Journal of Applied Ecology

Journal of Applied Ecology 2009, **46**, 1011–1017 doi: 10.1111/j.1365-2664.2009.01705.x

METHODOLOGICAL INSIGHTS

Camera trapping photographic rate as an index of density in forest ungulates

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Summary

1. Calibrating indices of animal abundance to true densities is critical in wildlife studies especially when direct density estimations are precluded by high costs, lack of required data or model parameters, elusiveness and rarity of target species. For studies deploying camera traps, the use of photographic rate (photographs per sampling time) as an index of abundance potentially applies to the majority of terrestrial mammals where individual recognition, and hence capture–recapture analysis, are unfeasible. The very few studies addressing this method have either been limited by lack of independence between trapping rates and density estimations, or because they combined different species, thus introducing potential bias in camera trap detection rates. This study uses a single model species from several sites to analyse calibration of trapping rates to independently derived estimations of density. The study also makes the first field test of the method by Rowcliffe *et al.* (2008) for density derivation from camera trapping rates based on modelling animal-camera contacts.

2. We deployed camera traps along line transects at six sites in the Udzungwa Mountains of Tanzania and correlated trapping rates of Harvey's duiker *Cephalophus harveyi* with densities estimated from counts made along the same transects.

3. We found a strong, linear relationship ($R^2 = 0{\cdot}90$) between trapping rate and density. Sampling precision analysis indicates that camera trapping rates reach satisfactory precision when trapping effort amounts to 250–300 camera days. Density estimates using Rowcliffe *et al.*'s (2008) gas model conversion are higher than from transect censuses; we discuss the possible reasons and stress the need for more field tests.

4. *Synthesis and applications*. Subject to rigorous and periodic calibration, and standardization of sampling procedures in time and over different sites, camera trapping rate is shown to be, in this study, a valid index of density in the target species. Comparative data indicate that this may also apply to forest ungulates in general. The method has great potential for standardizing monitoring programmes and reducing the costs of wildlife surveys, especially in remote areas.

Key-words: abundance estimation, camera traps, density estimation, duikers, Eastern Arc, index surveys, trap rate, Udzungwa

Introduction

Automatic cameras triggered by passing animals have been widely used to inventory elusive mammals (e.g. Silveira, Jácomo & Diniz-Filho 2003; Rovero & De Luca 2007; Tobler *et al.* 2008), study activity patterns and habitat-use (Bowkett, Rovero & Marshall 2007) and estimate density using capture–recapture models for species with distinguishable individuals, e.g. tiger *Panthera tigris* Mazak (Karanth & Nichols 1998), jaguar *Panthera onca* Linnaeus (Silver *et al.* 2004) and ocelot *Leopardus pardalis* Linnaeus (Maffei *et al.* 2004). However, few studies have addressed the use of camera trapping rate (the ratio of photographs to camera trapping time) as an index of abundance. This is, in principle, of wide potential application as it is relevant to the great majority of species for which individuals cannot be distinguished from photographs.

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The first study to address the potential of camera trapping rate as an index of abundance showed that trapping rates from 19 studies on tigers correlated with estimates of density (Carbone *et al.* 2001). However, densities were estimated from the number of individuals photographed per unit area, therefore trapping rate and density were not independent (Jennelle, Runge & Mackenzie 2002). This limited the general applicability of the study, and more work on density calibration for a range of species and areas was recommended (Carbone *et al.* 2002). The first robust case found significant correlations between trapping rate and density derived from both capture–recapture analysis of tigers and line transect counts of six prey species (O'Brien, Kinnaird & Wibisono 2003). This study, however, by pooling different species, did not control for the likely variations in trapping rates associated with factors such as different body size (Kelly & Holub 2008; Tobler *et al.* 2008), trail use (Trolle & Kéry 2003) and daily range (Rowcliffe *et al.* 2008; Tobler *et al.* 2008). Whilst the need for calibration of an index of abundance to true density is an unavoidable limit of this approach (Williams, Nichols & Conroy 2002; Rowcliffe *et al.* 2008; O'Brien, in press), it remains a very promising tool (Kelly 2008). This is particularly so for temporal monitoring of populations within sites, as the sources of variation of detection probability can be minimized and standardized (O'Brien, in press). Despite the clear potential of this method, however, it is yet to be tested over a range of field conditions and target animal species. An alternative method to calibration was recently proposed by Rowcliffe *et al.* (2008), using captive animal data to produce a gas model of the likelihood of contact between animals and cameras. This too has not been tested on wild populations.

In this study, we present a test of trapping rate as an index of abundance using a single model species, the Harvey's duiker *Cephalophus harveyi* Thomas in the Udzungwa Mountains of Tanzania, and discuss the potential of this method for standardizing sampling procedures and designing monitoring programmes. We also test the conversion method based on gas modelling and compare the resulting density estimates. The study area is of exceptional importance for biodiversity, particularly forest mammals (Rovero & De Luca 2007). Previous work on the five species of forest antelope showed that whilst transect counts are feasible only for the common and diurnal Harvey's duiker (Rovero & Mashall 2004), camera trapping allows detection of the rarest and/or nocturnal and crepuscular species, such as the threatened Abbott's duiker *Cephalophus spadix* True (Rovero, Jones & Sanderson 2005). For all species, camera trapping has provided a higher detection rate than both dung and transect counts (Bowkett *et al.* 2006). Moreover, unbiased species identification from dung requires genetic testing (Bowkett *et al.* 2009).

Materials and methods

STUDY AREA AND SITES

We conducted camera trap and transect surveys between July 2004 and September 2005 at five sites in three forests [Mwanihana (two sites: 'Mwanihana peak' and 'Campsite 3'), Matundu (two sites: 'Ruipa' and 'Lumemo') and Uzungwa Scarp (one site)] in the Udzungwa Mountains (Fig. 1). An additional site in Mwanihana forest (Sanje trail) was sampled between December 2008 and March 2009. The six sites represent a large variation in both forest habitat type and antelope abundance. Data from the three sites in Mwanihana forest were considered independent as these sites are located approximately 6 km apart. We assumed that such spacing was more than sufficient to avoid multiple recording of the same individuals across sites. Mwanihana and Uzungwa Scarp have continuous vegetation cover 300–2000 m in elevation, from deciduous to montane forest. However they contrast markedly in protection levels, as the latter suffers from high human encroachment including hunting. Matundu forest is a lowland forest consisting of semi-deciduous and regenerating forest (Ruipa site, 300–400 m) and semi-deciduous to semi-evergreen forest (Lumemo site, 600–800 m).

LINE TRANSECT DENSITY ESTIMATION

Linear transect routes 3·1–4 km in length were established at each of the six sites. We obtained counts of forest antelope through 10–23 repetitions of these transects, conducted twice per month. Details of census methods are reported in Rovero & Marshall (2004). Transects were walked at a pace of 1 km h^{-1}, beginning at 7:00–7:30 h. Upon observing any duiker, the observer's location was noted and the horizontal distance and bearing to the first duiker seen were measured using a laser rangefinder and compass. The perpendicular distance between transect and duiker was also measured.

Densities and 95% bootstrapped confidence intervals were estimated using DISTANCE 5·0 (http://www.ruwpa.st-and.ac.uk/distance). We used the global data set to build a detection function and then applied it to estimate densities for each line transect because of the small number of sightings at some sites. This was justified because understorey visibility was similar across sites. The uniform detection probability function with cosine adjustment was chosen to fit the distance data, based on the Akaike Information Criterion, a standard output of DISTANCE (Buckland *et al.* 2001). For each transect we pooled data from all repetitions and considered the sampling effort as transect length multiplied by the number of repetitions (following Buckland *et al.* 2001; S. Buckland, personal communication).

CAMERA TRAPPING

Heat and motion, infrared-triggered CamTrak and Vision Scouting 35-mm film cameras (CamTrak South Inc., Watkinsville, Georgia, USA, and Non-Typical Inc., Park Falls, Wisconsin, USA) were used. We found no difference in detection efficiency between the two models (Bowkett *et al.* 2007). Camera traps were set at 500-m intervals along each of the six transects (total eight cameras per transect). Only five to six cameras per transect were set in Mwanihana forest, because of the risk of theft near settlements, and only six cameras in Uzungwa Scarp because rough terrain constrained the transect length to 3·1 km. To assess the usefulness of using paired cameras, two cameras were set every 500 m at Ruipa, one on either side of the transect (total 16 cameras). Cameras were positioned within about 25 m of the transect lines, selecting the specific locations using presence of animal trails and dung piles.

Cameras were set to take pictures 24 h per day on 36-exposure 200ASA colour film, with a 1-min delay between exposures. The date and time of each exposure were recorded by the cameras. Cam-

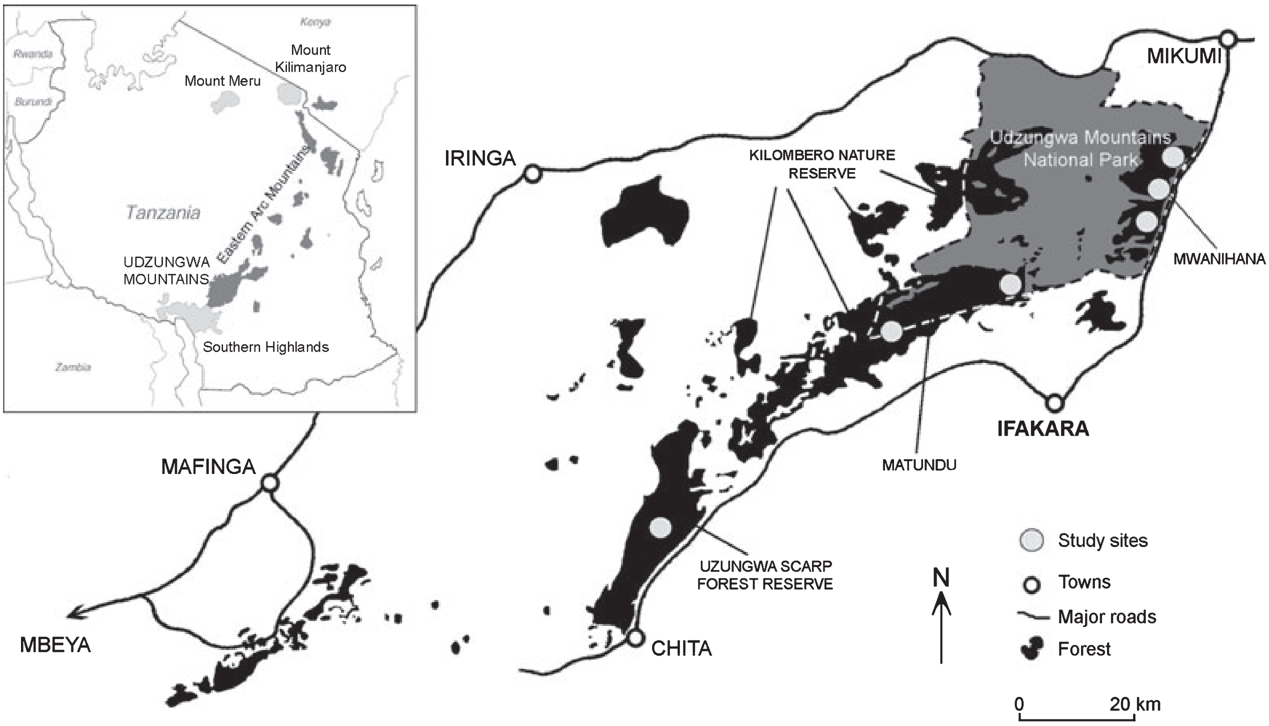

Fig. 1. Map of the Udzungwa Mountains of Tanzania showing major forest blocks (in black) and the six study sites where line transect counts and camera trapping were conducted (adapted from Marshall *et al.* 2005). Inset shows the Udzungwa Mountains within the Eastern Arc Mountains of Kenya and Tanzania.

eras were left in the field for 30–80 days. Camera trapping rate was defined as the ratio of independent photographs to the number of trap days (number of 24-h periods during which cameras were operating, i.e. until film was full or cameras were retrieved) and multiplied by 100. Consecutive photographs of the same species at the same site were deemed independent when there was at least 1-h interval between them (following Bowkett *et al.* 2007). For Harvey's duiker, linear regression was used to analyse the relationship between density estimates from transects and mean trapping rates at the six sites. Linear regression was selected following visual assessment of distribution and variance plots of residuals, and a Shapiro-Wilk test for normality (Conover 1999).

Sampling effort totalled 2984 trap days from 43 camera trap sites (Table 1). Of the 47 camera traps originally set, two were stolen and two malfunctioned. For Harvey's duiker, camera trapping sampling precision was assessed as the coefficient of variation (CV) of trap rates with cumulative trapping effort (cameras times days). We used data from Ruipa as this site had the highest number of cameras and the longest sampling period. One of each pair of cameras was randomly selected, to avoid spatial auto-correlation, when assessing precision of using single cameras. The average results for both cameras were used to assess precision when using paired cameras. Precision was computed for intervals of 50 camera days, each obtained by pooling 10 values of trapping rates (photos per five trapping days) selected randomly. The computation was repeated 10 times to derive mean profiles of CV.

DENSITY ESTIMATES USING ROWCLIFFE *ET AL.*'S (2008) CONVERSION

For Harvey's duiker, eqn 4 from Rowcliffe *et al.* (2008) was used to convert camera trapping rates to densities. Sensitivity of several cameras set at the height of 45 cm from ground was measured. Detection distance averaged 3·5 m and detection arc 48·5°. Since no data on day range or speed of movement are available for Harvey's duiker, data for the related, albeit larger black-backed duiker *Cephalophus dorsalis* Grey were used. A day range of 1·85 km was obtained by following four individuals for a mean period of 150 days, taking radio-tracking fixes every 15 min (Feer 1989). This value was scaled for Harvey's duiker using the allometry relationship between day range and body mass, fed with the empirically estimated slope of 0·133 suggested for Artiodactyls (Carbone *et al.* 2005). The resulting day range is

Table 1. Camera trapping effort at the six study sites in three forests in the Udzungwa Mountains of Tanzania

	Matundu		Mwanihana			Uzungwa
	Ruipa	Lumemo	Campsite 3	Mwanihana	Sanje	Scarp
Camera trapping days	1163	548	466	443	109	255
Mean trapping days per camera	72·7	78·3	28·6	35·5	21·8	51·0
Successful cameras	16	7	5	5	5	5
Cameras broken/stolen	0	1	1	0	1	1

Table 2. Results of Harvey's duiker line transect counts at the six study sites in the Udzungwa Mountains of Tanzania

	Ruipa	Lumemo	Campsite 3	Mwanihana	Sanje	Uzungwa Scarp
No. transect repetitions	12	12	14	13	10	23
Total number of sightings (mean ±95% confidence interval per walk)	26 (2·17 ± 0·87)	16 (1·33 ± 0·61)	18 (1·29 ± 0·48)	20 (1·54 ± 0·96)	7 (0·70 ± 0·82)	6 (0·26 ± 0·18)
Density estimate (95% confidence intervals; individuals km^{-2})	13·32 (12·06–14·71)	8·20 (7·42–9·05)	7·90 (7·16–8·73)	9·46 (8·56–10·44)	4·78 (4·33–5·28)	2·07 (1·87–2·28)

1·83 km. Body mass data were from Feer (1989) and Kingdon (1997) for *C. dorsalis* and *C. harveyi* respectively.

Results

From line transect counts, Harvey's duiker was sighted a total of 93 times along the six transects (Table 2). Blue duiker *Philantomba monticola* Thunberg was sighted only once in Uzungwa Scarp, while suni *Neotragus moschatus* Von Dueben and bushbuck *Tragelaphus scriptus* Pallas were detected from vocalizations only. Abbott's duiker was neither seen nor heard. The number of observations for estimating density and calibrating camera trapping rates was therefore insufficient for all species besides Harvey's duiker. As inferred from preliminary surveys, Harvey's duiker density estimates varied considerably among sites, ranging from 2·07 to 13·32 individuals km^{-2} (Table 2).

From camera trapping, 815 independent photographs of forest antelope were obtained (Table 3). Pooling all sites, the most photographed species was Harvey's duiker (600 photographs), followed by suni (157), bushbuck (27), Abbott's duiker (24) and blue duiker (7). Harvey's duiker was the only species captured at all sites, with a mean trapping rate of 15·2 independent photographs 100 day^{-1} of sampling. Suni was the second most frequently photographed species (6·5) and was detected at four sites. Abbott's duiker was also photographed at four sites with mean rate of 0·7. Bushbuck and blue duiker were photographed at three and one site, respectively, both at a mean rate of 0·5.

Along the six transects, Harvey's duiker mean trapping rate varied from 2·8 to 28·9 photographs 100 day^{-1}. The linear regression of mean trapping rate on density was highly significant ($y = 2{\cdot}26x - 2{\cdot}01$; $F_{1,4} = 36{\cdot}53$, $P = 0{\cdot}003$, $R^2 = 0{\cdot}90$; Fig. 2). Camera trap sampling precision for Harvey's duiker increased until a trapping effort of 250–300 camera days, with profiles levelling off considerably after this point (Fig. 3). Using paired camera traps at Ruipa allowed for increased sampling precision (by about 4% in CV), but profiles were similar (Fig. 3). Duiker density estimates using the Rowcliffe *et al.*'s (2008) conversion were significantly higher than from line transect counts (Table 4; Wilcoxon test: $Z = -2{\cdot}201$, $P = 0{\cdot}028$).

Discussion

The limits of wildlife surveys based on indices and, particularly, the use of camera trapping rates as an index of abundance, have been widely debated (Carbone *et al.* 2002; Jennelle *et al.* 2002; Williams *et al.* 2002; Karanth *et al.* 2003; O'Brien, in press), and they mainly relate to the need for calibrating the index with independent estimators of density. It is intuitive that camera trapping rate should be related to abundance. As density increases, the chance of encounters between individuals and cameras would be expected to increase. The likelihood of the observed relationship between trapping rates and density having general applicability in forest ungulates is strengthened by similar relationships found in previous studies (O'Brien *et al.* 2003 - tigers and six prey species, four of which were ungulates: $R^2 = 0{\cdot}79$; Rowcliffe *et al.* 2008 – four species in a semi-captive environment, including two ungulates: $R^2 = 0{\cdot}69$). This study, therefore, provides a convincing application of camera trapping that has been mostly overlooked. By studying one species across comparable forests, covariates of trapping rates associated with pooling different species have been minimized.

There are various possible reasons why the gas model method proposed by Rowcliffe *et al.* (2008) produced different density estimates. In general, while this method is based on robust theory, its application to field situations may be constrained, because (1) a gas model is not a true represen-

Table 3. Number of camera trap photographs and, in parenthesis, mean camera trapping rate (photographs 100 day^{-1}) ±95% confidence intervals for five species of forest antelope recorded at the six study sites in the Udzungwa Mountains of Tanzania

	Ruipa	Lumemo	Campsite 3	Mwanihana	Sanje	Uzungwa Scarp
Harvey's duiker	330 (28·9 ± 6·5)	98 (19·1 ± 6·1)	92 (18·0 ± 8·9)	65 (14·0 ± 9·1)	9 (8·2 ± 5·3)	6 (2·8 ± 0·4)
Abbott's duiker	2 (0·2 ± 0·2)	10 (1·7 ± 2·1)	7 (1·5 ± 1·1)	5 (1·0 ± 1·1)	0	0
Blue duiker	0	0	0	0	0	7 (3·2 ± 2·1)
Suni	42 (3·5 ± 1·2)	17 (3·5 ± 0·2)	45 (8·9 ± 8·9)	41 (8·3 ± 7·7)	12 (14·6 ± 12·1)	0
Bushbuck	25 (2·2 ± 1·8)	1 (0·3 ± 0·6)	0	0	0	1 (0·5 ± 0·9)

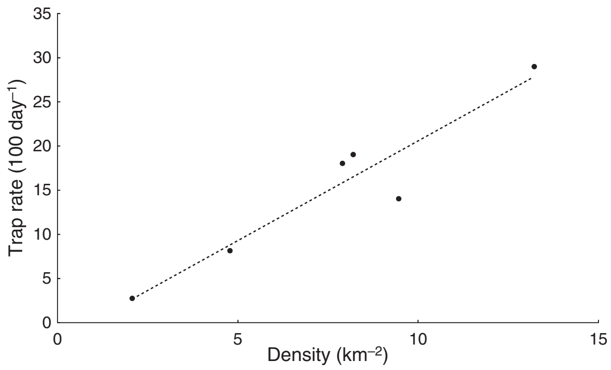

Fig. 2. Camera trapping photographic rates plotted against densities estimated from line transect counts of Harvey's duiker, recorded along six study sites in the Udzungwa Mountains of Tanzania (dashed line indicates linear regression; $R^2 = 0{\cdot}90$).

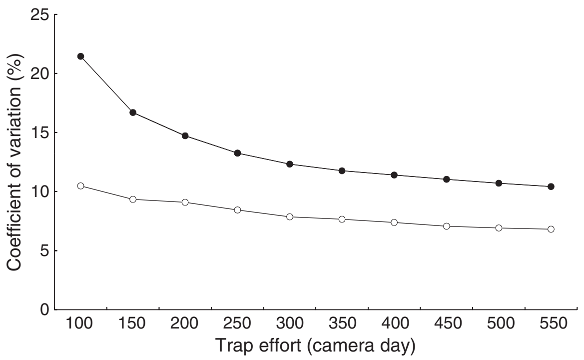

Fig. 3. Camera trapping sampling precision expressed as the coefficient of variation of Harvey's duiker's camera trapping rates with cumulative sampling effort (number of cameras times trapping days). Data are from both eight pairs of cameras (open circles) and single cameras (closed circles) set along a 4 km line transect at Ruipa in the Udzungwa Mountains.

Table 4. Comparison of density estimates (individuals km^{-2}) of Harvey's duiker obtained from line transect counts (left column) and (right column) from the conversion of camera trapping rates proposed by Rowcliffe *et al.* (2008)

Study site	Census density	Estimated density (mean ± 95% confidence intervals)
Ruipa	13·32	49·96 ± 11·16
Lumemo	8·2	32·83 ± 10·52
Uzungwa Scarp	2·07	4·74 ± 6·16
Campsite 3	7·9	31·10 ± 15·43
Mwanihana	9·46	24·18 ± 15·72
Sanje	4·78	14·05 ± 9·20

tation of animal movements and interactions, and (2) it depends on input parameters that are unavailable for most wild animals (speed of movement or day range). Borrowing day range from other species using allometry may result in biased estimates, and daily distances from telemetry may also be inaccurate depending on the time interval between localizations (M. Rowcliffe, personal communication). Moreover, camera sensitivity (i.e. detection arc and distance), varies greatly with camera models, and this too will affect estimates. The differences in estimates that were found may also partly reflect an underestimate of census density. Estimation of forest mammal densities using line transects can be problematic because of poor detectability (Marshall, Lovett & White 2008), which is especially critical for duikers dwelling in densely vegetated forest floors. Duikers were seen on the transect several times, however it is difficult to assess whether their shyness may result in missed sightings from transect lines (Struhsaker 1997; Rovero & Mashall 2004). That other species partially active at day time, especially suni, were detected frequently by camera traps but never sighted indicates that line transect observations are problematic for these species, potentially resulting in underestimation of density. Further field studies will be required to resolve these caveats, and alternative density estimation methods such as those based on counts of dung pellets should also be tested. Both calibration and modelling might not always be feasible because of lack of data, in which case occupancy models based on presence/absence data may be a useful surrogate (MacKenzie *et al.* 2002; Mackenzie & Nichols 2004). These do not estimate density, however, their application to camera trap data has shown promising results (Linkie *et al.* 2007).

Logistic problems constrained the sampling at some sites, especially Uzungwa Scarp and Sanje, where, in addition, one camera was stolen and one did not work. Accordingly precision analysis suggests that trapping effort was sub-optimal at these sites, as 250 camera days are required for optimal precision. The protocol of one camera every 500 m translates into eight cameras functioning for at least 30 days along a 4 km transect. Precision would be expected to be achieved earlier where densities are high, therefore raising some concern regarding the two low density sites. However, the sub-optimal sampling effort has not led to outlying points in the calibration (Fig. 2) and therefore crucially it does not appear that accuracy has been affected.

The advantages of camera trapping over density estimations from line transect counts relate to both standardization of sampling procedures and cost effectiveness. Camera trapping simplifies data collection since human error is reduced to placement and maintenance of the traps. These skills are easily acquired, rather than reliance on individual expertise such as estimating distance or detecting and identifying species (O'Brien in press). Inter-observer reliability has further been identified as a major constraint in monitoring programmes based on direct counts (e.g. Mitani, Struhsaker & Lwanga 2000; Rovero *et al.* 2006). In terms of cost, establishing the three transects and conducting the 23 censuses in the remote Uzungwa Scarp forest involved approximately 100 days of work by two people over 1 year, costing at least 3000 US$. In contrast, deploying and retrieving six camera traps at the same site required 12 days for the same team, costing 360 US$ plus approximately 1050 US$ for purchasing and maintaining the camera traps. Even if more advanced, digital camera trap models were to be used (currently up to 500 US$ each), the camera trap surveys would have remained more cost-effective. Thus, although camera trapping surveys involve high initial costs (Silveira *et al.* 2003), they are diluted by the decreased field time, and cameras can of course be used in future surveys.

Conclusions

Besides Harvey's duiker, the camera traps have revealed the presence of several secretive forest antelope in the Udzungwa Mountains. Assessing the overall antelope community was beyond the scope of this study. However, the results confirm the value of camera trapping for studying elusive forest mammals and obtaining useful information on the occurrence and conservation status of threatened species (see also Kinnaird *et al.* 2003; Tobler *et al.* 2008).

The use of camera trapping rate as an index of abundance is both promising and cost-effective for the rapid assessment of animal abundance in remote areas or where alternative methods are unfeasible (O'Brien *et al.* 2003; O'Brien in press). The method also has potential for temporal comparison of populations (O'Brien in press) and may facilitate to standardize and reduce costs of monitoring programmes, providing that (1) calibration is re-assessed periodically, (2) sampling precision is adequate and (3) sampling season is standardized. Future studies should further evaluate this method in relation to other camera trapping approaches in development (Linkie *et al.* 2007; Rowcliffe *et al.* 2008; O'Brien in press). Ongoing development of camera trapping protocols and analytical frameworks is very important as these methods are relevant to the majority of forest mammals that cannot be identified to individuals using natural markings.

Acknowledgements

We are grateful to Chris Carbone, Tim O'Brien, Andy Bowkett, Thomas Struhsaker and two anonymous reviewers for constructive comments on the manuscript, and to Marcus Rowcliffe for advice on applying the density derivation method. F.R. was funded by a post-doctoral grant from the Provincia Autonoma di Trento through the Museo Tridentino di Scienze Naturali. A.R.M. was funded by the Natural Environment Research Council (NER/S/A/2002/11177). Additional funding was from National Geographic Society and Margot Marsh Biodiversity Foundation (through Thomas Struhsaker). A.R.M. thanks Jon Lovett and Piran White for facilitate with supervision, and Steve Buckland for advice on analysing line transect data from repeat counts. Andy Bowkett collaborated on some phases of fieldwork; John Msirikale, Arafat Mtui and Ruben Mwakisoma facilitated collecting data. Research permits were by Tanzania Wildlife Research Institute, Tanzania National Parks, Forestry and Beekeeping Division and Tanzania Commission for Science and Technology.

References

Bowkett, A.E., Lunt, N., Rovero, F. & Plowman, A.B. (2006) How do you monitor rare and elusive mammals? Counting duikers in Kenya, Tanzania and Zimbabwe. *Animals, Zoos and Conservation* (eds E. Zgrabczyńska, P. Ćwiertnia & J. Ziomek), pp. 21–28. Zoological Garden in Poznan, Poland.

Bowkett, A.E., Rovero, F. & Marshall, A.R. (2007) The use of camera trap data to model habitat use by antelope species in the Udzungwa Mountain forests, Tanzania. *African Journal of Ecology*, **46**, 479–487.

Bowkett, A.E., Plowman, A.B., Stevens, J.R., Davenport, T.R.B. & van Vuuren, B.J. (2009) Genetic testing of dung identification for antelope surveys in the Udzungwa Mountains, Tanzania. *Conservation Genetics*, **10**, 251–255.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling. Estimating Abundance of Biological Populations*. Oxford University Press, Oxford.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., MacDonald, D.W., Martyr, D., McDougal, C., Nath, L., O'Brien, T., Seidensticker, J., Smith, D., Sunquist, M., Tilson, R. & Wan Shahruddin, W.N. (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, **4**, 75–79.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kinnaird, M., Laidlaw, R., Lynam, A., MacDonald, D.W., Martyr, D., McDougal, C., Nath, L., O'Brien, T., Seidensticker, J., Smith, J.L.D., Tilson, R. & Wan Shahruddin, W.N. (2002) The use of photographic rates to estimate densities of cryptic mammals: response to Jennelle *et al. Animal Conservation*, **5**, 121–123.

Carbone, C., Cowlishaw, G., Isaac, N.J.B. & Rowcliffe, M. (2005) How far do animals go? Derminants of day range in mammals. *The American Naturalist*, **165**, 290–297.

Conover, W.J. (1999) *Practical Nonparametric Statistics*, 3rd edn. John Wiley & Sons, New York.

Feer, F. (1989) Occupation de l'espace par deux bovidés sympatriques de la foret dense africaine (Cepahlophus callipygus et C. dorsalis): influence du rythme d'activité. *Revue d'Ecologie – La Terre et La Vie*, **44**, 225–248.

Jennelle, C.S., Runge, M.C. & Mackenzie, D.I. (2002) The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. *Animal Conservation*, **5**, 119–120.

Karanth, K.U. & Nichols, J.D. (1998) Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, **79**, 2852–2862.

Karanth, K.U., Nichols, J.D., Seidensticker, J., Dinerstein, E., David Smith, J.L., McDougal, C., Johnsingh, A.J.T., Chundawat, R.S. & Thapar, V. (2003) Science deficiency in conservation practice: the monitoring of tiger population in India. *Animal Conservation*, **6**, 141–146.

Kelly, J.M. (2008) Design, evaluate, refine: camera trap studies for elusive species. *Animal Conservation*, **11**, 182–184.

Kelly, J.M. & Holub, E.L. (2008) Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species on Salt Pond Mountain, Giles Country, Virginia. *Northeastern Naturalist*, **15**, 249–262.

Kingdon, J. (1997) *The Kingdon Field Guide to African Mammals*. Academic Press, London.

Kinnaird, M.F., Sanderson, E.W., O'Brien, T.G., Wibisono, H.T. & Woolmer, G. (2003) Deforestation trends in a tropical landscape and implications for forest mammals. *Conservation Biology*, **17**, 245–257.

Linkie, M., Dinata, Y., Nugroho, A. & Haidir, I.A. (2007) Estimating occupancy of data deficient mammalian species living in tropical rainforests: sun bears in the Kerinci Seblat region, Sumatra. *Biological Conservation*, **137**, 20–27.

Mackenzie, D.I. & Nichols, J.D. (2004) Occupancy as a surrogate for abundance estimation. *Animal Biodiversity and Conservation*, **27**, 461–467.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.

Maffei, L., Noss, A.J., Cuellar, E. & Rumiz, D.I. (2004) Ocelot (*Felis pardalis*) population densities, activity, and ranging behaviour in the dry forests of eastern Bolivia: data from camera trapping. *Journal of Tropical Ecology*, **21**, 1–6.

Marshall, A.R., Topp-Jørgensen, J.E., Brink, H. & Fanning, E. (2005) Monkey abundance and social structure in two high elevation forest reserves in the Udzungwa Mountains of Tanzania. *International Journal of Primatology*, **26**, 127–145.

Marshall, A.R., Lovett, J.C. & White, P.C.L. (2008) Selection of line-transect methods for estimating the density of group-living animals: lessons from the primates. *American Journal of Primatology*, **70**, 452–462.

Mitani, J.C., Struhsaker, T.T. & Lwanga, J.S. (2000) Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. *International Journal of Primatology*, **21**, 269–286.

O'Brien, T.G. (in press) Abundance, density and relative abundance: conceptual framework. *Camera Traps in Animal Ecology: Methods and Analyses* (eds A.F. O'Connell, J.D. Nichols & U.K. Karanth). Springer Tokyo Inc., Tokyo.

O'Brien, T.G., Kinnaird, M.F. & Wibisono, H.T. (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, **6**, 131–139.

Rovero, F. & De Luca, D.W. (2007) Checklist of mammals of the Udzungwa Mountains of Tanzania. *Mammalia*, **71**, 47–55.

Rovero, F. & Mashall, A.R. (2004) Estimating the abundance of forest antelope by using line transect techniques: a case from the Udzungwa Mountains of Tanzania. *Tropical Zoology*, **17**, 267–277.

Rovero, F., Jones, T. & Sanderson, J. (2005) Notes on Abbott's duiker (*Cephalophus spadix* True 1890) and other forest antelope of Mwanihana Forest, Udzungwa Mountains, Tanzania, as revealed by camera trapping and direct observations. *Tropical Zoology*, **18**, 13–23.

Rovero, F., Struhsaker, T.T., Marshall, A.R., Rynne, T.A., Pedersen, U.B., Ehardt, C.L., Butynski, T.M. & Mtui, A.S. (2006) Abundance of Diurnal Primates in Mwanihana Forest, Udzungwa Mountains, Tanzania. *International Journal of Primatology*, **27**, 675–697.

Rowcliffe, J.M., Field, J., Turvey, S.T. & Carbone, C. (2008) Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, **45**, 1228–1236.

Silveira, L., Jácomo, A.T.A. & Diniz-Filho, J.A.F. (2003) Camera trap, line transect census and track surveys: a comparative evaluation. *Biological Conservation*, **114**, 351–355.

Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gomez, H. & Ayala, G. (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx*, **38**, 148–154.

Struhsaker, T.T. (1997) *Ecology of an African Rainforest: Logging in Kibale and the Conflict Between Conservation and Exploitation*. University Press of Florida, Gainesville.

Tobler, M.W., Carrillo-Percastegui, S.E., Leite Pitman, R., Mares, R. & Powell, G. (2008) An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation*, **11**, 169–178.

Trolle, M. & Kéry, M. (2003) Estimation of ocelot density in the Pantanal using capture–recapture analysis of camera trapping data. *Journal of Mammalogy*, **84**, 607–614.

Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego.

Received 12 May 2009; accepted 3 August 2009
Handling Editor: Nathalie Pettorelli