ORIGINAL RESEARCH

Camera trapping reveals trends in forest duiker populations in African National Parks

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Abstract

Bushmeat hunting is widely cited as cause for declines of wildlife populations throughout Africa. Forest duikers (Bovidae, Cephalophinae) are among the most exploited species. Whether current harvest rates imperil duikers is debated because of the difficulty of accurately assessing population trends. To assess population trends, we first reviewed literature for historical duiker population estimates. Second, we used systematic camera-trap monitoring to assess population trends for 15 populations of nine duiker species in six national parks in Central and East Africa. We analysed annual monitoring data using Royle-Nichols heterogeneity-induced occupancy models to estimate abundance/sample point and derive occupancy estimates. Published density estimates indicate that duiker populations declined significantly throughout Africa between 1973 and 2013. There was a wide range of densities depending on species ($\bar{x}$ range: 0.26–20.6 km^{-1}) and whether populations were hunted ($\bar{X}$ =6.3 km^{-1}) or unhunted ($\bar{X}$ = 16.3 km^{-1}). More recent analysis of camera-trap monitoring produced different results. Estimated mean point abundance over time was between 0 and 0.99 individuals/point for four populations, between 1.0 and 1.99 for six populations, and greater than 2.0 for five populations. We observed five populations of duikers with negative trends in point abundances, although only one trend was significant and point abundance estimates for three populations were above 2.0 in the final survey year. Six populations showed positive trends in point abundance (three significant), and the remaining populations displayed no trends. Average occupancy was high ($\Psi > 0.60$) except for three populations. While literature indicates that historical population declines have occurred, most duiker populations appear relatively healthy in monitored parks. Our results indicate that these parks are effective in protecting most duikers despite hunting pressure. We recommend that systematic, standardized camera-trap monitoring be initiated in other African parks in combination with point-abundance models to objectively assess forest ungulate population trends.

Introduction

Hunting of wildlife to provide meat for subsistence and as a source of income (bushmeat) is widespread (Robinson and Bennett 2004; Ripple et al. 2016) in Africa (Wilkie and Carpenter 1999; Nasi et al. 2011), Latin America (Robinson and Redford 1991) and Asia (Bennett 2007; Lee et al. 2014). In Africa, hunting of wildlife for bushmeat is widely cited as a cause for declines of wildlife populations (East 1999; Craigie et al. 2010). Duikers (Cephalophinae: *Cephalophus* spp., *Philantomba* spp., *Sylvicapra grimmia*) are among the most hunted species in the Congo Basin, both in terms of numbers and biomass (van Vliet and Nasi 2008), and are among the top bushmeat species confiscated at international airports in Europe (Chaber et al. 2010; Wood et al. 2014). In Central and West Africa, forest ungulates, primarily duikers, comprise 63% of carcasses sold at markets (Nasi et al. 2011). Despite the close link between bushmeat exploitation and declines of wildlife populations (Ripple et al. 2016), the impact of hunting on duiker population remains unclear. The continuing presence of duiker bushmeat in markets has led some researchers to question whether harvest models (Robinson and Redford 1991; Robinson and Bennett 2004) indicating unsustainable off-take are reliable, and also to question the quality of monitoring data underlying the status of wildlife populations (Noss 2000; van Vliet and Nasi 2008).

Accurate monitoring data are difficult to collect in forest environments, and therefore scarce. Generally, methods to monitor wildlife result in 'indices' or 'estimates' of abundance and distribution. Index methods do not attempt to account for imperfect detection and include catch per unit effort (unreplicated sign surveys, call counts, drive counts), interviews and market surveys (Williams et al. 2002; Fa et al. 2006). Estimation methods attempt to account for imperfect detection, and include spatial and non-spatial capture-recapture (Royle et al. 2014), line-transect surveys using distance sampling (including deposition-decay-calibrated dung surveys: Thomas et al. 2010; Maisel et al. 2013), point counts and replicated presence-absence surveys (MacKenzie et al. 2006). Methods for estimation are designed specifically so the data can be used to develop unbiased estimates of abundance, density and distribution (MacKenzie et al. 2006; Thomas et al. 2010; O'Brien 2011). Although line-transect and point count surveys are widely used to monitor bird and mammal populations, they can be difficult to implement in forest conditions, and for nocturnal or elusive species (van Vliet and Nasi 2008; Breuer and Hockemba 2012).

Occupancy surveys (MacKenzie et al. 2006), using sign or camera traps to generate replicated detection-nondetection data have been proposed as an alternative to line-transect and point count surveys for elusive species in forest environments (Gopalaswamy et al. 2012; Ahumada et al. 2013; Linden et al. 2017). For example, Gopalaswamy et al. 2012 used an appropriately scaled sampling design and a point abundance model of occupancy (Royle-Nichols model: Royle and Nichols 2003) to estimate density of ungulates in a moist deciduous forest in India. They found that results were comparable to line-transect density estimates for four of five species considered. In addition, Linden et al. (2017) compared Royle-Nichols models with spatial capture-recapture (SCR) models and found a close relationship between densities generated by Royle-Nichols models and SCR models. Both studies noted that densities in Royle-Nichols models were lower than line-transect and SCR estimates but coefficients of determination (r^2) values were high, indicating that changes in Royle-Nichols estimates accurately reflect changes in density. Thus occupancy surveys combined with Royle-Nichols point abundance modeling may provide a robust approach for quantifying changes in duiker populations.

In this paper, we assess abundance and distribution trends of nine species of forest duikers in African parks that experience hunting for bushmeat. We first review historical density estimates of forest duikers. We then assess recent trends in duiker abundance and distribution in parks based on annual camera-trap monitoring data analysed using Royle-Nichols point abundance models. We conclude with recommendations for improvement of forest duiker monitoring.

Materials and Methods

Study species

The duiker family includes 19 species in three genera (Table 1) distributed primarily in rainforests of Sub-Saharan Africa, especially in the Congo Basin and Guinean forests (Kingdon 2015). Duikers are small- to medium-sized antelopes, ranging in body mass from 3 to 70 kg and are primarily browsers, feeding on leaves, shoots, seeds, fruits, buds and bark. Although most duiker species are diurnal, they tend to be shy and elusive, and therefore difficult to survey using direct observation techniques. IUCN considers all species of duikers to be declining range-wide due to hunting, often in relation to encroachment, habitat loss and road development (Laurance et al. 2006). Full descriptions of the species within the duiker genera can be found in Kingdon (2015).

Population trends from published density estimates

We conducted an online search of duiker literature using the Web of Science on 6 December 2016. We used search

Table 1. Characteristics of forest duikers potentially occurring within study sites including weight, elevation range, IUCN Redlist status in 2008 and 2016 (changes in bold), IUCN expected trend for the future, geographic range, and preferred habitat notes

Species	Common name	Weight (Kg)	Elevation (m)	Redlist 2008	Redlist 2016[†]	Trend	Range	Habitat
S. grimmia	Common	18	<5600	LC	LC	declining	Most widely distributed duiker outside forests	Savanna, woodland
C. spadix	Abbott's	55	300–2800	EN	EN	declining	Endemic to Tanzania	Mature montane/sub-montane forest
C. leucogaster	White-bellied	12.7	<1000	**LC**	**NT**	VU under a2[‡]	Disjunct distribution (2 populations)	Lowland equatorial closed-canopy forests
C. callipygus	Peter's	18.25	<1200	LC	LC	declining	Endemic to western central africa	Primary/secondary forest, farm bushland
C. sylvicultor	Yellow-backed	72.5	<1200	**LC**	**NT**	VU under a2	Most widely distributed forest duiker	Forests and thickets
C. dorsalis	Bay	20	<1500	**LC**	**NT**	VU under a2	Disjunct distribution (2 populations)	Primary/old secondary forest
C. ogilbyi	Ogilby's	20	<2260	LC	LC	NT under A[§]	Disjunct distribution (4 populations)	Primary moist lowland forest
C. harveyi	Harvey's	15	<2400	LC	LC	declining	Disjunct distribution (6–7 populations)	Forests, habitat with thick cover
C. weynsi	Weyns'	15	400–3000	LC	LC	declining	Widespread	Primary/old secondary lowland to montane forest
P. monticola	Blue	4.6	<3000	LC	LC	declining	Widespread	Forest and wooded habitats
C. nigrifrons	Black-fronted	13.9	<4000	LC	LC	declining	Widespread	Poorly drained lowland to montane forests

[1]source: IUCN redlist 2016 ver 3.1 (www.iucnredlist.org) accessed 10 January 2017.

[2]a2- a decline of more than 20% over 3 generations (15 years), based on increasing levels of bushmeat hunting across its range, with documented local declines and extirpations.

[3]A - reduction in population size.

words 'duiker', 'Cephalophus', 'Philantomba', 'Sylvicapra', 'bush-meat' and 'bushmeat'. For each publication, we evaluated whether density estimates were included and reviewed references for additional unpublished reports and book chapters. Before analysis, we eliminated estimates collected by literature review ($n = 6$), camera traps ($n = 1$) and call counts ($n = 3$). The literature review failed to provide references for the estimates, the camera trap method only represented a single species studied in a single year, and the call count estimates used an audio lure that may have attracted animals within broadcast range causing a concentration of duikers and inflated density estimates. For each density estimate, we noted species, density, sampling method, year of survey, average elevation, annual rainfall, and whether the study area was subject to hunting. We considered average elevation because most duikers have an upper limit to their distribution (Table 1), and average rainfall because mammalian biomass tends to decline in forests with increasing rainfall (Robinson and Bennett 2004).

We first determined if there was a trend over time in published duiker density estimates, ignoring species identity and survey methods. We then conducted an analysis of covariance with categorical effects (species identity, survey method, presence of hunting) and covariates (elevation and rainfall), using SPSS version 16.0 (SPSS Inc. Chicago, IL).

Population trends from standardized camera-trap monitoring

To assess recent trends in duiker populations, we analysed data from multi-year camera-trap surveys conducted between 2009 and 2017 in six unfenced national parks (Fig. 1; Table 2). Five sites were part of the Tropical Ecology Assessment and Monitoring Network (TEAM): Korup National Park (Cameroon), Nouabale-Ndoki National Park (Republic of Congo), Bwindi National Park (Uganda), Volcanoes National Park (Rwanda), and Udzungwa Mountains National Park (Tanzania). All sites followed a standardized camera-trap sampling protocol (TEAM Network 2011a,2011b, Jansen et al. 2014). Camera traps were deployed annually at 60 sample points arranged in a systematic grid with a trap density of 0.5 camera points km^{-2}.
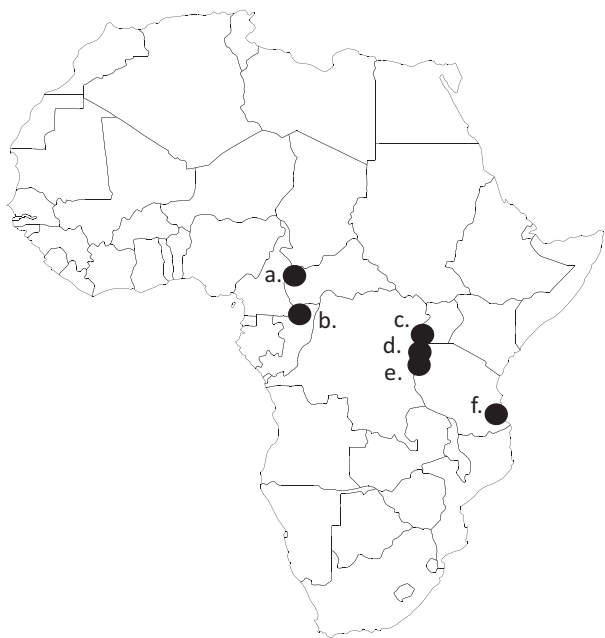
Figure 1. Map of Africa showing national park locations: a. Korup NP, Cameroon; b. Nouabale Ndoki NP, Republic of Congo; c. Bwindi NP, Uganda; d. Volcanoes NP, Rwanda; e. Nyungwe NP Rwanda; f. Udzungwa NP, Tanzania.

The sixth park, Nyungwe National Park (Rwanda), followed TEAM protocol standards for camera spacing and operations but used 82 camera points at the beginning and end of 2-km transects spaced uniformly throughout the park in 2014 as part of a biodiversity monitoring program.

Between 2015 and 2017, subsets of 36–52 of these points were sampled as part of annual monitoring efforts.

All surveys were conducted using Reconyx RM45 Rapidfire IR, HC500 and HC600 Hyperfire Semi-Covert IR, PC800 and PC900 Hyperfire Professional IR (Reconyx, Holmen, WI) or Bushnell Trophy Cam HD - 119437 (Bushnell Corporation, Overland Park, KA) camera traps. Mixing of Reconyx camera models was minimal, and no site mixed Bushnell and Reconyx cameras. Traps were deployed for at least 30 days per point per year, during the dry season. For analysis, we truncated sampling to 30 trap days for all camera traps and used 5-day sampling periods as replicates. More details on the field methods can be found in TEAM (2011a), and Appendix S1.

For each duiker species at each site, we extracted 5-day detection records and scored each of six replicates as having at least one detection (1) or a non-detection (0). We constructed matrices in which rows corresponded to camera trap points and columns corresponded sample periods. We considered three potential covariates influencing detection and point abundance: habitat type, elevation and distance to nearest accessible edge (hereafter distance), defined as the closest public road, navigable river or a park boundary adjacent to agriculture. Habitat types were determined for the location of each camera trap point, based on technician's knowledge of the study area. Elevation was obtained from a 90 m spatial resolution digital elevation model (Jarvis et al. 2008). Some species have altitudinal limits to their distribution within the range of camera trap elevations (Tables 1 and 2) so elevation may influence local abundance and detection probability. Distance to edge was

Table 2. Characteristics of national parks including length of time series, landscape setting, habitat type, human density on park border, annual rainfall, mean and range of elevation of camera trap points, and mean and range of distance from camera trap points to nearest accessible edge, and types of edge

Site	Country	Time series (Yrs)	Landscape	Habitats within Study Area[†]	Human density (/km²)	Hunting Pressure[‡]	Mean rainfall	Mean elevation (m)	Elevation range (m)	Mean distance to edge (m)	Distance range (m)	Type of edge
Korup NP	Cameroon	5	patchy	1	21.9	High	5011	168	92–463	868	47–2616	Agriculture, River
Nouabale-Ndoki NP	Republic of Congo	6	intact	1, 2	0.5	None	1645	461	411–519	3486	896–7382	River
Udzungwa NP	Tanzania	9	isolated	3, 4	32.1	High	1750	1142	378–1798	1580	7–6343	Agriculture, Road
Bwindi NP	Uganda	8	isolated	1	358.4	Moderate	2390	1906	1445–2395	1915	1–5278	Agriculture
Nyungwe NP	Rwanda	4	isolated	1	314.0	High	2150	2357	2175–2570	667	5–2998	Agriculture, Road
Virunga NP	Rwanda	4	isolated	5, 6	386.0	High	1800	2994	2509–3884	1748	144–4249	Agriculture

[1]Habitat Types: 1. Closed canopy mixed forest; 2. Monodominant forest; 3. Deciduous forest; 4. Montane forest; 5. Bamboo/Mixed forest; Open herbaceous bush.
[2]Source: Supplemental Materials Beaudrot et al. 2016.

Table 3. Number of density estimates, mean density and range, and mean for hunted and unhunted populations for each duiker species

Species	# estimates	$\bar{x}$	Range	$\bar{x}$ (# unhunted)	$\bar{x}$ (# Hunted)
C. adersi	1	7.30	7.3	7.1 (1)	
C. callipygus	7	6.44	0.6–7.62	15.85 (2)	2.67 (5)
C. dorsalis	11	3.16	0–19.0	12.40 (2)	1.11 (9)
C. maxwelli	13	5.22	0.04–22.5	5.37 (4)	5.17 (9)
C. nigrifrons	4	4.00	0.27–14	14.00 (1)	0.47 (3)
C. rufilatus	10	1.97	0.14–6.2	4.04 (3)	1.08 (7)
C. sylvicultor	7	0.65	0 0–2.5	1.18 (3)	0.25 (4)
Philontoba monticola	33	20.59	1.54–83	29.97 (10)	16.51 (20)
C. ogilbyi	8	2.37	0.07–6.53	ND	2.37 (8)
C. zebra	2	0.26	0.08–0.44	ND	0.26 (2)
C. harveyi	6	7.62	2.07–13.3	ND	7.62 (6)
Sylvicapra grimmia	8	0.38	0.03–0.64	ND	0.38 (8)

ND indicates no density estimates for unhunted populations.

determined using a geoprocessing tool in ArcGIS and used as a proxy of potential hunting pressure (Kinnaird et al. 2003; Laurance et al. 2006; Benítez-López et al. 2017). We rescaled distance and elevation measurements within each park using a z-transformation.

We used Royle-Nichols models (Royle and Nichols 2003) to estimate annual point abundance and occupancy. These models assume that heterogeneity in detection probability p_i is caused by variation in local abundance N_i around the sampling point i. This relationship can be expressed as

$$p_i = 1 - (1 - r)^{N_i}$$

where r is the binomial sampling probability that an individual is detected.

Point abundance is an appropriate metric for forest duikers, because they live as territorial pairs and offspring (2 – 4 individuals/home range) with home ranges estimated at less than 1 km^2 (range 3.4–63 ha: Wilson 2001). Our sampling design is expected to result in one camera trap/duiker territory on average. We expect that an average point abundance ≥ 2.0 indicates a healthy duiker population, and numbers less than 2.0 indicate vacant territories and/or territories occupied by single individuals. Changes in average point abundance over time should mirror changes in population size at the site (Royle and Nichols 2003; O'Brien 2011). Each species at each site was analysed separately. Analyses used a single season Royle-Nichols model treating year as a covariate to separate the annual point abundance estimates (Linden and Roloff 2013; Linden et al. 2017), and evaluated the effect of elevation and distance on point abundance and

detection. This model is similar to a multi-season model with implicit dynamics (MacKenzie et al. 2006) but does not estimate colonization or extinction rates. Occupancy can be estimated as a derived parameter of local abundance (Royle and Nichols 2003).

All models were fitted using maximum likelihood methods and the *unmarked* library (Fiske and Chandler 2011) in the R statistical software (R Core Team, 2019). Pearson chi-square goodness-of-fit tests (MacKenzie and Bailey 2004) were run using the *AICmodavg* library (Mazerolle 2019), which were first applied to Royle-Nichols models by Linden et al. (2017). A parametric bootstrap was used to obtain MacKenzie and Bailey test statistics for each of 1000 simulated datasets based on a given model. The resulting p-value corresponds to the proportion of the simulated test statistics greater than or equal to the observed test statistic. The test statistic was calculated using the chi-square table of observed (actual or simulated) detection histories and expected theoretical distribution of values for a Royle-Nichols model. An estimate of the overdispersion or variance inflation parameter ($\hat{c}$; Burnham and Anderson 2002) was also obtained and can be used as an indicator of lack-of-fit. It was calculated by dividing the observed test statistic by the average of the simulated test statistics. $\hat{c} > 1$ usually indicates overdispersion whereas $\hat{c} > 4$ may indicate lack of fit (Mazerolle 2019). In each analysis, competing models were ranked by minimum AIC_c values or $QAIC_c$ for models with $\hat{c} > 1$, and evaluated using AIC weights (Burnham and Anderson 2002).

For each species in each park, we estimated the linear trend in point abundance by setting the first year to 0 and using a simple linear regression with the intercept set to the initial point abundance value ($\lambda_i = \lambda_0 + m(Year_i)$). We used a probability of 0.1 to assess significance of change in λ over time as a conservative measure based on the precautionary principle because of relatively small datasets (4 to 9 years), the limited set of covariates common to all sites and the asymmetric consequences for conservation of Type I and Type II errors (Meyers 1993; Root et al. 2005).

Results

Historical duiker density estimates

We found 110 published estimates of density for 12 of a total of 19 duiker species, in 31 publications, reporting surveys conducted from 1973 to 2013 (Table 3). Methods used include call counts, track counts, pellet group counts, net captures, diurnal and nocturnal line-transect surveys, and extrapolation from radio telemetry. The most common survey method was diurnal line-transect surveys, accounting for 69% of estimates. Duiker density, independent of species and method of estimation, was
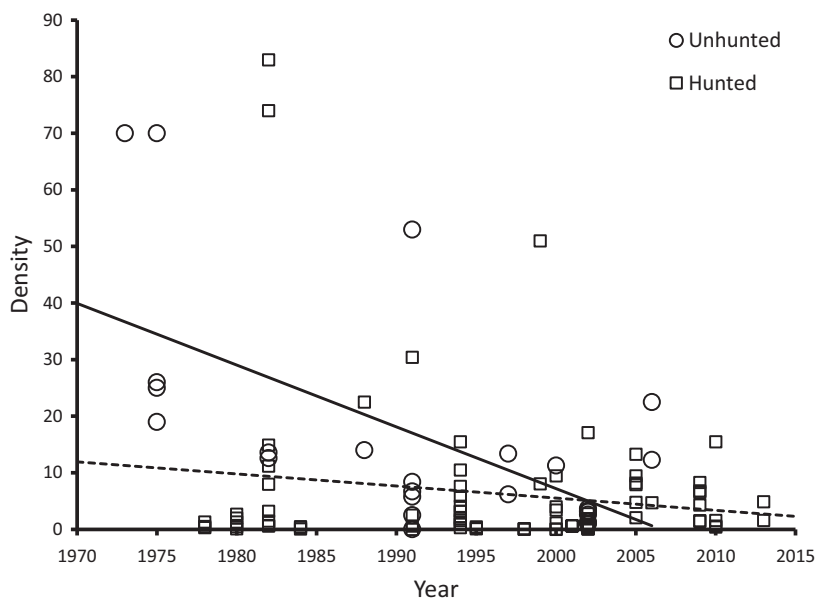
Figure 2. Published duiker densities between 1973 and 2013. Solid line indicates trend over time for unhunted populations and dashed line indicates trend for hunted populations.

negatively correlated with year of survey (Fig. 2; $r = -0.328$, $n = 110$, $P < 0.001$), indicating a general, historical decline in density estimates across sites over time. Most of this decline is associated with unhunted populations ($r = -0.60$, $n = 26$, $P < 0.01$: Fig. 2); densities of hunted population did not decline significantly over time ($r = -0.156$, $n = 84$, $P > 0.1$: Fig. 2). Unhunted duiker populations occurred at more than twice the density compared to hunted duiker populations (16.3 ± 19.7 vs. 6.28 ± 13.62: Table 3). Only *C. maxwelli* had comparable densities among hunted and unhunted populations.

To conduct the analysis of covariance, we reduced the dataset by eliminating species represented for only a single year and a single study. A full main effects model showed no relationship of duiker density with rainfall or elevation. A reduced model with a year x hunting interaction showed no relationship of density estimates with census method or with the interaction term. Our final model indicated that duiker density depended on Species Identity ($F_{8,90} = 5.330$, $P < 0.001$), were lower in populations subject to hunting ($F_{1,90} = 4.683$, $P = 0.033$), and declined with Year of Survey ($F_{1,90} = 17.000$, $P < 0.001$). Effect size (h^2) was greatest for Year of Survey ($h^2 = 0.61$), followed by Species Identity ($h^2 = 0.19$) and presence of hunting ($h^2 = 0.17$).

Recent trends in duiker populations

We considered 20 potential duiker population time series from camera trap data representing 10 species known to

occur in the six national parks from historical species lists, and lasting from 4 to 9 years. Five potential populations were either not detected (*C. sylvicultor* and *C. weynsii* in Volcanoes NP) or had insufficient data for analysis (*C. silvicultor* and *C. weynsii* in Nyungwe NP and *C. weynsii* Bwindi NP), resulting in 15 populations for analysis.

The best Royle-Nichols model differed between species, but received strong support, (AIC$_c$ weights > 0.89) in 6 of 15 analyses (Table 4). The top two models received strong support (combined AIC$_c$ weight > 0.89) in 11 of 15 analyses. Ten model sets had c-hat > 1.0 (P < 0.05) indicating some overdispersion in the data, and coefficient variances were adjusted accordingly. *C. leucogaster* models showed significant lack of fit. The top models for most populations included distance to nearest accessible edge and elevation as covariates of detection whereas only a few included these covariates for point abundance. Specifically, we found positive effects of elevation on point abundance for species in Udzungwa Mountains NP, Bwindi NP, Volcanoes NP and Nyungwe NP. These parks all are high elevation parks with large elevation gradients (Table 2). Distance to accessible edge also affected point abundance in these parks but those effects were variable by species. Habitat type affected detection probability for four species, but was not an important covariate affecting point abundance.

Point abundance estimates varied across species ranging from 0 for *C. sylvicultor* in Volcanoes NP to 4.07 for *C. callipygus* and 4.06 for *P. monticola* in Nouabale-Ndoki

Table 4. Top two Royle-Nichols models and AIC weights and goodness of fit test for each duiker population in each PA. Covariates include year (Yr), habitat (Hab), elevation (Elev) and distance to accessible edge (Dist). For models with significant lack of fit, standard errors are inflated using $\hat{c}$.

National Park	Species	Model #	Model	AIC wgt	Goodness of Fit		Abundance Covariates			Detection Covariates		
					$\hat{c}$	P-value	Hab.	Elev.	Dist.	Hab	Elev.	Dist.
Korup NP	C. ogilbyi	1	λ(Yr),p(Elev,Dist)	0.585	1.89	0.036					0.311 [0.140]	−0.010 [0.131]
		2	λ(Yr),p(Yr,Elev,Dist)	0.366	2.26	0.036					0.270 [0.143]	0.016 [0.140]
	C. sylvicultor	1	λ(Yr),p(Elev,Dist)	0.993	1.30	0.128					0.816 [0.562]	−1.988 [0.617]
		2	λ(Yr),p(.)	0.007	4.86	0.027						
	P. monticola	1	λ(Yr),p(.)	0.466	1.70	0.001						
		2	λ(Yr),p(Elev,Dist)	0.426	1.74	0.001					−0.094 [0.099]	0.153 [0.104]
Nouabale-Ndoki NP	C. callipygus	1	λ(Yr),p(Hab, Elev)	0.429	1.23	0.197				−0.787 [0.144]	0.148 [0.056]	
		2	λ(Yr),p(Hab, Elev, Dist)	0.385	1.25	0.175				−0.754 [0.148]	0.121 [0.062]	0.057 [0.057]
	C. dorsalis	1	λ(Yr),p(Elev,Dist)	0.736	1.68	0.006					0.271 [0.081]	−0.018 [0.080]
		2	λ(Yr),p(Yr,Elev,Dist)	0.264	1.59	0.015					0.285 [0.081]	−0.018 [0.080]
	C. leucogaster	1	λ(Yr),p(.)	0.791	237.00	0.001						
		2	λ(Yr),p(Elev,Dist)	0.209	80.47	0.001					−0.221 [0.195]	0.472 [0.190]
	C. nigrifrons	1	λ(Yr),p(.)	0.985	0.04	0.324						
		2	λ(Yr,Hab,Dist)p(Dist)	0.015	0.00	0.370	0.634 [0.767]		−1.486 [1.23]			1.480 [1.230]
	C. sylvicultor	1	λ(Yr),p(Hab, Elev)	0.500	1.42	0.021				−0.192 [0.180]	−0.206 [0.065]	
		2	λ(Yr),p(Elev,Dist)	0.300	1.42	0.016					−0.238 [.065]	0.015 [0.067]
	P. monticola	1	λ(Yr),p(Hab,Elev)	0.575	1.12	0.191				−0.825 [0.143]	−0.125 [0.058]	
		2	λ(Yr),p(Hab,Elev,Dist)	0.230	1.09	0.164				−0.831 [0.145]	−0.118 [0.065]	−0.015 [0.061]
Udzungwa NP	C. harveyi	1	λ(Yr),p(Elev,Dist)	0.993	2.89	<0.001					−0.109 [0.093]	−0.415 [0.093]
		2	λ(Yr),p(Yr,Elev,Dist)	0.007	2.90	<0.001					−0.109 [0.093]	−0.416 [0.093]
	C. spadix	1	λ(Yr,Elev,Dist),p(Elev,Dist)	0.897	2.38	0.036		0.804 [0.300]	0.182 [0.260]		−0.167 [0.340]	−0.058 [0.278]
		2	λ(Yr,Elev,Dist),p(Yr,Elev,Dist)	0.101	2.25	0.038		0.831 [0.302]	0.161 [0.256]		−0.205 [0.334]	−0.035 [0.273]
Bwindi NP	C. nigrifrons	1	λ(Yr,Elev,Dist),p(Elev,Dist)	0.895	1.20	0.154		0.466 [0.085]	−0.157 [0.078]		0.188 [0.112]	0.161 [0.107]
		2	λ(Yr,Elev,Dist),p(Yr,Elev,Dist)	0.105	1.22	0.134		0.429 [0.086]	−0.139 [0.079]		0.246 [0.116]	0.112 [0.110]
	C. sylvicultor	1	λ(Yr,Elev,Dist),p(Elev,Dist)	0.935	1.26	0.049		0.816 [0.104]	0.074 [0.093]		0.146 [0.144]	0.104 [0.126]
		2	λ(Yr,Elev,Dist),p(Yr,Elev,Dist)	0.065	1.24	0.051		0.862 [0.107]	0.016 [0.092]		0.020 [0.154]	0.216 [0.124]
Nyungwe NP	C. nigrifrons	1	λ(Yr),p(Yr,Elev,Dist)	0.509	1.92	0.011					1.206 [0.251]	0.124 [0.180]
		2	λ(Yr,Elev,Dist),p(Yr,Elev,Dist)	0.489	1.40	0.095		0.419 [0.165]	−0.018 [0.144]		0.456 [0.452]	0.125 [0.154]
Virunga NP	C. nigrifrons	1	λ(Yr,Dist),p(Hab,Elev)	0.565	1.63	0.043				1.382 [0.224]	−0.253 [0.117]	
		2	λ(Yr,Dist),p(Hab,Elev)	0.223	1.64	0.048			0.0726 [0.058]	1.397 [0.223]	−0.317 [0.131]	

Table 5. Trends in forest duiker point abundance (λ) and occupancy (Ψ)

Species	Site	Years of data	Mean λ	SD λ	Slope	P	r^2	Mean Ψ	SD Ψ
P. monticola	Korup NP	5	2.12	0.37	0.037	NS	0.009	0.873	0.042
C. olgilbyi	Korup NP	5	1.31	0.11	0.004	NS	0.004	0.729	0.029
C. sylvilocutor	Korup NP	5	0.17	0.06	−0.007	NS	0.103	0.157	0.050
P. monticola	NNNP	6	4.06	0.91	−0.452	NS	0.560	0.976	0.015
C. leucogaster	NNNP	6	0.14	0.13	0.057	<0.1	0.661	0.128	0.113
C. nigrifrons	NNNP	6	0.09	0.12	−0.020	NS	0.053	0.082	0.106
C. callipygus	NNNP	6	4.07	1.04	−0.612	NS	0.001	0.973	0.019
C. dorsalis	NNNP	6	1.97	0.31	−0.130	NS	0.244	0.856	0.041
C. sylvilocutor	NNNP	6	3.01	0.46	−0.187	<0.1	0.702	0.946	0.029
C. harveyi	Udzungwa NP	9	2.18	0.32	0.042	<0.1	0.384	0.882	0.035
C. spadix	Udzungwa NP	9	1.47	0.30	−0.018	NS	0.251	0.644	0.061
C. nigrifrons	Bwindi NP	8	1.41	0.68	0.094	NS	0.263	0.674	0.137
C. sylvicultor	Bwindi NP	8	1.40	0.58	0.121	<0.1	0.406	0.603	0.110
C. nigrifrons	Nyungwe NP	4	1.02	0.28	0.072	NS	0.243	0.631	0.092
C. nigrifrons	Virunga NP	4	0.941	0.127	0.017	NS	0.626	0.610	0.049

Duiker species are listed by park population, number of years in time series, mean and SD of λ and Ψ over time, slope of time series, *P*-value of slope, and coefficient of determination (r^2) of trend. Figures for each population are in Appendix Appendix S2.

NP (Table 5). On average, four populations had mean point abundance between 0 and 0.99, six populations had mean point abundance between 1 and 1.99, and five populations had mean point abundance greater than 2 (Table 5). Nouabale-Ndoki NP possessed the most species and had robust point abundance estimates (mean 1.97–4.07) for four species. Only *C. leucogaster* and *C. nigrifrons* were considered rare with average point abundance of 0.14 and 0.09 respectively. In Korup NP, populations of *C. sylvicultor* and *C. ogilbyi* had low mean point estimates (0.17 and 1.31 respectively) whereas *P. monticola* average point abundance was 2.12. In Nyungwe NP, Volcanoes NP and Bwindi NP, average point estimates of *C. syvlicultor* were low (> 0, 0 and 1.4, respectively) as were estimates for *C. nigrifrons* in Nyungwe NP and Bwindi NP (1.02 and 1.41, respectively). The average point abundance estimate of *C. nigrifrons* in Volcanoes NP was relatively high at 2.81.

Occupancy values were derived from point abundance values and thus closely reflected those values (*r* = 0.88, *P* < 0.01: Table 5). Average occupancy over time was high for most species in most parks. Only *C. leucogaster* and *C. nigrifrons* in Nouabale-Ndoki NP, and *C. sylvicultor* in Korup NP were considered rare (Ψ = 0.128, 0.082, and 0.157, respectively). These populations also had average point abundances < 0.2. The remaining populations averaged occupancy estimates of Ψ = 0.81 (range 0.603–0.976).

Among the 15 populations, we observed six populations with increasing point abundance trends, six populations with decreasing trends and three populations with no trends (Table 5, Appendix S2). Only four trends,

however, were significantly different from 0 at *P* = 0.1. *C. sylvicultor* in NNNP declined significantly over time, whereas *C. sylvicultor* in Bwindi NP, *C. harveyi* in Udzungwa NP and *C. callipygus* in NNNP all increased significantly. Among all populations with declining trends, final point abundance estimates in NNNP for *C. callipygus*, *C. sylvicultor* and *P. monticola* all remained above 2.0, whereas *C. dorsalis* dropped from 2.4 to 1.8. All populations showing significant trends came from parks with the longest monitoring histories (6–9 years), but there was no correlation between magnitude of trends and length of time series (r = 0.003, NS).

Discussion

African forest duikers are among the top species exploited for bushmeat, but how hunting affects duiker populations has been debated due to the difficulty of accurately assessing abundance trends of duikers over large, forested landscapes. Our literature review of abundance estimates indicated that unhunted African duiker populations generally declined between 1973 and 2013, whereas hunted duiker populations remained relatively stable at low densities Compared to unhunted populations. The historical decline result should be treated cautiously, however, because it was based on 30 years of short-term studies, combines census methods, and does not control for variation in quality of survey between and within census methods. The overall trend however, is consistent with the consensus of conservation biologists working in African forests and IUCN prognoses (Table 1).

Our analysis of systematic camera-trap monitoring with standardized protocols in six African protected areas indicated that average point abundance of duikers declined for six populations ($P < 0.1$ for one populations), increased for six populations ($P < 0.1$ for 3 populations) and remained relatively constant for three populations. During the last survey year, point abundance estimates were above 2.0 for six populations, between 1.0 and 1.99 for five populations, and between 0 and 0.99 for four populations. Overall, the last survey year point abundance averaged 1.82 ± 1.07, close to the expected one pair per territory. Across species, occupancy remained higher than 0.6 for 12 of 15 populations. Significant declines in duiker populations occurred primarily in the unhunted Nouabale-Ndoki NP, rather than the five parks with higher hunting pressure. Thus, overall, duiker populations appear relatively healthy in the six parks.

Among sparse populations, *C. leucogaster* is considered rare wherever it occurs (Kingdon 2015) and *C. nigrifrons*, considered a swamp specialist, may lack suitable habitat in the survey area in Nouabale-Ndoki NP. Only the rarity of *C. sylvicultor* in Korup NP is possibly related to hunting, as indexed by distance to edge. Bwindi NP, Volcanoes NP and Nyungwe NP have human population densities above 300 km^{-2} on the borders, and high hunting pressure (Table 2). Despite this, populations of *C. nigrifrons* have average point abundance > 1.0, positive growth trends and occupancy > 0.6 in the three parks. The Bwindi *C. sylvicultor* population has a mean point abundance of 1.4, an increasing trend in abundance, and occupancy = 0.60. Udzungwa NP duikers also have estimates above 1.4, stable or increasing abundance trends, and are widespread within the park. This is especially noteworthy for *C. spadix*, a Tanzanian endemic which is found only in a few montane forests (Rovero et al. 2013).

We failed to investigate a number of potential covariates in this study that might affect the point abundance of duiker species. The presence of other, larger forest ungulates such as bushbuck (*Tragelaphus scriptus*) and sitatunga (*Tragelaphua spekii*) that co-occur with many duiker communities may result in competition for food resources. Our habitat classification was coarse scale, involving only 2-3 habitat types and we failed to find habitat differences in point abundance that might be discovered with a finer scale habitat analysis. The presence and complexity of carnivore communities including leopard (*Panthera pardus*), golden cat (*Caracal aurata*), serval (*Leptailurus serval*) and chimpanzee (*Pan troglodytes*) could affect local abundance of duikers. This possibility is being explored for the duiker and predator community in Nouabale Ndoki (Moore, *in litt.*). Finally, disease may have affected the duiker populations. Duikers are susceptible to Ebola (Leroy et al. 2004; Lahm et al. 2007),

leptospirosis, bluetongue, infectious bovine rhinotracheitis and epizootic hemorrhagic disease (Karesh et al. 1995). Disease outbreaks may affect duiker population dynamics and trends, but remain understudied. Declines in point abundance across several duiker species in Nouabale-Ndoki NP could result from an increase in predation or a disease outbreak, but neither has been confirmed.

There have been a number of reports of severe reductions and local extinction of duiker populations involving at least 11 of the 19 recognized species. Several declines exceeding 50% of baseline have occurred for *C. adersi* (Finnie 2008), *P monitcola* and *C. harveyi* (Nielson 2006), *C. maxwelli* (Fischer and Linsenmair 2001; Brugiere and Magassouba 2009), *C. rufilatus* and *S. grimmia* (Fischer and Linsenmair 2001). Local extinctions have been reported for *C. sylvicultor* (Brashares et al. 2001; Jimoh et al. 2012) *C. dorsalis* (Jimoh et al. 2012; Akomo-Okoue et al. 2015), *C spadix* (Nielson 2006; Rovero et al. 2013), *C. niger*, *C. maxwelli*, *C. rufilatus*, *C. ogilbyi* and *S. grimmia* (Brashares et al. 2001). These declines and local extirpations are attributed to hunting and have occurred in species with both low and high resilience to hunting. Yet, we found no consistent link between trends in point abundance and whether parks were hunted (Table 2). Yasuoka et al. (2015) point out that hunting methods can be selective among duiker species resulting in mixed trends for duiker species in a single park. We did not measure hunting pressure or law enforcement efforts to prevent hunting. However, Volcanoes NP and Bwindi NP are tourist destinations for mountain gorilla viewing and have good protection; Udzungwa NP has adequate staff capacity to ensure efficient law enforcement, and Nyungwe NP and Nouabale-Ndoki NP have long-term law enforcement support from NGOs.

Our camera-trap surveys failed to record several duiker species that were historically known from study sites, indicating the possibility of local extinctions. For example, Viquerat et al. (2012) reported that *C. dorsalis* and *C. sylvicultor* were at risk of local extinction in Korup NP. We found no evidence of *C. dorsalis* and only nine records of *C. sylvicultor* in five years of sampling. East (1999) and Hart (2013) report *C. weynsi* from Nyungwe and Bwindi National parks; we found *C. weynsi* to be extremely rare in both parks (Moore et al. 2018). Neither *C. rufilatus* (Treves et al. 2010) nor *P. monticola* were detected in Bwindi NP in 8 years of surveys. Only Nouabale-Ndoki NP and Udzungwa NP had historically intact duiker communities during our surveys.

There is a possibility that our sampling effort was too localized for the size of parks surveyed to be representative. Study areas were 300 to 600 km^2, while park sizes ranged from 342 to > 4000 km^2. However, the study areas were large enough to encompass hundreds of duiker

territories and the camera-traps points, on average, should have included a single territory ensuring adequate sample sizes. Historically, estimates of duiker density were made for much smaller areas than this study. Thus, we feel that our data are suitable for drawing reasonable conclusions.

It is also possible that duikers were sometimes misidentified. We discount this since most sites included one to three species of duiker that were distinctive based on body size, markings and diurnal/nocturnal habit. Nouabale-Ndoki NP had six duiker species, including the smallest (*P. monticola*) and largest (*C. silvicultor*) species. White undersides and a fluffy tail (Kingdon, 2015) distinguish *C. leucogaster* from the three similar duiker species. *C. callipygus*, *C. dorsalis,* and *C. nigrifrons* are similar but the diurnal *C. nigrifrons* lacks a dorsal stripe and possesses a black forehead, whereas the diurnal *C. callipygus* possesses a black dorsal midline that flairs at the tail. The nocturnal *C. dorsalis* possesses a black dorsal midline that narrows at the tail. These morphological and behavioural distinctions give us high confidence in species identification.

Methods for monitoring forest duikers

Currently, line-transect surveys, deposition-decay-calibrated dung transect surveys, and call counts are the most commonly used methods for monitoring duikers (Breuer et al. 2009; van Vliet et al. 2009a,2009b; Breuer and Hockemba 2012). Direct observations on line-transects, either audio or visual, are challenging to collect in rainforest environments (Breuer and Hockemba 2012). Breuer and Hockemba (2012) found that duiker observations were so rare that 60 km to 1875 km of transects are needed to achieve a sample size of 30 observations for *P. monticola*. Rovero and Marshal (2004; 2009) walked approximately 83 km to attain a sample size of 30 for *C. harveyi*.

During dung line-transect surveys, grouping of duiker species by dung pellet size is necessary due to inability to accurately identify species and small species-specific sample sizes (Ntie et al. 2010). Often, small and large individuals of the same species occur in different size classes, limiting the interpretation of dung surveys of forest duikers. Grouping duiker species together can mask the dynamics in the duiker community and limits inferences from dung surveys. This is especially troublesome when the duiker community is a mix of resilient and non-resilient species with different diets. To distinguish duiker species effectively, dung transect monitoring requires DNA analysis (Bowkett et al. 2009; Ntie et al. 2010), local dung decay rates estimated concurrently with the surveys, and defecation rates for all species in question (Viquerat et al. 2012; Ahrestani et al. 2018). Currently there are few published dung decay studies or defecation rates for most sites and species (Breuer et al. 2009; van Vliet et al. 2009a; Viquerat et al. 2012). Duiker dung decay rates can be highly variable within and between species, ranging from a few hours (Breuer and Hockemba 2012) to 21 days (Koster and Hart 1988), and defecation rates vary with diet and species (Koster and Hart 1988).

Call counts using distress calls as a lure have potential, but to date have been used as indices only (van Vliet et al. 2009b) because of uncertainty about the area affected by the calls. Buckland et al. (2006) describe a point-count design to estimate density using call lures that corrects for detection and species' response to the calls for a range of known distances. To date, this method has not been used for duikers.

We have shown that grid-based camera-trap surveys are an effective alternative sampling method for monitoring duiker populations, corroborating findings from earlier studies that tested applications of camera-trapping to study forest ungulates in tropical forests (e.g. Rovero and Marshall 2009; Treves et al. 2010). Developing and deploying a camera-trap monitoring program is well-understood. As cost of labour increases and cost of camera-traps declines, comparative cost effectiveness of camera-trap monitoring increases (Rovero and Marshall 2009). Observers had few problems classifying duiker to species from photos (Nakashima 2015) which is a significant improvement over dung-based surveys. Also, observations come with photographic evidence that can be validated by experts. Malfunctions and damage from wildlife were uncommon at the sites in this study, but may be an important consideration elsewhere. Most importantly, camera-traps allowed us to develop species-specific, point abundance and distribution trends over time that accounted for imperfect detection and did not require extraordinary effort to develop adequate sample sizes over large landscapes (Linden et al. 2017). Recent work by Rossman et al. (2016) extends this approach to multi-season models that can estimate demographic rates in point abundance models.

In conclusion, our study shows that forest duikers, primary targets of subsistence and commercial bushmeat trade, have declined historically in Africa. Yet, most duiker populations in parks that we monitored in the last decade were still in good health, some despite declining trends. Our findings will inform authorities and managers that these parks are relatively effective in protecting duikers despite poaching pressure. We recommend that systematic, standardized camera-trap monitoring be initiated in other African parks, beginning with the most important strongholds for duikers. In parks where camera-trap monitoring is already occurring, we recommend the use of unbiased indicators such as point abundance as the monitoring metric.

Acknowledgments

Data Accessability

All TEAM data are freely available at http://www.teamnetwork.org/data/query. TEAM and WCS data will also be available through WildlifeInsights at https://wildlifeinsights.org/ in the near future.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Details of camera trap surveys
Appendix S2. Trends in 15 duiker populations across six national parks in east and central Africa.