Habitats comprise mangrove, coral rag, thicket, groundwater forest, woodland and forest edge, plantations and gardens (*shamba*) at elevations between sea level and 110 m.

Methods

During January 2013–January 2015 various methods were employed to determine distribution and abundance. Distribution data were collected using presence/absence surveys, whereas census data were recorded using total counts made while following groups.

Presence/absence surveys

Forests were selected for presence/absence surveys based on our prior knowledge of the areas, information from previous surveys, village interviews and the habitat type from which *P. kirkii* was already known. At each site, 3–4 pairs (teams) of observers searched concurrently for *P. kirkii* along separate pre-planned routes, using 1 : 50,000 topographic maps (Tanzania Surveys and Mapping Division, Series Y742), global positioning system (GPS) units and binoculars. Each team comprised a scientist and a field assistant. Only sightings were considered to be positive indicators of presence. New areas were surveyed each day, adjacent to the area covered the previous day. Some areas were revisited if poor weather hindered earlier work. Survey routes followed wildlife trails, human tracks and off-track, to survey a large area thoroughly. Each team walked slowly (c. 2 km per hour) and quietly during 06.30–18.00, no more than 100 m apart, scanning the understorey and canopy for monkeys. Surveys were paused in heavy rain. When an individual or group was detected, the observer remained until they were confident that the species was correctly identified as *P. kirkii*, and then the follow would begin.

Census

The methods employed were those we had devised previously and used successfully for complete census counts of the ashy red colobus in Sumbawanga (Davenport et al., 2007) and the kipunji in the Southern Highlands (Davenport et al., 2008). To ascertain the total *P. kirkii* population as accurately as possible, we adapted the complete count method, which is accepted as being the most precise primate census technique (Plumptre & Cox, 2006; Davenport et al., 2007, 2008). Unlike gorilla census methods developed by Harcourt & Fossey (1981) and McNeilage et al. (2001, 2006), based on complete counts of indirect sign, our collection methods used direct observations of individuals only (Davenport et al., 2007, 2008). In this way our calculation of the population was neither an estimate nor an extrapolation based on density, but an absolute figure.

To count all individuals directly within every group, we aimed to locate and follow every group for a minimum of 3 consecutive days, tracking all movements and distances with a GPS. When a team located a group, it remained with the group at a distance that was sufficient to maintain contact while minimizing stress on the group (Cipolletta, 2003). Grid reference positions of the group were recorded routinely by GPS every 15 minutes. Teams maintained contact with one another via mobile phone. During the follows, the numbers of individuals, adult males, adult females, infants and subadults/juveniles in each group were counted eight times daily and/or whenever the opportunity arose.

The four field assistants had a combined total of 61 years' experience (a mean of 15 years each) in *P. kirkii* research, including in determining sex and age-class. Extensive inter-observer reliability training was carried out in Masingini Forest Reserve prior to the study, and the same person did all the counting in each team, reducing potential errors resulting from a change of observers. Age classes were defined according to Siex (2003).

At any particular site, *P. kirkii* groups were considered to be unique if (1) they were seen at the same time by different observation teams, spending more than 75% of the observation time at a distance of at least 300 m apart (this was verified a posteriori); (2) one team saw a group other than the one they were following, at least 300 m away, and later verified that no other team had been near the group(s); (3) the groups were recorded > 300 m apart, at the same time, and subsequently moved in different directions. In cases where there was any doubt, at least two teams returned to the location at a later date to verify group identity through location, size and demography.

We used *ArcGIS 9.3* (ESRI, Redlands, USA) to analyse observation data from all *P. kirkii* groups recorded in the census. Using these data we could calculate the area of occupancy (AOO), defined as the area within the species' extent of occurrence (EOO) that a taxon occupies, excluding cases of vagrancy (IUCN, 2017). This definition reflects the fact that a taxon will not usually occur throughout its EOO, which may contain unsuitable or unoccupied habitats. We employed the grid method of AOO representation and calculation proscribed by IUCN (2017), whereby a 2 × 2 km grid of cells is overlain on observation points, although we acknowledge that with this grid size in Zanzibar, AOO may

TABLE 2 Total number of *P. kirkii* groups, adult males, adult females, subadults/juveniles, infants, individuals in groups and total individuals per site, on Unguja Island, Zanzibar (Fig. 1).

Site	Groups	Adult males	Adult females	Subadults/ Juveniles	Infants	Total individuals in groups	Total individuals
Chwaka	3	6	14	6	6	32	34
Dunga Forest Reserve Plantation	1	2	2	1	0	5	5
Jambiani	11	23	67	18	24	132	134
Jozani–Chwaka Bay National Park	141	437	1,574	415	481	2,907	2,907
Cheju	7	18	39	8	24	89	90
Kiwengwa Forest Reserve	37	115	330	72	111	628	628
Kizimkazi	15	24	74	13	18	129	130
Maji Mekundu	1	1	7	3	2	13	13
Marumbi	4	8	11	5	6	30	30
Bungi Usalaama	2	6	41	9	9	65	65
Mchangamle	23	56	220	48	42	366	366
Kitogani	17	36	105	26	33	200	200
Uzi/Vundwe	16	39	125	32	38	234	234
Ukongoroni	24	53	192	52	47	344	344
Umbuji	2	8	17	6	6	37	37
Uroa	4	13	12	4	4	33	34
Masingini Forest Reserve	10	36	192	25	56	309	309
Michamvi	1	1	1	1	0	3	3
Jambiani–Muyuni Proposed Forest Reserve	9	16	52	13	22	103	103
Shambas south of Jozani–Chwaka Bay National Park	10	22	79	15	23	139	139
Unguja Ukuu	4	8	23	20	6	57	57
Total	342	928	3,177	792	958	5,855	5,862

be overestimated. A taxon's EOO is the area contained within the shortest continuous boundary that can be drawn to encompass all the known, inferred or projected sites of present occurrence (IUCN, 2017). We measured the EOO by calculating the area of minimum convex polygons and using a geographical information system (GIS). As this measure excludes discontinuities within the total distribution, such as areas of unsuitable or heavily degraded habitat, we produced separate polygons for the isolated *P. kirkii* groups in Maji Mekundu, Masingini and Michamvi.

Results

The total effort spent searching for and following *P. kirkii* was 4,725 team hours. The surveys revealed the full extent of *P. kirkii* distribution across Unguja (Fig. 1). The introduced group in Ngezi on Pemba Island was not considered. Despite extensive surveys, *P. kirkii* was not recorded (and is presumed to be extirpated) from Bambi, Jendele and Kichwele Forest Reserves and Nungwi, where the species was once present. The species' absence from these areas was supported by discussions in adjacent villages. One group only was found in each of Kibele and Dunga Forest Reserves and Maji Mekundu. We calculated an AOO of 376 km² and an EOO of 428 km². The census data and EOO yield a species-wide density estimate of 13.7 individuals per km². *P. kirkii* distribution in terms of total time spent in each habitat type is illustrated in Fig. 2.

A total of 342 *P. kirkii* groups were identified during the census, as well as three singletons and four doubletons. The numbers of groups, individuals, adult females, adult males, subadults/juveniles and infants per site and site type are in Table 2. We estimate the total *P. kirkii* population to be 5,862 individuals, with 3–52 individuals per group ($\mu = 17.12 \pm$ SE 0.48; n = 342); this is 2.93–3.98 times higher than all previous extrapolated estimates (Table 2). Circa 4,042 individuals (69%) live within protected areas and 1,820 (31%) live outside protected areas.

Mean group size was considerably higher in protected areas ($\mu = 20.57 \pm$ SE 0.63; n = 190) compared to non-protected areas ($\mu = 12.80 \pm$ SE 0.58; n = 152) (Fig. 3) and this difference was highly significant (Wilcoxon signed rank test: $W = 6815$, $P < 0.05$). The total number of adult females was 3,179 (54.21% of the total), with a mean of 9.29 ± SE 0.29 adult females per group (n = 342). The total number of adult males was 932 (15.89%), with a mean of 2.71 ± SE 0.08 per group (n = 342). These data demonstrate a ratio of 3.31 adult females to adult males across the species' range (Fig. 4). However, the ratio differed significantly between protected and non-protected areas ($\chi^2(340) = 3.39$, $P = < 0.05$), with a significantly lower ratio outside protected areas. The total number of subadults/juveniles was 793 (13.52% of the total), with a mean of 2.32 ± SE 0.11 per

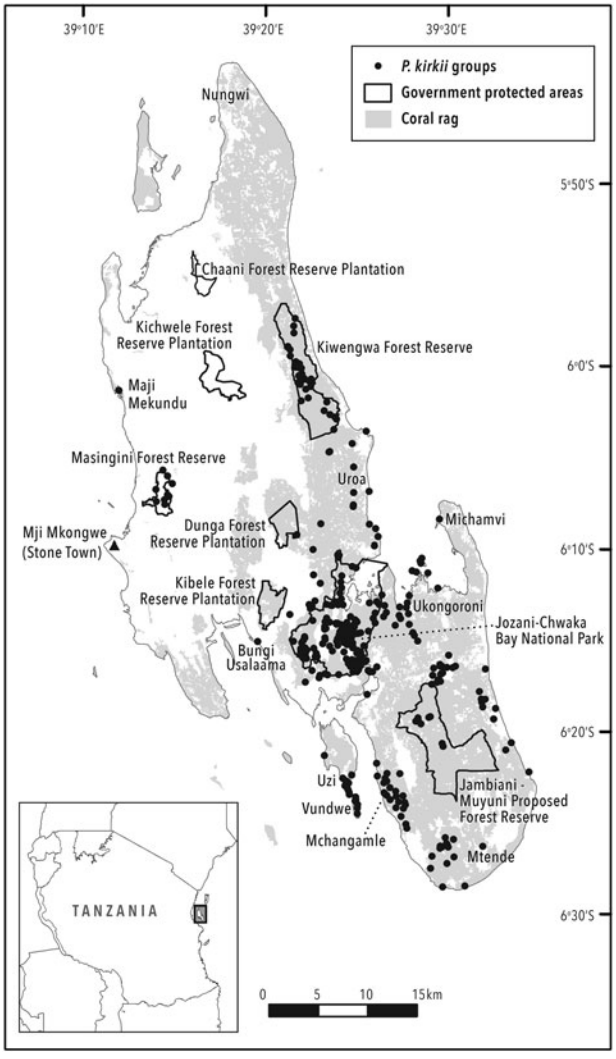

FIG. 1 Locations of all *Piliocolobus kirkii* groups located and counted on the island of Unguja, Zanzibar.

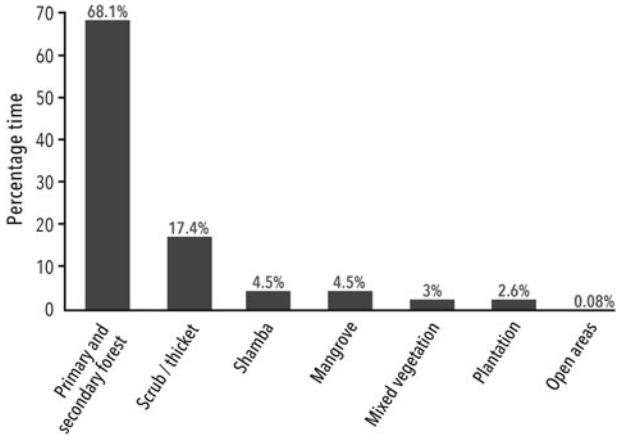

FIG. 2 Distribution of all *P. kirkii* groups according to time spent in each habitat type.

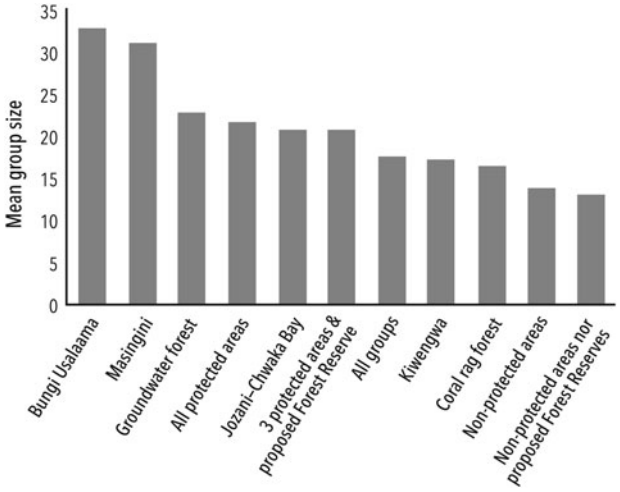

FIG. 3 Mean group size of *P. kirkii* in various protected and non-protected areas and habitat types.

group (n = 342), and the total number of infants was 958 (16.34%), with a mean of 2.80 ± SE 0.11 per group (n = 342), yielding ratios of 0.30 infants to adult females, and 0.25 subadults/juveniles to adult females. The ratio of infants to adult females did not differ between protected and non-protected areas ($\chi^2(340) = 0.584$, P = 0.449), nor did the ratio of subadults/juveniles to adult females ($\chi^2(340) = 0.627$, P = 0.427).

Discussion

Although there have been a number of previous estimates of the population size of *P. kirkii* (Table 1), we present the first systematically derived data on the total abundance and distribution of this primate. The conservation value of *P. kirkii*, the immediacy of threats posed by a growing human population and tourist sector, and the resources at our disposal guided our decision to perform a complete count by sweep census across Zanzibar's main island of Unguja. Having developed the methods and employed them successfully on two other primate species (Davenport et al., 2007, 2008), our aim was to ensure as precise a population assessment as possible. The complete count relies on locating and following every group (Davenport et al., 2008). However, despite the considerable effort undertaken, we acknowledge the possibility that double-counting may have occurred as a result of occasional challenges associated with dense habitat, fission–fusion, sampling bias or group overlap. We also recognize potential problems associated with inter-observer consistency regarding the identification of age–sex categories. Nevertheless, the methods we employed and the training we provided were designed to minimize potential errors, and we aimed to provide one of the few demographic datasets for an entire primate species.

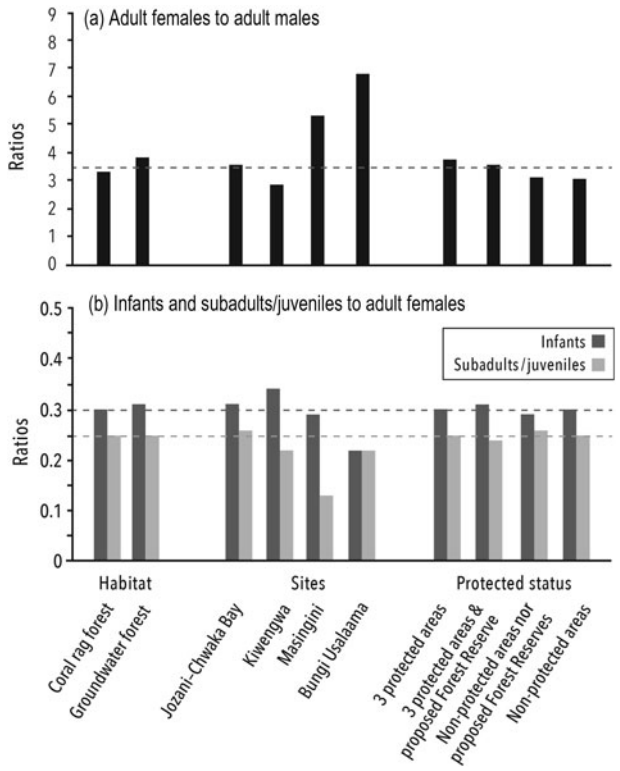

FIG. 4 Ratios of (a) adult females to adult males and (b) infants to adult females, and subadults/juveniles to adult females of *P. kirkii*, for various key habitats, selected sites and levels of protection. Dotted lines represent mean ratio across all groups.

Although comparatively small for a primate population, a total population of 5,862 individuals is almost three times larger than the highest previous estimate for this species. The reasons behind this disparity are unclear. From its discovery to science in 1886 to the early 20th century *P. kirkii* was described as very rare and on the verge of extinction. A century later the total population was estimated to comprise 1,000–2,400 individuals. It is tempting to assume that these latter estimates (Table 1) were based on incomplete samples and insufficient knowledge of the species' full extent of occurrence. However, it may also be the case that the former descriptions reflected the widespread forest clearance that took place across Zanzibar in the mid 19th century for clove plantations (Hazell, 2011). It is possible that after the collapse of the clove industry following the hurricane of 1872, and the market crash of the 1920s, forests and associated fauna began to recover. The assumption that *P. kirkii* was, and always has been, in decline may be incorrect, and the population may have been increasing. The data from Jozani–Chwaka Bay National Park, Uzi, and especially Masingini Forest Reserve, indicate that marked population growth of the species is possible even in conditions that are less than ideal (Struhsaker & Siex, 1998a, b). Our count of 309 individuals in Masingini Forest Reserve is the latest point in an exponential increase (Fig. 5) for this small forest since *P. kirkii* was introduced there (Table 1). The current

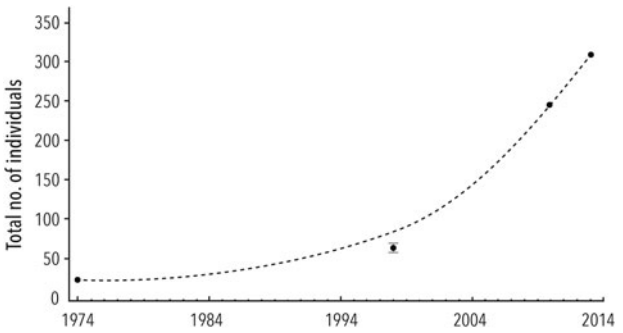

FIG. 5 *P. kirkii* population increase in Masingini Forest Reserve (Fig. 1) during 1974–2014.

recruitment in Masingini is low, as reflected by a subadult/juvenile to adult female ratio of 0.13, compared to 0.74 in 1994 (Struhsaker & Siex, 1998a,b), although this may reflect an isolated subpopulation that has now reached capacity. What is clear is that the red colobus is a more resilient and abundant animal than anyone since 1868 had thought.

However, the species faces serious challenges and, with 5,862 individuals, *P. kirkii* is rare by most primate standards. In Tanzania, an important country for primate conservation (Davenport et al., 2006, 2014), it is the third most threatened diurnal primate, after *R. kipunji* (1,117 individuals; Davenport et al., 2008) and *Cercocebus sanjei* (2,800–3,500 individuals; McCabe et al., in press); *P. gordonorum* is fourth, with 30,000–40,000 individuals (Rovero et al., in press). Furthermore, mean recruitment/survivorship is low, indicating a population in decline across Unguja. Subadult/juvenile to adult female ratios as low as 0.25 are rare among all red colobus species that have been studied (15 samples from six taxa; Struhsaker, 2010), and the two populations with similar ratios were threatened by habitat loss or predation.

Tourism continues to have a negative effect on *P. kirkii* across Unguja, and recent hotel and residential developments have destroyed forest habitat and/or connectivity in Uroa, Mchangamle, Kiwengwa, Jambiani, Chwaka, Nungwi, Fumba and Michamvi. Meanwhile, demographic data indicate that mean group size is significantly smaller outside protected areas than within. Group size in red colobus species is determined by predation pressure, habitat quality and sociological dynamics (Struhsaker, 2010). Following the probable extinction of the Zanzibar leopard *Panthera pardus pardus* in the 1980s, people are the only predators of *P. kirkii*. Predation by people may be considerable, and hunting has been shown to result in smaller group sizes in *P. tephrosceles* (Stanford, 1998). Although the effect of predation tends to be less strong than that of habitat (Struhsaker, 2010), in Zanzibar at least, it appears to be significant. Nonetheless, large groups of red colobus usually occur in large forest blocks of good habitat, whereas smaller groups typically occur in small forest patches or degraded forest

(Struhsaker, 2010). This is consistent with our finding significantly smaller group sizes outside protected areas, probably as a result of fragmentation, and reduced resources and food availability, as found in other colobines (Chapman et al., 2002; Struhsaker et al., 2004), as well as higher levels of hunting by people. Barelli et al. (2015) reported that α-diversity of gut microbiota in *P. gordonorum* in the Udzungwa Mountains was significantly higher in undisturbed forest. This variation may be associated with food plant diversity and may also influence the survival of *P. kirkii*.

Siex (2003) found the male to female sex ratio in *P. kirkii* in and around Jozani–Chwaka Bay National Park was high (1 : 4.6) and variable. In 1992–1993 the sex ratio in the *shambas* outside the Park was 6.9, much higher than inside; however, by 1999 this had declined to 3.8 as a result of population compression into the *shamba* from degraded forest, and male immigration (Siex, 2003). Our data indicate a lower sex ratio of 1 : 3.31 across Unguja (and the species), as well as significantly lower ratios outside protected areas compared to inside. This overall ratio suggests that compression may not have been the cause of the decline in sex ratio, or at least not completely. Van Schaik & Hörstermann (1994) argued that where predators are common there are more males and thus lower sex ratios. Our surveys showed the extent of human predation on *P. kirkii*, and the sex ratio may not only provide ecological evidence of this, but also show that it is much more prevalent, unsurprisingly, outside protected areas. The impact of mortality can be reflected more strongly in the ratio of adult females to subadults/juveniles than infants (Struhsaker, 2010), but like Siex (2003) we found no significant differences between these ratios, or between female to infant ratios inside and outside protected areas, although our data indicate there has been a 3.4–5.7 fold decline in recruitment in and around Jozani–Chwaka Bay National Park since 1992 (Siex & Struhsaker, 1999; Siex, 2003).

Circa 85.5% of *P. kirkii* were located in forest (primary, secondary, forest edge and thicket), with 4.5% occurring in each of *shamba* and mangroves. Although the species is clearly capable of surviving, and even thriving, in degraded habitat, forest in some form is essential. Although mangroves may be a refuge for a few individuals, notably in Maji Mekundu, Ukongoroni and parts of Uzi, it does not appear to be an important or source habitat at the species level as postulated by Nowak & Lee (2011).

It is likely that most of the groups and individuals outside protected areas will not survive in the long term as habitat is lost. This puts 1,820 individuals (the 31% of the total population that live outside protected areas) in jeopardy, with isolated groups in Kibele, western Uzi, Maji Mekundu, Mtende, Michamvi and the eastern coastal strip most at risk. The species has already been extirpated from Nungwi, Matemwe, Kichwele, Jendele and Dunga since the late 1990s. The proposed Jambiani–Muyuni Forest Reserve has only 103 individuals in nine groups and will therefore protect only a small portion (1.8%) of the total *P. kirkii* population. Nonetheless, greater protection for this area resulting from its gazettement as a Forest Reserve may facilitate *P. kirkii* population growth.

Nowak (2007) reported that the Uzi/Vundwe population was at least twice the size of that in Kiwengwa. However, according to our data there are currently 2.7 times as many *P. kirkii* individuals in Kiwengwa as in Uzi/Vundwe. There is justification for improved management of Uzi/Vundwe (Nowak & Lee, 2011; Davenport et al., 2014), although the assertion that this is needed because mangrove-dwelling groups are a behaviourally and ecologically distinct subpopulation (Nowak & Lee, 2011) may now be open to debate. However, there is certainly a strong case for the gazettement of a new protected area to protect > 600 *P. kirkii* individuals and other biodiversity, covering southern Uzi, Vundwe and Mchangamle across Pete Inlet. Mchangamle offers greater potential for long-term viability, with extant habitat corridors to the north and south. Vundwe Islet is not officially inhabited, but during visits in April and August 2017 we found that migrant fishing camps there have expanded and become more permanent.

Hunting with dogs, guns and sometimes poison is a significant threat to wildlife. *Piliocolobus kirkii* and *Cercopithecus mitis albogularis* are both killed for meat for people and for dogs, and as a pest. This is despite traditional beliefs that *kima punju* (poison monkeys) are unfit for human or canine consumption. The practice is widespread, and monkey hunters were observed during the surveys in Kibele, Marumbi, Ufufuma, Mchangamle, Jozani and Kiwengwa. During 2007–2013 poisoned water was routinely left out to kill *P. kirkii* in mangroves on Uzi. The last known individual in Kichwele Forest Reserve was killed by hunters in 2010, and monkey carcasses are sold for USD 3–6 each.

The total AOO calculated as the sum of the occupied grid squares is 376 km² and the total EOO (species range) is 428 km² (i.e. 24.6 and 28% of the total land area of Unguja, respectively), although these figures could be smaller if calculated with grid cells smaller than 2 × 2 km. The occurrence of *P. kirkii* across a quarter of the island is in contrast to Kirk and Johnson's observations in 1884 and 1886, respectively, that the monkey was 'lingering on in one clump of forest' only (Forbes, 1894).

A taxon is considered to be threatened if the best available evidence indicates that it meets any one of a number of criteria (IUCN, 2017). *P. kirkii* was most recently assessed as Endangered based on criteria B1a,b(ii,iii,v) (Struhsaker & Siex, 2016); however, our data do not support this unequivocally, as there is no empirical evidence of 'extreme fluctuations' or a reduction in population size, even with hunting by humans. It could be argued that the population is increasing, especially within protected areas, which contain 69% of the global population. Nonetheless, low recruitment,

forest loss, an increasing human population, and development all justify a projected reduction. The crucial factor, therefore, lies in a subjective assessment of whether the population is severely fragmented. If we adopt the precautionary principal and accept that it is, based on the isolation of several subpopulations, then we recommend a categorization of Endangered based on criteria B1a,b(i,ii,iii).

This survey did not include *P. kirkii* in Ngezi Forest Reserve on Pemba Island and we do not include them as part of the census. In 1973 c. 15 individuals were introduced to the island from Unguja (Silkiluwasha, 1981), and the latest reports are that 35–40 now survive there (Butynski & De Jong, 2011). Although it is possible that *P. kirkii* may have existed in Masingini and other sites on Unguja, this small population in Ngezi is definitely exotic and its conservation there is hard to justify, not least because of its possible impact on indigenous flora and fauna. We believe there is a case for the re-location of these individuals back to Unguja.

The results we present are surprising and they offer some grounds for optimism. Although Zanzibar's forests continue to be lost, and resources to manage them are meagre, income from well-managed primate and forest tourism can help. In 2016 Jozani–Chwaka Bay National Park accrued revenue of USD 334,700 (Tahir Abasi, pers. comm.), most of which was attributable to *P. kirkii* viewing. This could be further developed, with additional habituated groups in Kiwengwa, Masingini, Uzi or Jambiani–Muyuni, for example. We also recommend that *P. kirkii* be adopted by the Revolutionary Government of Zanzibar as the official national animal, as there can be few more charismatic and appropriate candidates. The persistence of Zanzibar's unique red colobus would be a fitting tribute to the efforts of the Government, as well as John Kirk, the man whose name the species bears and who accomplished so much for science and humanity alike.

Acknowledgements

All work was funded by the Wildlife Conservation Society (WCS). Research permission was granted by the Department of Forestry and Non-Renewable Natural Resources in Zanzibar. We thank Shaabani Iman, Ali Kassim Ali, Almasi Ramadhani, Hilali Akiba, Abasi Juma Mzee, Tahir Abasi, Lazaro Benedict, Sarah Markes and Rob Critchlow for their varied and considerable assistance. We also thank the Community Conservation Committees on Unguja for their support. Thomas Struhsaker and an anonymous referee provided helpful comments.

Author contributions

TRBD conceived the research, raised the funds, designed the methods, directed the fieldwork, visited all sites, analysed the data, and wrote the article. SAF, SPK and LUK coordinated with village authorities, led teams in the field, managed data collection and edited the text. LSF carried out GIS work and text editing. DWDL provided technical advice, oversaw project logistics and human resources, and carried out statistical analysis and edits.

References

Aylward, A.G. (2001) *Population census of the Zanzibar red colobus monkey (*Procolobus kirkii*) on Uzi Island. Zanzibar*. BSc thesis. School for International Training, Zanzibar, Tanzania.

Barelli, C., Albanese, D., Donati, C., Pindo, M., Dallago, C., Rovero, F. et al. (2015) Habitat fragmentation is associated to gut microbiota diversity of an endangered primate: implications for conservation. *Scientific Reports* 5, 14862, http://dx.doi.org/10.1038/srep14862.

Brockelman, W.Y. & Ali, R. (1987) Methods of surveying and sampling forest primate populations. In *Primate Conservation in the Tropical Rain Forest* (eds C.W. March & R.A. Mittermeier), pp. 23–62. Alan R. Liss, New York, USA.

Butynski, T.M. & De Jong, Y.A. (2011) Zanzibar red colobus on Pemba Island Tanzania: population status 38 years post-introduction. In *Global Reintroduction Perspectives: 2011* (ed. P.S. Soorae), pp. 168–174. IUCN/SSC Reintroduction Specialist Group, and Environment Agency-Abu Dhabi, UAE.

Camperio Ciani, A., Palentini, L. & Finotto, E. (2001) Survival of a small translocated *Procolobus kirkii* population on Pemba Island. *Animal Biodiversity & Conservation*, 24, 15–18.

Chapman, C.A., Chapman, L.J., Bjorndal, K.A. & Onderdonk, D. A. (2002) Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. *International Journal of Primatology*, 23, 283–310.

Cipolletta, C. (2003) Ranging patterns of a western gorilla group during habituation to humans in the Dzanga-Ndoki National Park, Central African Republic. *International Journal of Primatology*, 24, 1207–1226.

Davenport, T.R.B., De Luca, D.W., Jones, T., Mpunga, N.E., Machaga, S.J., Kitegile, A. & Picton Phillipps, G. (2008) The Critically Endangered kipunji *Rungwecebus kipunji* of southern Tanzania: first census and conservation status assessment. *Oryx*, 42, 352–359.

Davenport, T.R.B., Mpunga, N.E. & Machaga, S.J. (2007) Census and conservation assessment of the red colobus (*Procolobus rufomitratus tephrosceles*) on the Ufipa Plateau, southwest Tanzania: newly discovered, threatened and extinct populations. *Primate Conservation*, 22, 97–105.

Davenport, T.R.B., Nowak, K. & Perkin, A. (2014) Priority primate areas in Tanzania. *Oryx*, 48, 39–51.

Davenport, T.R.B., Stanley, W.T., Sargis, E.J., De Luca, D.W., Mpunga, N.E., Machaga, S.J. & Olson, L.E. (2006) A new genus of African monkey, *Rungwecebus*: morphology, ecology and molecular phylogenetics. *Science*, 312, 1378–1381.

Forbes, H.O. (1894) *A Hand-Book to the Primates*. W.H. Allen & Co. Ltd., London, UK.

Harcourt, A.H. & Fossey, D. (1981) The Virunga gorillas: decline of an 'island' population. *African Journal of Ecology*, 19, 83–97.

Hazell, A. (2011) *The Last Slave Market*. Constable, London, UK.

Hedberg, I. & Hedberg, O. (eds) (1966) *Conservation of Vegetation in Africa South of the Sahara*. Association Pour I' Etude Taxonomique de la Flora d' Afrique Tropicale, Uppsala, Sweden.

Hettige, M.L. (1990) *Land Evaluation and Land Suitability Classification—Unguja & Pemba Island*. Food and Agriculture Organization of the United Nations, Zanzibar, Tanzania.

IUCN (2017) *The IUCN Red List of Threatened Species*. Http://www.iucnredlist.org [accessed 6 May 2017].

Johansen, L.N. (2016) *A conservation re-assessment of the endangered Zanzibar red colobus* Piliocolobus kirkii. MSc thesis. University of Copenhagen, Copenhagen, Denmary.

Khamis, M.S. (2010) *Masingini Forest Reserve*. Unpublished report. Department of Forestry & Non-renewable Natural Resources, Zanzibar, Tanzania.

Kukkonen, M. & Käyhkö, N. (2014) Spatio-temporal analysis of forest changes in contrasting land use regimes of Zanzibar, Tanzania. *Applied Geography*, 55, 193–202.

Mansfield-Aders, W. (1919) The natural history of Zanzibar and Pemba. In *Zanzibar Island Metropolis of Eastern Africa* (ed F. B. Pearce), pp. 326–339. Gallery Publications, Zanzibar, Tanzania.

McCabe, G., Rovero, F., Fernández, D., Struhsaker, T. & Butynski, T. (in press) *Cercocebus sanjei*. In *The IUCN Red List of Threatened Species*. Http://www.iucnredlist.org.

McNeilage, A., Plumptre, A.J., Brock-Doyle, A. & Vedder, A. (2001) Bwindi Impenetrable National Park, Uganda: gorilla census 1997. *Oryx*, 35, 39–47.

McNeilage, A., Robbins, M.M., Gray, M., Olupot, W., Babaasa, D., Bitariho, R. et al. (2006) Census of the mountain gorilla *Gorilla beringei beringei* population in Bwindi Impenetrable National Park, Uganda. *Oryx*, 40, 419–427.

Moreau, R.E. & Pakenham, R.H. (1940) The land vertebrates of Pemba, Zanzibar, and Mafia: a zoo-geographical study. *Proceedings of the Zoological Society of London*, 110, 7–128.

Mturi, F.A. (1991) *The feeding ecology and behavior of the red colobus monkey (*Colobus badius kirkii*)*. PhD thesis. University of Dar es Salaam, Dar es Salaam, Tanzania.

Nowak, K. (2007) *Behavioral flexibility and demography of* Procolobus kirkii *across floristic and disturbance gradients*. PhD thesis. University of Cambridge, UK.

Nowak, K. & Lee, P.C. (2011) Demographic structure of Zanzibar red colobus populations in unprotected coral rag and mangrove forests. *International Journal of Primatology*, 32, 24–45.

Nowak, K. & Lee, P.C. (2013) Status of Zanzibar red colobus and Sykes's monkeys in two coastal forests in 2005. *Primate Conservation* 27, 65–73.

Othman, W.J. & Rijali, H.A. (1997) *Islandwide red colobus census in Zanzibar. Zanzibar Forestry Technical Paper 90*. Department of Commercial Crops, Fruits and Forestry, Zanzibar, Tanzania.

Pakenham, R.H.W. (1984) *The Mammals of Zanzibar and Pemba Islands*. Unpublished report to Zanzibar Department of Environment, Zanzibar, Tanzania.

Plumptre, A.J. & Cox, D. (2006) Counting primates for conservation: primate surveys in Uganda. *Primates*, 47, 65–73.

Rodgers, W.A. (1981) The distribution and conservation status of colobus monkeys in Tanzania. *Primates*, 22, 33–45.

Rovero, F., Barelli, C., Butynski, T., Marshall, A. & Struhsaker, T. (in press) *Piliocolobus gordonorum*. In *The IUCN Red List of Threatened Species*. Http://www.iucnredlist.org.

Rovero, R., Struhsaker, T.T., Marshall, A.R., Rinne, T.A., Pedersen, U.B. & Butynski, T.M. (2006) Abundance of diurnal primates in Mwanahina Forest, Udzungwa Mountains, Tanzania: a multi-observer comparison of line-transect data. *International Journal of Primatology*, 27, 675–697.

Siex, K.S. (2003) *Effects of population compression on the demography, ecology and behavior of the Zanzibar red colobus monkey (*Procolobus kirkii*)*. PhD thesis. Duke University, Durham, USA.

Siex, K.S. & Struhsaker, T.T. (1999) Ecology of the Zanzibar red colobus monkey: demographic variability and habitat stability. *International Journal of Primatology*, 20, 163–192.

Siex, K.S. & Struhsaker, T.T. (2013) Zanzibar red colobus *Procolobus kirkii*. In *Mammals of Africa, Volume II* (eds J. Kingdon, D. Happold & T. Butynski), pp. 151–154. Bloomsbury Publishing, London, UK.

Silkiluwasha, F. (1981) The distribution and conservation status of the Zanzibar red colobus. *African Journal of Ecology*, 19, 187–194.

Snyder, M. (1996) *Ecology and behaviour of the Zanzibar red colobus monkey (*Procolobus kirkii*) on Uzi Island, Zanzibar*. BSc thesis. School for International Training, Zanzibar, Tanzania.

Stanford, C.B. (1998) *Chimpanzees and Red Colobus: The Ecology of Predator and Prey*. Harvard University Press, Cambridge, USA.

Struhsaker, T.T. (1992) *Conservation and Natural Resource Management of Jozani Forest Reserve and Adjacent Areas, Zanzibar*. Unpublished report. Zanzibar Forest Department, Zanzibar, Tanzania.

Struhsaker, T.T. (2010) *The Red Colobus Monkeys: Variation in Demography, Behavior, and Ecology of Endangered Species*. Oxford University Press, New York, USA.

Struhsaker, T.T., Marshall, A.R., Detwiler, K.M., Siex, K., Ehardt, C.L., Lisbjerg, D.D. & Butynski, T.M. (2004) Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. *International Journal of Primatology*, 25, 615–658.

Struhsaker, T. & Siex, K. (2016) *Piliocolobus kirkii*. In *The IUCN Red List of Threatened Species 2016*: e.T39992A92630131. Http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T39992A92630131.en [accessed 6 May 2017].

Struhsaker, T.T. & Siex, K.S. (1996) The Zanzibar red colobus monkey: conservation status of an endangered island endemic. *African Primates*, 2, 54–61.

Struhsaker, T.T. & Siex, K.S. (1998a) The Zanzibar red colobus monkey: conservation status of an endangered island endemic. *Primate Conservation*, 18, 51–58.

Struhsaker, T.T. & Siex, K.S. (1998b) Translocation and introduction of the Zanzibar red colobus monkey: success and failure with an endangered island endemic. *Oryx*, 32, 277–284.

van Schaik, C. & Hörstermann, M. (1994) Predation risk and the number of adult males in a primate group: a comparative test. *Behavioral Ecology & Sociobiology*, 35, 261–272.

Whitesides, G.H., Oates, J.F., Green, S.M. & Kluberdanz, R.P. (1988) Estimating primate densities from transects in a West African rainforest: a comparison of techniques. *Journal of Animal Ecology*, 57, 345–367.

Biographical sketches

Tim Davenport set up and directs the WCS Tanzania Program. His research interests are broad and include anything with applied conservation relevance. Said Fakih is a botanist, forester and assistant director of the WCS Zanzibar Program. Sylvanos Kimiti manages field teams in the Southern Highlands studying carnivores, primates and ungulates. Lydia Kleine is a biologist who spent 2010–2013 in Zanzibar, and currently works as a commercial salmon fisher in Alaska. Lara Foley manages the WCS Tarangire Elephant Project and uses GIS technology to study wildlife across the Tarangire ecosystem. Daniela De Luca is a carnivore biologist who specializes in carnivore and threatened species ecology, conservation and monitoring. She set up the Uganda mongoose project in 1990.