# The use of camera-trap data to model habitat use by antelope species in the Udzungwa Mountain forests, Tanzania

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## Abstract

The ecology of many species of duiker, and other African forest antelope, is poorly known and yet knowledge of the factors determining their distribution and abundance is critical to the conservation of this increasingly threatened group. Camera-trapping was used to investigate forest antelope ecology in the biologically diverse Udzungwa Mountains, Tanzania. The relationship between camera-trapping rates and vegetation (and other habitat variables) was investigated using generalized linear modelling. Over 630 photographs of antelope were obtained, with Harvey's duiker being the most recorded species. The camera-trap rate of Harvey's duiker was positively related to the species diversity of small plant stems and negatively related to an index of visibility, while that of suni antelope was negatively related to the percentage ground cover of leaf-litter. The camera-trap rate of Harvey's duiker was also negatively related to distance to the nearest village, as predicted for a species targeted for subsistence hunting. Camera-traps also recorded bushbuck and the threatened Tanzanian endemic Abbott's duiker, but there were insufficient captures to model habitat use for these species. Results of this study illustrate the potential of camera-trapping for modelling habitat requirements and providing guidelines for the conservation management of threatened antelope populations in forest habitats.

*Key words: Cephalophus harveyi*, Eastern Arc, generalized linear models, Harvey's duiker, *Neotragus moschatus*, suni

## Résumé

L'écologie de nombreuses espèces de céphalophes et celle d'autres antilopes forestières africaines sont mal connues, et pourtant la connaissance des facteurs qui déterminent leur distribution et leur abondance est critique pour la conservation de ce groupe de plus en plus menacé. On a utilisé des pièges photographiques pour étudier l'écologie des antilopes de forêt dans les Udzungwa Mountains, en Tanzanie, qui sont biologiquement variées. La relation entre le taux de piégeage photo et la végétation (et d'autres variables de l'habitat) a été étudiée au moyen d'une modélisation linéaire généralisée. On a obtenu plus de 630 photos d'antilopes, l'espèce la plus souvent piégée étant le céphalophe de Harvey. Le taux de piégeage photo de ce céphalophe était positivement lié à la diversité des espèces végétales de petite taille et négativement lié à un indice de visibilité, alors que celui de l'antilope suni était négativement lié au pourcentage de la couverture du sol par une litière de feuilles. Le taux de piégeage photo du céphalophe de Harvey était aussi lié négativement à la distance jusqu'au village le plus proche, ce qui est prévisible pour une espèce victime de la chasse de subsistance. Les pièges photos ont aussi révélé la présence de bushbucks et du céphalophe d'Abbott, endémique à la Tanzanie et menacé, mais il y eut trop peu de prises de vues pour permettre la modélisation de l'utilisation de l'habitat par ces espèces. Les résultats de cette étude illustrent le potentiel du piégeage photographique pour la modélisation des exigences en matière d'habitat et pour la préparation de directives pour la gestion de la conservation des populations d'antilopes menacées dans les habitats forestiers.

## Introduction

Antelope are an important, if often poorly known, component of African forest ecosystems (Wilson, 2001; Plowman, 2003). Duikers (*Cephalophus* spp.), and sympatric antelope species fulfil important ecological roles including

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seed dispersal (Gautier-Hion, Emmons & Dubost, 1980; Feer, 1995) and prey for top predators (Boshoff *et al.*, 1994; Hart, Katembo & Punga, 1996). Many populations of forest antelope are under heavy pressure from habitat disturbance and hunting (Eaves, 2000; Newing, 2001).

In common with other African forest species, knowledge of the factors determining distribution and abundance of forest antelope is important for their conservation (e.g. Barnes *et al.*, 1991; Wasserman & Chapman, 2003). Habitat requirements for forest antelope species have rarely been quantified nor have models been developed. However, multispecies studies in west and central Africa (Dubost, 1979, 1980; Hart, 1985; Feer, 1989) and South African coastal forests (Bowland & Perrin, 1994, 1995, 1998) provide important clues as to which ecological factors might predict habitat quality for forest antelope.

Many forest antelope predominantly feed on fallen fruit (Gautier-Hion *et al.*, 1980; Hart, 1985) and fallen leaves (Lawson, 1989; Bowland & Perrin, 1998). The forest canopy layer therefore may be an important primary food source. Forest antelope also browse the understorey and take a variety of ancillary food items including fungi, crop tubers and animal matter (e.g. Wilson, 2001; Hoffman & Roth, 2003; Apio & Wronski, 2005). Plant species diversity is likely to be an important factor for habitat quality with forest antelope feeding on a wide variety of plant parts and species to meet their nutritional requirements and avoid plant defences (Bowland & Perrin, 1998; Perrin, Bowland & Faurie, 2003).

Other ecological factors that may determine forest antelope abundance are cover and refuge from predators. Dubost (1979) found that duiker species in Gabon were negatively associated with plant stem density and interpreted this as selection for foraging sites that allow duiker to flee rapidly. However, forest antelope have also been found to utilize dense vegetation for cover whilst resting and during frequent rumination bouts (Perrin *et al.*, 2003).

Hunting pressure is also likely to be an important predictor of forest antelope habitat use. Forest antelope species are a common target for subsistence hunting and the commercial bushmeat trade (Noss, 1998; Fa *et al.*, 2006) and are generally less abundant in areas where they are subjected to hunting (e.g. Wilkie & Carpenter, 1999; Hart, 2000).

A key factor that has limited quantitative habitat modelling for forest antelope is the difficulty in estimating density or relative abundance. This is because of low detection rates from methods based on direct sightings and methodological problems extrapolating from indirect signs such as dung or tracks (Bowland & Perrin, 1994; Struhsaker, 1997; Lunt, Bowkett & Plowman, 2007). However, camera-trapping has shown excellent potential for studying elusive animals in comparison with more traditional methods (Jácomo, Silveira & Diniz-Filho, 2004) and has proven useful for forest antelope in the Udzungwa Mountains of Tanzania, where it has a high detection efficiency and has recorded species otherwise undetected (Rovero & Marshall, 2004; Rovero, Jones & Sanderson, 2005; Bowkett *et al.*, 2006).

In this study, we used camera-trap data to determine ecological and anthropogenic factors affecting habitat use by two forest antelope species in the Udzungwa Mountains. The Udzungwas are part of an internationally recognized hotspot for biodiversity conservation (Myers *et al.*, 2000; Burgess *et al.*, 2007), and have a diverse forest antelope community including at least five species: Harvey's duiker *Cephalophus harveyi*, bushbuck *Tragelaphus scriptus*, suni *Neotragus moschatus*, blue duiker *C. monticola* and the highly threatened Tanzanian endemic, Abbott's duiker *C. spadix* (Dinesen *et al.*, 2001; Rovero *et al.*, 2005). While several of these species may also occupy woodland and thicket habitats, we employ the term 'forest antelope' to refer to all antelope species found in our study site rather than just those that are strictly forest dependent.

## Materials and methods

### *Study area*

Camera-trap surveys were conducted between July 2004 and September 2005 in two forests (Mwanihana and Matundu) within the Udzungwa Mountains National Park (UMNP, 1990 km$^2$, centred on 7°46′S and 36°43′E; Fig. 1). Two areas within each forest were chosen for deploying camera-traps. The four areas represent a large variation in terms of both forest habitat type and antelope abundance as inferred from preliminary transect surveys. Mwanihana is a large forest block (*c.* 150 km$^2$) with continuous vegetation cover from 300 to over 2000 m above sea level on the eastern side of UMNP. The altitude range of the two camera-trapping areas was 400–1000 m in semi-deciduous to sub-montane forest. Matundu (*c.* 180 km$^2$), is in the southern UMNP, extending into a Forest Reserve, and consists of lowland, semi-deciduous forest at 300–800 m. The altitude range of the two camera-trapping areas was 300–700 m.

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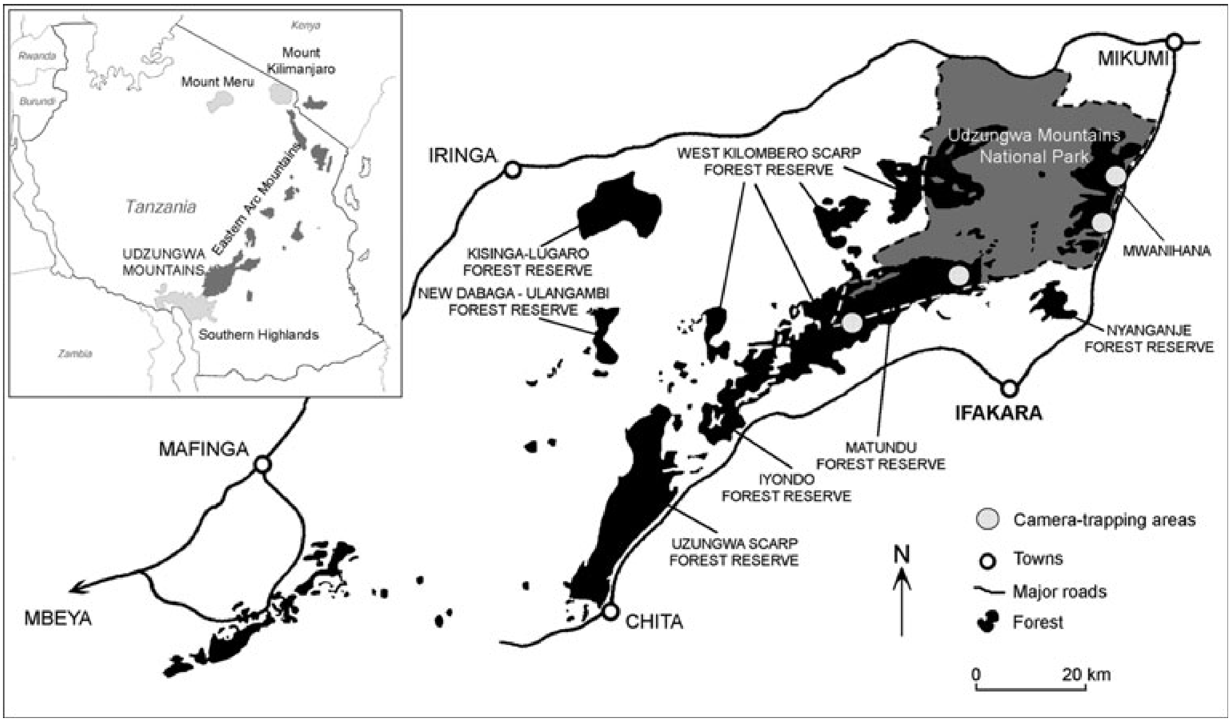


**Fig 1** Map showing the Udzungwa Mountains, Tanzania, including the four camera-trapping areas used to study forest antelope habitat selection (adapted from Marshall *et al.*, 2005)

*Camera-trapping*

Heat and motion, infrared-triggered CamTrak and Vision Scouting cameras were used (CamTrak South Inc., Watkinsville, GA, U.S.A. and Non Typical Inc., Park Falls, WI, U.S.A., respectively). Consistency in sensitivity between the two camera models was assessed by setting two cameras at the same site for 16 days and verifying that the number of antelope photographed per day was not significantly different between the two models (Mann–Whitney test: $U = 110$, $P = 0.51$). Cameras were set to take pictures 24 h day$^{-1}$ on 200 ASA colour print film, with a 1-min delay between exposures. The date and time of each exposure were shown on the film. Cameras were kept in the field for 60–80 days.

Camera-trap sites were located at 0.5-km intervals along four 4 km transect routes established for primate and forest antelope surveys (Rovero *et al.*, 2006; Marshall, 2007), two transects in each of Matundu and Mwanihana Forests. Cameras were set within about 25 m of the line used for transect counts, the specific locations being selected upon the presence of animal trails and dung piles. We assume that the position along the transect is random with respect to duiker habitat use, but the specific camera location is selected to maximize photographic capture rate. Therefore, our strategy is a compromise between completely random sampling and intentional selection of duiker habitat. Cameras were set at a height of 30–50 cm and at distances from the trail that gave clear images of captured antelope. One camera was set every 0.5 km along each transect with the exception of one transect in Matundu where two cameras were set every 0.5 km, one each side of the transect (totalling 16 cameras along the 4 km of transect). Five cameras were set per transect in Mwanihana Forest instead of eight to avoid placing cameras in proximity to the forest edge where the risk of theft was greater. Twenty-five camera-trap locations were originally used in the study.

*Habitat description*

Habitat variables were measured for each 0.5 km transect section containing a camera-trap or camera-trap pair (Table 1). All sampling was undertaken during the dry season between June and September 2005. Large trees

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**Table 1** Habitat variables recorded from four areas in the Udzungwa Mountains, Tanzania, and used to predict forest antelope camera-trap rate as a proxy of abundance. DBH, diameter at breast height, D at 1m = diameter at 1m height

| Variables presented to regression models | Inter-correlated variables not presented to models (correlation coefficients) |
|---|---|
| 1. Canopy cover | |
| 2. Large tree (>10 cm DBH) density | |
| 3. Large tree (>10 cm DBH) diversity (*D*) | |
| 4. Medium tree (5–10 cm DBH) density | |
| 5. Medium tree (5–10 cm DBH) diversity (*D*) | |
| 6. Small stem (<5 cm D at 1 m) diversity (*D*) | 10. Small stem (<5 cm D at 1 m) density[a] (−0.74**)11. Per cent grass[a] (−0.42*) |
| 7. Visibility | |
| 8. Per cent leaf-litter | 12. Per cent woody and herbaceous[b] (−0.54**) |
| 9. Distance to village (km) | 13. Per cent seedling[b] (0.53**) |

Right-hand column lists redundant variables and their Spearman rank correlation coefficient with opposing variables listed in the left column (n = 25, $^{*}P < 0.05$, $^{**}P < 0.01$).
[a]Small stem (<5 cm D at 1 m) density also correlated with per cent grass (0.54**).
[b]Per cent seedling also correlated with per cent woody and herbaceous (0.61**).

(>10 cm diameter at breast height) were counted within a 5 m by 200 m linear plot along each transect. All other variables were measured within 50 m by 50 m plots centred on the 50 m transect marker nearest the camera-trap. Percentage canopy cover was estimated visually as the amount of sky visible overhead whilst walking the 50 m transect section. Density was calculated for medium-sized trees (5–10 cm diameter at breast height) in 25 m by 25 m subplots and small plant stems (<5 cm diameter at 1 m height) in five randomly located 3 m by 3 m subplots.

Simpson's diversity index (*D*) was calculated for each plant size-class within each plot, pooling subplots for smaller plant stems. Simpson's index was employed rather than the Shannon diversity index as it is less affected by sample size (Magurran, 2004). Per cent ground cover was estimated visually in ten 1 $m^2$ subplots per plot. Standardized habitat variables (e.g. plant diversity) were chosen rather than more site-specific variables (e.g. abundance of particular plant species) so that results would be widely applicable.

A visibility index was calculated for each plot by estimating the percentage of a 1 by 1 m plastic sheet visible at a distance of 20 m from the centre of the plot. This was repeated four times at different bearings to give a mean value for each plot. This method was taken to incorporate the extent of horizontal vegetation growth not measured by stem density.

The distance to the nearest village for each camera-trap was calculated using a Garmin e-trex GPS unit (Garmin Corporation, Olathe, KS, U.S.A.). In the case of the Lumemo site, this distance was taken to be from a village within the National Park boundaries that had been abandoned following the relocation of its inhabitants. This distance was used instead of that to the nearest inhabited village because evacuation of the village within the park occurred recently (1998) and people still hunt in the surrounding area.

### *Data analysis*

Camera-trap rate was calculated as the number of photographs of a species divided by the number of trap-days per site. Trap-days were computed as the number of 24-h periods from deployment of camera until the film was used up or the camera was retrieved. Instances where the same species were captured by the same camera more than once within 1 h were excluded from trap rate calculation. This was a compromise between scoring the same individual multiple times and missing individuals (Rovero *et al.*, 2005) and is more conservative than other published studies (e.g. Kinnaird *et al.*, 2003). Camera-trap rate was used as a proxy for antelope abundance as camera-trap rates for Harvey's duiker were significantly correlated with population density as estimated from transect sightings in the same area (F. Rovero and A. R. Marshall, unpublished data; see also O'Brien, Kinnaird & Wibisono, 2003). We therefore used camera-trap rate as the response variable to vegetation and other habitat variables.

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Mean camera-trap rate was used for the Matundu transect where pairs of cameras were set at each 0.5-km interval. One data point was excluded following preliminary data exploration because of an outlying regression residual score for both species models. The excluded camera captured Harvey's duiker four times (trap rate: 0.059, no other antelope captured). Prior to model building, redundancy between habitat variables was tested for using Spearman rank correlation, whereby only one of any two variables that were significantly correlated was retained for further analysis (Table 1).

Generalized linear model (GLM) analysis (McCullagh & Nelder, 1989) was used to construct a model describing the relationship between camera-trap rate and habitat variables for each antelope species. Variables were not transformed prior to model building because this is achieved through the link function in GLM (Maindonald & Braun, 2003). A quasi-Poisson error distribution was assumed (using a logarithmic link function) as appropriate for proportional response variables and allowing for over-dispersion from a standard Poisson distribution (A. Zuur, personal communication; Zuur, Ieno & Smith, 2007). GLM was implemented in the computer package R (version 2.1.0; http://cran.r-project.org).

## Results

We obtained 663 independent photographs of four species of forest antelope (Table 2). Harvey's duiker was the most recorded species (n = 524), followed by suni (n = 99). There were insufficient data available for the habitat selection analysis for Abbott's duiker and bushbuck (15 and 25 captures, respectively). Moreover, images of bushbuck were captured at only one of the four study areas. No images of blue duiker were captured during the study. Therefore, habitat-use modelling was only carried out for Harvey's duiker and suni.

Harvey's duiker's camera-trap rate was positively and significantly related to small stem diversity and distance to the nearest village and negatively affected by visibility (Table 3). The model explained 70.11% of the deviance in camera-trap rate, and small stem diversity was the most significant variable (Fig. 2). Camera-trap rate for suni was negatively affected by the percentage of leaf-litter ground

**Table 2** Sampling details and camera-trap rate (number of captures) for forest antelope species for four areas in the Udzungwa Mountains

| Forest | Area (number of cameras) | Mean trap-days | Abbott's duiker | Harvey's duiker | Suni | Bushbuck |
|---|---|---|---|---|---|---|
| Mwanihana | Campsite 3 (4) | 62.8 | 0.005 (2) | 0.248 (59) | 0.081 (20) | 0 |
| Mwanihana | Mwanihana trail (5) | 61.2 | 0.004 (1) | 0.112 (37) | 0.071 (20) | 0 |
| Matundu | Ruipa (16) | 72.7 | 0.002 (2) | 0.291 (330) | 0.037 (42) | 0.022 (25) |
| Matundu | Lumemo (7)[a] | 78.3 | 0.017 (10) | 0.190 (98) | 0.035 (17) | 0 |

[a]Originally eight cameras but one malfunctioned.

**Table 3** Variables from generalized linear models of forest antelope habitat use as measured by camera-trap rate in the Udzungwa Mountains, Tanzania (n = 24, $^*P < 0.05$)

| | Harvey's | | Suni | |
|---|---|---|---|---|
| Variables | $z \pm$ SE | $P$-value ($z$) | $z \pm$ SE | P-value ($z$) |
| Canopy cover | −0.003 ± 0 | 0.419 | −0.008 ± 0.01 | 0.415 |
| Large tree (>10 cm DBH) density | −4.002 ± 8.69 | 0.652 | 27.28 ± 17.81 | 0.148 |
| Large tree (>10 cm DBH) diversity (*D*) | −0.018 ± 0.04 | 0.645 | −0.064 ± 0.08 | 0.452 |
| Medium tree (5–10 cm DBH) density | 7.034 ± 5.07 | 0.187 | −8.769 ± 10.69 | 0.426 |
| Medium tree (5–10 cm DBH) diversity (*D*) | 0.031 ± 0.04 | 0.455 | 0.075 ± 0.08 | 0.347 |
| Small stem (<5 cm D at 1 m) diversity (*D*) | 0.111 ± 0.04 | 0.02* | 0.175 ± 0.08 | 0.058 |
| Visibility | −0.015 ± 0.01 | 0.032* | 0.0004 ± 0.01 | 0.965 |
| Per cent leaf-litter | 0.005 ± 0.01 | 0.718 | −0.082 ± 0.03 | 0.008* |
| Distance to village (km) | 0.0001 ± 0 | 0.035* | −0.00002 ± 0 | 0.9 |

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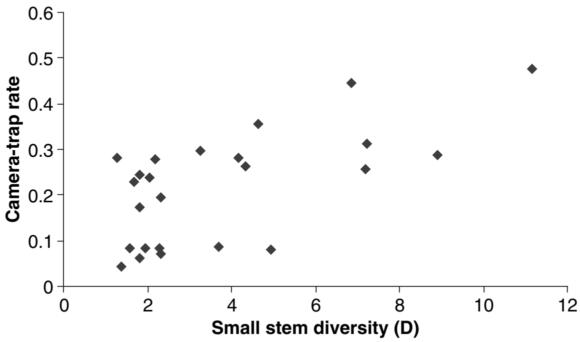


**Fig 2** Harvey's duiker camera-trap rate in the Udzungwa Mountains in relation to small stem diversity (*D*). The most significant variable in a generalized linear model

cover with the model explaining 65.13% of the deviance. The positive relationship between camera-trap rate and small stem diversity approached statistical significance for suni (Table 3).

## Discussion

### *Habitat selection by forest antelope*

The most significant variable indicated by the Harvey's duiker model was small stem diversity, which supports the prediction that plant species diversity is important to forest antelope (Perrin *et al.*, 2003). Together with the lack of a relationship between abundance and diversity of larger plants, this may indicate that this duiker is primarily feeding on small stemmed plants in the undergrowth. This suggestion fits well with the traditional classification of small antelope as concentrate selectors (Jarman, 1974), a view that has been shown not to hold for all duiker species (Bowland & Perrin, 1998; Plowman, 2002).

That distance to the nearest village was positively related to camera-trap rate for Harvey's duiker is likely to reflect the negative effects of human activity. Possibly, this result could also reflect natural habitat changes coincident with distance from village, as shifts in species composition may be independent of our measures of diversity and density. However, while we cannot rule out the effect of unmeasured habitat variables, we have observed snares, traps and abandoned skins within the National Park. This activity is likely to have been even greater until 1998 when settlements were still present near the study area in Matundu forest. Several studies have documented lower forest antelope abundance where hunting and trapping occur (Wilkie & Carpenter, 1999; Hart, 2000; Nielson, 2006) including those revealing a similar relationship between abundance and distance from human habitation as suggested here (Muchaal & Ngandjui, 1999; Noss, 1999).

The only significant relationship indicated by the model for suni was a negative effect of leaf-litter ground cover. Leaf-litter was negatively related to percentage cover of herbaceous and woody plants on the forest floor, which might in turn indicate preference for low, dense vegetation. The relationship with small stem diversity was similar to that for Harvey's duiker and may be interpreted similarly. Despite the fairly robust sample size for our analysis (number of photographs of suni per area = 17–42), it may be that by only recording and identifying small plant stems above 1 m height, we failed to take account of important habitat features for this small species.

Habitat use results were not entirely consistent with previous reports in the literature. Our models did not reflect the importance of canopy cover or large trees as the primary provider of food. This result is perhaps not surprising as studies documenting suni and *Cephalophus natalensis*, sister taxa to Harvey's duiker (Van Vuuren & Robinson, 2001), as feeding mainly on fallen leaves from canopy trees (Lawson, 1989; Bowland & Perrin, 1998) were carried out in dry coastal forests and, therefore, in habitat very different from that of our study. The visibility index was a negative significant variable in the Harvey's duiker model indicating a preference for dense vegetation. This does not concur with Dubost's (1979) finding that some other duiker species avoid high stem densities. However, in this case, visibility was not related to stem density and so other vegetative growth such as herbaceous plants and lianas are likely to be responsible for reducing visibility.

### *Camera-trap rate as a measure of habitat selection*

Camera-traps are widely and increasingly being used as a survey tool by conservationists and wildlife managers to investigate differences in abundance between broad habitat and land-use types (Kinnaird *et al.*, 2003; Jácomo *et al.*, 2004). This study has demonstrated clear associations between camera-trap rates and quantifiable habitat characteristics for forest antelope, thus showing, for the first time, the potential of camera-trapping for fine-scale habitat analysis (but see Di Bitetti, Paviolo & De Angelo, 2006). However, it must be emphasized that this method may not

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be applicable to rare species (at least over the short-term). We failed to obtain robust sample sizes for three of the five antelope species in the area.

In comparison with other methods, camera-traps have clear advantages including easier species identification, decreased time and costs associated with fieldwork and better representation of nocturnal and crepuscular species, such as suni and Abbott's duiker (Rovero *et al.*, 2005; Bowkett *et al.*, 2006).

There are problems in interpreting camera-trap rates even when precautions are taken to reduce multiple scoring (as in this study). It is often not possible to distinguish between scoring several individuals and regular use of a particular camera location by the same individuals. However, this distinction may not matter, if both measures reflect the relative importance of habitat components at different sites.

Measuring habitat use with camera-trap rates assumes that differences in trap rate represent selection of surrounding habitat rather than unmeasured microhabitat features such as paths or water sources. Potentially, animals may regularly visit unsuitable habitat to access an important resource. In this study, cameras were placed on animal paths; if these paths are used more often in dense vegetation (see Struhsaker, 1997), this could result in higher trap rates for those areas. Other census methods such as net drives (Noss, 1998) and territory mapping (Bowland & Perrin, 1994) may avoid this problem, but are far more invasive and usually more expensive.

### *Conservation implications and recommendations*

We were unable to quantify habitat use for the threatened Abbott's duiker. Recent surveys and opportunistic sightings indicate that this species is more common in moist forest above 1000 m, thus at higher altitudes than we generally sampled (A. E. Bowkett and F. Rovero, unpublished data; Rovero, Davenport & Jones, in press). Whether this difference is because of habitat requirements or the effects of hunting at lower altitudes requires further research. Data relevant to the conservation of this species are urgently needed (Moyer, 2003).

Our study area was not reflective of the different levels of hunting within the Udzungwas, as all sites were situated within a generally well-protected National Park. Nevertheless, the fact that distance from the nearest village was a significant variable in the model for Harvey's duiker suggests that Park management should take this potential effect into account when planning anti-poaching activities.

Despite the methodological caveats mentioned above, our approach proved useful to derive quantitative models of habitat use, which explain a large amount of the deviance in the data. These models help point to new areas of investigation concerning habitat use by antelope species in tropical forests. For example, the effect of invasive plant species and ongoing removal of firewood on small plant diversity also requires further research given our findings for Harvey's duiker. Additional data from a variety of habitat and disturbance levels, and for those species undersampled in this study, will be required to test and refine further our habitat use models.

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