Why do models fail to assess properly the sustainability of duiker (*Cephalophus* spp.) hunting in Central Africa?

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Abstract Hunting of wildlife in Central Africa is largely considered to be unsustainable. Several studies indicate that most mammal species should already have disappeared from many Central African forests but markets continue to be supplied with bushmeat, with no sign of large scale extinction of the most common species. Most studies of the sustainability of duiker (*Cephalophus* spp.) hunting in Central Africa are based on the same index of hunting. We illustrate how uncertainty is accumulated in these estimations of sustainability. We show that the results obtained in different sites are not comparable because a variety of methods have been used to calculate the parameters of the model and each of the methods has different sources of error. For the assessment of maximum sustainable harvest for duikers, the studies reviewed differ mainly in the value chosen for the hypothetical adjustment factor, and the method used to calculate the rate of maximum population increase and to estimate duiker population densities. For the assessment of annual hunting offtake the studies differ mainly in the scale at which they were conducted (village or regional), and sampling and extrapolation methods. Without evaluation of accuracy and standardization of methods for the estimation of maximum sustainable harvest and annual offtake, conclusions regarding harvesting based on biological indices should be treated with extreme caution.

Keywords *Cephalophus*, density, duiker, hunting offtake, maximum sustainable harvest, production rate, Robinson & Redford model.

Introduction

Many studies have documented that bushmeat is the main source of protein, and in some cases the most important source of income, for rural people in the Congo Basin (Lahm, 1993; Wilkie & Carpenter, 1999; Bakarr *et al.*, 2001). With the rapid increase of human population densities since the 1920s (Hochschild, 1998), a growing number of studies have expressed concern about the scale of bushmeat exploitation in the Congo Basin.

An increasing number of authors have tried to determine the effect of hunting and the level at which it becomes unsustainable in the Democratic Republic of Congo (Hart, 2000), Central African Republic (Noss, 1998a,b, 2000), Gabon (Feer, 1993, 1996; Lahm, 1993), Cameroon (Dethier, 1995; Delvingt *et al.*, 1997; Muchaal & Ngandjui, 1999; Ngandjui & Blanc, 2000; Bousquet *et al.*, 2001) and Equatorial Guinea (Fa *et al.*, 1995, 2005). Most authors have based their studies on small forest duikers (*Cephalophus* spp.), given their importance in hunting offtake. Duikers are among the most hunted species in Central Africa both in terms of number and biomass (Lahm, 1991; Juste *et al.*, 1995; Muchaal & Ngandjui, 1999; see Wilkie & Carpenter, 1999, for a review).

Different methods have been used to assess hunting sustainability. Some authors have used the comparison of hunting offtake over time (Fa *et al.*, 2005) or the comparison of mammal abundance and age structure between hunted and non-hunted sites (Lahm, 1993; Hart, 2000). These methods do not indicate the intensity at which hunting becomes unsustainable. Others have used biological indices to assess sustainability, the three most popular of which are Robinson & Redford's model (1991), the Unified Harvest Model (Bodmer *et al.*, 1994), and the Stock Recruitment Model, which has its origin in fisheries research.

These biological indices allow the assessment of a maximum sustainable harvest based on the density and productivity of the population. Of 17 publications dealing with the estimation of hunting sustainability for duikers in Central Africa, 13 have used biological indices (Feer, 1993, 1996; Fa *et al.*, 1995; Fitzgibbon *et al.*, 1995; Noss, 1998a,b, 2000; Dethier & Ghuirgui, 1999; Muchaal & Ngandjui, 1999; Ngandjui & Blanc, 2000; Delvingt *et al.*, 1997; Wilkie *et al.*, 1998). These studies warn of the unsustainability of hunting practices and the risk of extinction, and the term bushmeat has become synonymous with overexploitation (Cowlishaw *et al.*, 2005).

Meanwhile, urban markets continue to be supplied with fresh bushmeat, indicating a contradiction between the unsustainability demonstrated by biological indices and the apparent abundance of the resource. Alvard *et al.* (1997), Robinson & Bodmer (1999) and Novaro *et al.* (2000) recognized that, according to biological models, many studies report levels of harvest above sustainable values, yet these levels have been maintained or increased over

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Received 19 February 2007. Revision requested 4 May 2007.
Accepted 29 November 2007.

time with no sign of population depletion (Salas & Kim, 2002). Noss (2000) suggested that models for calculating sustainable harvest may produce conservative estimates.

Milner-Gulland & Akçakaya (2001) demonstrated the general uncertainty inherent in the use of biological indices to assess sustainability. Our purpose here is to illustrate these uncertainties using duiker hunting as an example. We review the existing literature on estimations of the sustainability of duiker hunting based on biological indices, and describe the variety of methods used to estimate the parameters of Robinson & Redford's (1991) model. Using a step-by-step approach we highlight the different sources of error in each of the methods and demonstrate how uncertainty is accumulated in the estimation of duiker hunting sustainability.

Maximum sustainable harvest

Robinson & Redford's (1991) index of sustainability is a simple, practical equation to calculate a maximum sustainable harvest (MSH):

$$MSH = hP_{max} = h(e^{r_{max}} - 1)D$$

where h is a hypothetical adjustment factor, P_{max} = maximum production of the population, r_{max} = rate of maximum population increase, and D = population density. Studies of duiker hunting sustainability have used a variety of methods to estimate the parameters of the model (Fig. 1), and the 13 studies considered here differ in (1) the value chosen for h, (2) the method used to calculate r_{max}, and (3) the method to determine D.

Hypothetical adjustment factor (h)

Robinson & Redford (1991) assume that hunting substitutes for a proportion of the natural mortality, rather than increases total mortality of a population. Therefore, they suggested that the maximum sustainable harvest is equal to the maximum production (P_{max}) multiplied by a hypothetical adjustment factor that accounts for pre-reproductive and adult reproductive mortality. The value of the hypothetical factor was estimated for Neotropical species and is 0.6, 0.4 or 0.2 for animals whose longevity is <5 years, 5–10 years, and >10 years, respectively. The same values were applied by different authors to African species without any readjustment (Robinson & Redford, 1991). Although duiker species do not form a homogeneous group (e.g. they have body weights of 5–80 kg), the same hypothetical factor has been used for different species. Discrepancies among authors in considering duikers as relatively short- or long-lived species result in using h = 0.4 (Fa *et al.*, 1995; Noss, 1998b; Wilkie *et al.*, 1998; Muchaal & Ngandjui, 1999; Ngandjui & Blanc, 2000) or h = 0.2 (Fitzgibbon *et al.*, 1995; Delvingt *et al.*, 1997; Noss, 1998a, 2000).

Rate of maximum population increase (r_{max})

The rate of maximum population increase (r_{max}) has been calculated either with Cole's (1954) or, less frequently, Caughley & Krebs' formula (1983). Following Cole's (1954) formula, r_{max} is estimated from:

$$1 = e^{-r_{max}} + be^{-r_{max}}a - be^{-r_{max}}(w + 1)$$

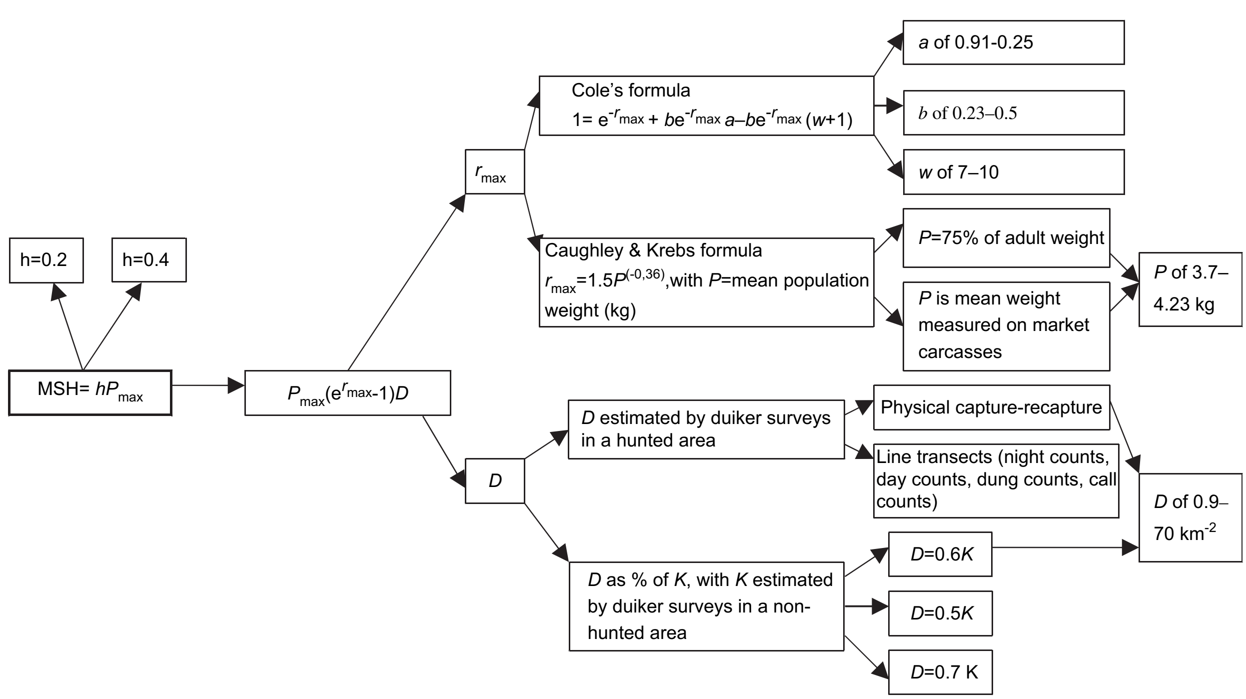

FIG. 1 Flowchart indicating the different methods used to assess maximum sustainable harvest (MSH), taking the blue duiker as an example.

where a = age at first reproduction, w = age at last reproduction, and b = annual birth rate of female offspring. This equation can take into account changes in r_{max}, depending on the variation of reproductive parameters with hunting pressure. However, possible variations for duikers have not been studied.

Cole's formula has two major disadvantages. Firstly, it uses the unrealistic assumption that there is no mortality of juveniles or adults prior to age w. However, studies of ungulate population dynamics have shown that the rate of adult survival is one of the most important parameters influencing the rate of population increase (Bourgarel, 2004). Secondly, the minimal population information required for Cole's formula is unknown for most duiker species. In most studies, identical values for reproduction parameters were used for all duiker species without distinguishing between blue *C. monticola*, red (*C. callipygus, C. dorsalis, C. nigrifrons, C. leucogaster, C. ogylbi*) or yellow *C. sylvicultor* duikers. Delvingt *et al.* (1997) and Noss (1998a, 2000) used unpublished data gathered by V.J. Wilson for duikers in captivity. Noss (1998a, b) used species specific data from Haltenorth & Diller (1985). Fa *et al.* (1995), Wilkie *et al.* (1998), Muchaal & Ngandjui (1998) and Ngandjui & Blanc (2000) used population data derived from Payne (1992), where maximum longevity is used as a substitute for w.

Because knowledge of duiker mortality and fecundity rates are poor, some authors (Feer, 1996; Delvingt *et al.*, 1997; Noss, 1998b; Dethier & Ghuirgui, 1999) used Caughley & Krebs' (1983) formula:

$$r_{max} = 1.5P^{(-0.36)}$$

where r_{max} is only a function of the mean population weight (P) in kg. To take into account the age structure of the population, Feer (1996) and Delvingt *et al.* (1997) used 75% of the mean weight of an adult for P. Dethier & Ghuirgui (1999) used data from Noss (1998b), who measured mean population weight based on carcasses sold in markets (Table 1).

TABLE 1 Estimations of minimum and maximum mean population weight and population maximum increase rate (r_{max}) based on Caughley & Kreb's (1983) equation for six duikers (*Cephalophus* spp.).

Species	Min. mean population weight (kg)	Max. mean population weight (kg)	r_{max} (kg year^{-1})
C. callipygus	15.7[1]	17.8[2]	0.53–0.56
C. dorsalis	15.4[1,3]	17.8[4]	0.53–0.56
C. leucogaster	10.3[1,3]	10.3[1,3]	0.65
C. monticola	3.7[1,3]	4.23[2,4]	0.89–0.94
C. nigrifrons	11.0[1,3]	11.0[1,3]	0.63
C. sylvicultor	51.0[1,3]	51.0[1,3]	0.36

[1]Feer, 1996. [2]Dethier & Ghuirgui, 1999. [3]Delvingt *et al.*, 1997. [4]Noss, 1998b.

Density (D)

Because the population density is difficult to measure in the field, Robinson & Redford (1991) suggested using a predictive value of D based on the carrying capacity (K). K is estimated as equal to the population density of a forest where there is no hunting. A logistic growth curve suggests that P_{max} is reached for a density of 0.5K but based on population curves for Neotropical species, Robinson & Redford (1991) showed that for species that do not breed until late in life, maximum productivity occurs at 0.6K, thus:

$$P_{max} = (e^{r_{max}} - 1)D = (e^{r_{max}} - 1)\,0.6K$$

Feer (1996) and Dethier & Ghuirgui (1999) used density measured in an undisturbed site as the value of K. Feer (1996) compared the results obtained with $D = 0.5K$ with a more conservative formula, where P_{max} is reached when the population density = 0.7K.

Other authors (Fa *et al.*, 1995; Delvingt *et al.*, 1997; Noss, 1998a,b; Muchaal & Ngandjui, 1999; Ngandjui & Blanc, 2000) have used a direct value of D, measured in hunted sites, as recommended by Bodmer *et al.* (1994), using a variety of techniques: capture-recapture methods using nets (Dubost, 1980; Hart, 1985; Koster & Hart, 1988; Feer, 1989); line transect methods using either night-time visual counts (Lahm, 1993; Noss, 1998a), day-time visual counts (Payne, 1992; Lahm, 1993; Dethier, 1995; Delvingt *et al.*, 1997; Koster & Hart, 1998; Lannoy *et al.*, 2003), pellet counts (Wilkie & Finn, 1990; Payne, 1992; WCS, 1996) or call counts (Hart 1985, Dethier, 1995; Koster & Hart, 1998; Struhsaker, 1998). Other methods include net hunting encounters by counting the number of animals seen per searched area (Noss, 2000) and densities estimated from home range size and population structure (Feer, 1996). For *C. leucogaster, C. nigrifrons* and *C. sylvicultor* the number of observations did not always allow densities to be determined; Feer (1996) estimated densities using their relative abundance in a sample compared to the abundance of *C. callipygus*.

Uncertainty in assessment of maximum sustainable harvest

The estimation of maximum sustainable harvest suffers from two main sources of uncertainty: one related to the values and methods used to assess the parameters of the model, the other related to the variety of calculation methods used.

For the estimation of r_{max}, Cole's formula gives heterogeneous results depending on the reproductive parameters chosen (Table 2). The available reproductive parameters come from data on a few duikers in captivity. There is

TABLE 2 Estimation of maximum population increase rate (r_{max}) based on Cole's (1954) equation for *C. callipygus, C. dorsalis* and *C. monticola*.

Species	Reference	Age at first reproduction (*a*)	Annual birth rate of female offspring (*b*)	Age at last reproduction (*w*)	r_{max} (kg yr^{-1})
C. callipygus	Noss, 1998b	1.5–2.5	0.18–0.43	10	0.34–0.7
	Noss, 1998a	1.5–2.5	0.5	10	0.32
	Fitzgibbon *et al.*, 1995	1	0.5	10	0.39
	Noss, 2000	0.91	0.43	10	0.29
C. dorsalis	Noss, 1998b	1.5–2.5	0.17–0.43	10–11	0.34–0.5
	Noss, 1998a	1.5–2.5	0.5	10	0.32
	Payne, 1992; Fa *et al.*, 1995	1.67	0.5	8	0.20
	Fitzgibbon *et al.*, 1995	1	0.5	10	0.39
	Noss, 2000	0.91	0.43	10	0.29
C. monticola	Noss, 1998b	1.5–2.5	0.23–0.43	10	0.12–0.34
	Noss, 1998a	1.5–2.5	0.5	10	0.32
	Payne, 1992; Fa *et al.*, 1995	1.09	0.33	7	0.49
	Fitzgibbon *et al.*, 1995	1	0.5	10	0.39
	Noss, 2000	0.91	0.43	10	0.29

particular disagreement on the annual birth rate of female offspring (0.17–0.5), age at first (0.91–2.5 years) and last reproduction (7–11) years. For *C. monticola* the values of r_{max} calculated with Cole's formula are particularly variable, from 0.12 (Noss, 1998b) to 0.49 (Fa *et al.*, 1995).

We compared results for the value of maximum sustainable harvest (Table 3) with r_{max} calculated using either Cole's ($r_{max}1$) or Caughley & Krebs' equation ($r_{max}2$) for *C. monticola*, *C. dorsalis* and *C. callipygus*. We used data from Feer (1996) for the estimation of *D*. For *C. callipygus* and *C. dorsalis*, maximum sustainable harvest calculated with $r_{max}2$ is within the range of that calculated with $r_{max}1$. For *C. monticola*, $r_{max}2$ gives a value four times higher than with $r_{max}1$.

The values of *D* obtained with different methods are highly variable, sometimes by a factor of > 100. In the Ituri forest, Democratic Republic of Congo, Koster & Hart (1988) estimated a duiker biomass of 174 kg km^{-2} using visual counts, whereas Wilkie & Finn (1990) estimated 1,497 kg km^{-2} counting pellet groups. Such differences raise the problem of the accuracy of existing duiker survey techniques. Each method has possible biases (Koster & Hart, 1998; Struhsaker, 1998; Newing, 2001; Lannoy *et al.*, 2003) because of poor visibility in dense vegetation, shy animal behaviour, and the resemblance of different species. The difficulty and low rate of direct sightings explains the wide use of dung counts. However, van Vliet *et al.* (in press), have assessed the rate of error in species identification using dung and found that field identification was only reliable for *C. sylvicultor*.

We compared the results obtained for maximum sustainable harvest using call counts and day time visual counts for *C. monticola, C. callipygus* and *C. dorsalis* in Dja, Cameroon (Delvingt *et al.*, 1997; Table 4). The authors used Cole's formula for the assessment of r_{max} and MSH = 0.2 P_{max}. For *C. monticola* and *C. callipygus* maximum sustainable harvest is more than seven times higher when densities are assessed using call counts than with day counts. For *C. dorsalis* maximum sustainable harvest obtained using call counts is less than twice that obtained with day counts.

Methods used to estimate hunting offtake, and possible sources of error

To analyse the sustainability of hunting the maximum sustainable harvest is compared to the observed annual offtake. If the offtake exceeds the estimated maximum sustainable harvest then hunting is not sustainable and can leave exploited populations vulnerable to extinction or disrupt ecosystem functioning. Harvest profiles have been obtained using sampling methods that differ according to the: (1) level at which studies were conducted (local or regional scale), (2) sampling method, (3) way authors extrapolated their data (Table 5).

TABLE 3 Comparison of r_{max} calculated with Cole's (1954; $r_{max}1$) and Caughley & Krebs' (1983; $r_{max}2$) equations and related values of maximum sustainable harvest (MSH) for *C. callipygus*, *C. dorsalis* and *C. monticola*.

Species	$r_{max}1$ (kg yr^{-1})	$r_{max}2$ (kg yr^{-1})	K[4] (km^{-2})	*D* (60% *K*; kg km^{-2})	$P_{max}1$ (kg km^{-2} yr^{-1})	$P_{max}2$ (kg km^{-2} yr^{-1})	MSH1 (kg km^{-2} yr^{-1})	MSH2 (kg km^{-2} yr^{-1})
C. callipygus	0.29[1]–0.7[2]	0.53–0.56	10.7	0.642	0.2–0.6	0.4–0.5	0.008–0.024	0.016–0.02
C. dorsalis	0.2[3]–0.5[2]	0.53–0.56	7.1	0.426	0.1–0.3	0.3–0.3	0.004–0.012	0.012–0.012
C. monticola	0.12[2]–0.49[2]	0.89–0.94	70	4.2	0.5–2.6	6–6.5	0.02–0.104	0.24–0.26

[1]Noss, 2000. [2]Noss, 1998a. [3]Payne, 1992. [4]Feer, 1996.

TABLE 4 Values of maximum sustainable harvest (MSH) using the density obtained from both call counts and day counts for *C. callipygus, C. dorsalis* and *C. monticola;* r_{max} (= 34%) was calculated using the method of Cole (1954) and MSH was calculated with $h = 0.2$ (i.e. MSH = 0.2* P_{max}).

	Density (km^{-2})		MSH
Species	Value	Method	($kg\ km^{-2}\ yr^{-1}$)
C. callipygus	58.13	Call counts	3.95
	7.62	Daytime visual counts	0.52
C. dorsalis	3.75	Call counts	0.25
	1.94	Daytime visual counts	0.13
C. monticola	44.38	Call counts	3.02
	5.86	Daytime visual counts	0.4

Some authors have conducted studies at a regional level, registering the number and nature of carcasses sold in city markets (Fa *et al.*, 1995, 2000; Juste *et al.*, 1995). Fa *et al.* (2000) have shown that bushmeat markets can be useful as indicators of the status of wildlife prey in the surrounding catchment area as long as the sampling effort is well designed. The available studies gathered data for one or two markets only, and thus their use in determining the impact of bushmeat extraction is limited to relatively small areas (Fa *et al.*, 2004). The main difficulties when working at a regional level are the assessment of the catchment area and the sampling method. The catchment area is often calculated by evaluation of the total surface covered by all locations mentioned as bushmeat sources by bushmeat sellers. Fa *et al.* (2004) assessed the efficiency of a number of methods for measuring the volume of bushmeat extracted and the proportion of total species traded, and found that: (1) only a large sample of markets permits useful inferences at a regional scale, (2) timing and coordination of sampling may be highly influential, and (3) sampling in blocks of days was as efficient as random sampling in estimating species richness but not carcass volume.

Harvest rates calculated from animals sold in markets underestimate the real harvest rate because only part of the hunting offtake is sold to markets. Colell *et al.* (1994) show that 20% of the antelopes caught in villages of southern Bioko, Equatorial Guinea, are for own consumption. Lahm (1996) showed in three villages of north-east Gabon that 34% of ungulates are are eaten in the village and not sold in cities. Some cultural taboos explain why some species are not sold in markets, e.g. *C. sylvicultor* and *C. leucogaster* in north-east Gabon (van Vliet, 2008), thus resulting in an underestimation of offtake for these particular species.

Other studies were based on data collected at the village or household level while participating in hunting, or with regular (daily, weekly or monthly) interviews and monitoring of kills brought from the forest (Fitzgibbon *et al.*, 1995; Delvingt *et al.*, 1997; Noss, 1998a,b, 2000; Wilkie *et al.*, 1998; Dethier & Ghuirgui, 1999; Muchaal & Ngandjui, 1999; Ngandjui & Blanc, 2000). In some cases only one hunting method was assessed (e.g. snares or nets) so that Maximum Sustainable Harvest was compared to offtake corresponding to one hunting method only.

The catchment area was estimated approximately for most of the studies either through the use of a global positioning system (Noss, 1998a,b, 2000) or considering a 15 km radius circle around the settlement (Wilkie *et al.*, 1998). Delvingt *et al.* (1997), Muchaal & Ngandjui (1999), Dethier & Ghirgui (1999) and Ngandjui & Blanc (2000) made a more precise estimation by mapping the area with the participation of volunteer hunters. Some authors did not mention the method used to estimate the catchment area.

For village level studies, because only a proportion of the total number of hunters per village was surveyed, data was extrapolated to the whole village to estimate the total hunting offtake per unit area per year. When only a few months were surveyed, the mean offtake per month was calculated and extrapolated for 1 year, without taking into account the temporal variability of hunting effort. The offtake rate (R_{offtake}) per duiker species was calculated as follows:

$$R_{\text{offtake}} = (N_s N_h)/S$$

where N_s is the number of animals of the species captured per hunter, N_h the number of hunters, and S the total catchments area. For snare hunters, the number of animals of a given species caught per hunter was assessed as the number of animals captured per snare multiplied by the number of snares per hunter.

Discussion

This review shows that maximum sustainable harvest for duikers is estimated with an accumulation of errors because of the difficulties in estimating model parameters for duiker species. Knowledge of duiker biology and ecology has remained poor because, as for many other shy tropical forest animals, their ecology is particularly difficult to study. Furthermore, research funds for ecology have focussed more on charismatic mammal species than on small, common mammal species. Studies of the sustainability of duiker hunting based on Robinson & Redford's index (1991) have used such a variety of methods to assess the parameters of the model that any comparisons between sites are largely meaningless. The major areas of divergence concern: (1) the value of the hypothetical adjustment factor, the method used to calculate the rate of maximum population increase, and the assessment of duiker population densities, and (2) the scale at which studies were conducted, and the sampling and extrapolation methods for assessing annual offtake.

Our analyses suggest that for *C. callipygus* and *C. dorsalis* maximum sustainable harvest obtained using

Table 5 Methods used to assess hunting offtake in studies of the sustainability of duiker hunting.

Author	Site	Scale	Hunting method	Offtake assessment method	Date	Sample	Data extrapolation	Method to estimate the catchment area
Feer, 1996	Makokou, Gabon	Villages around Makokou	All	F. Feer, unpubl. data				
	Ituri, Congo	Villages around Okapi Reserve	All	Hunting offtake surveys	1993–1994	Not mentioned	Not mentioned	Catchment's area a circle of 15 km radius
Fa *et al.*, 1995	Bioko, Equat. Guinea	1 city: Rio Muni	All	2 city markets visited daily	10/1990–10/1991	All sellers	Total offtake	Interviews with key informants
Fa *et al.*, 1995	Bioko, Equat. Guinea	1 city: Malabo	All	1 city market visited daily	10/1990–10/1991	All sellers	Total offtake	Interviews with key informants
Delvingt *et al.*, 1997	Dja, Cameroon	1 village: Ekom	All	Hunting offtake surveys	10/1994–1/1995	12 volunteer hunters out of 62	Offtake supposed constant through year	Map of hunting territory
Dethier & Ghuirgui, 1999	N'Gotto, CAR	6 villages	All	Hunting offtake surveys	2/1999–5/1999	All hunters	Total offtake	Map of hunting territory as used during study period
Fitzgibbon *et al.*, 1995	Arabuko-Sokoke Forest, Kenya	75 households	All	Hunting offtake surveys	3/1991–5/1991	16 hunters	Offtake supposed constant through year	Method not mentioned: surface = 372 km^2
Muchaal & Ngandjui, 1999	Dja, Cameroon	1 village: Mekas	All	Hunting offtake surveys	10/1994–11/1995	14 hunters		Map of hunting territory
Ngandjui & Blanc, 2000	Dja, Cameroon	1 village: Mekas	All	Hunting offtake surveys	01/1994–12/1995	All hunters	Total offtake	Map of hunting territory
Noss, 1998b	Bayanga, CAR	1 city: Bayanga	Snares	Hunting offtake surveys	Not given	17 volunteer hunters out of 60	Extrapolation for 60 hunters with 70 snares each	Approx. estimation of hunting areas using GIS
Noss, 1998a	Mossapoula, CAR	1 city: Bayanga	Nets	Hunting offtake surveys	9/1993–12/1993	76 net hunts	Extrapolation from 90 days over 18 weeks	Approx. estimation of hunting areas using GIS
Noss, 2000	Dzanga-Sangha, CAR	1 city: Mossapoula	Snares	Hunting offtake surveys	9/1994–12/1997	17 snare hunters	Extrapolation for 60 hunters with 70 snares each	Approx. estimation of hunting areas using GIS
Noss, 2000	Dzanga-Sangha, CAR	1 city: Mossapoula	Nets	Hunting offtake surveys	9/1994–12/1997	All hunters	Offtake supposed constant through year	Rough estimation of hunting areas using GIS

https://doi.org/10.1017/S0030605308000288 Published online by Cambridge University Press

Cole's (1954) formula are within the range of that calculated with Caughley & Krebs' (1983) formula. For *C. monticola*, however, maximum sustainable harvest based on Cole's formula gives much more conservative results: maximum sustainable harvest is 13 times higher when calculated using Caughley & Krebs' equation. For *C. monticola* and *C. callipygus* maximum sustainable harvest is highly dependent on the survey method used to assess densities, with densities for abundant duiker species (*C. monticola*) more variable than those for rarer species (most red duikers and *C. sylvicultor*).

Hunting offtake in poorly known catchment areas is not accurately assessed when data are collected at the market level. At the village level, extensive effort to obtain the trust of hunters and their active participation must be foreseen prior to any offtake study. High temporal variability of hunting effort (van Vliet, 2008) should be taken into account when data collected during one season are extrapolated to 1 year. Careful participatory mapping of the hunting territory would help to identify the catchment area, taking into account seasonal distribution of hunting pressure and the existence of non-hunted areas within the village territory (van Vliet, 2008).

Prior to any further duiker sustainability studies based on Robinson & Redford's (1991) index, we propose that the following are required: (1) Adaptation of the model to African mammals (e.g. are the hypothetical adjustment factors suggested by Robinson & Redford (1991) accurate for African duikers?). (2) Determination of the most reliable and practical formula to assess the rate of maximum population increase for duikers, and testing of the variability of reproductive parameters under different hunting pressures. (3) Assessment of the accuracy and magnitude of error of duiker survey methods, with a large comparative study between classical methods (physical capture-recapture, line transects), and exploratory methods (call points, genetic capture-recapture) in an area of known population density (e.g. semi-captivity such as an enclosure). (4) Standardization of methods to assess the parameters of Robinson & Redford's (1991) index when applied to duikers, to allow spatial and temporal comparisons.

We suggest that the use of biological models, such as Robinson & Redford's (1991) index of sustainability, should not be used as an absolute measure of sustainability. Pure biological approaches should be coupled with ethno-biological and socio-economic approaches to assess changes in hunting practices, evolution of prey choice, and cultural and economical drivers of hunting activities for an integrated assessment of sustainability.

Acknowledgements

This document has been produced with the financial assistance of the IFAD and European Union. The views expressed herein can in no way be taken to reflect their official opinion.

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