# Distribution, habitat use and activity patterns of nocturnal small carnivores in the North Luangwa Valley, Zambia

Paula A. WHITE

## Abstract

Surveys of the diversity, distribution, habitat use and nocturnal activity patterns of small carnivores were conducted in a protected part of the North Luangwa Valley, Zambia, during three periods: dry season (September–November) 2003; dry season (September–November) 2004; and wet season (May–June) 2005. The first used direct-observation and camera-trap surveys across seven habitats, whereas the second and third took place in two forest habitats and used only camera-traps. Camera-traps were set over scented lures and operated nightly, during 17h30–05h30. In the first season, observations of animals were made while driving along 2,500 km (100 daylight hours) and 150 km (8 night-time hours) of dirt track. These first-period surveys detected 13 carnivore species. The camera-traps operated for 690 trap-nights exposing 315 frames, 62% of which contained an animal. Of the animals photographed ($n$ = 194), 68% ($n$ = 131) were carnivores, of 11 species in five families: Mustelidae, Herpestidae, Hyaenidae, Viverridae and Felidae. Viverrids accounted for nearly half (46%) of carnivores photographed, followed by mongooses (35%), hyaenas (13%), mustelids (4%) and cats (2%). No species of Canidae were camera-trapped, despite their confirmed occurrence in the area. Extreme daytime temperatures constrained camera-sensor operation to nights; thus, diurnal species were under-recorded. Species-specific differences observed in visitation times between habitats suggest differences in species activity patterns. During the second and third survey periods combined, camera-traps recorded 674 photographs of five carnivore species in the two forest habitats: mongooses (Bushy-tailed Mongoose *Bdeogale crassicauda* and Meller's Mongoose *Rhynchogale melleri*) were photographed most often (83%), followed by viverrids (genets *Genetta*, 9%; African Civet *Civettictis civetta*, 7%) and mustelids (Ratel *Mellivora capensis*, <1%). Within the two forest habitats, carnivore distribution, and both the timing and amount of visitation, varied by season. The highest visitation levels were in Hill Miombo in the wet season. The changing visitation rates through the night suggest that spotlighting (a popular nocturnal carnivore survey method, rarely conducted uniformly through the night) may bias detection and thus status assessments for some species.

*Keywords*: *Bdeogale crassicauda*, camera-trap, *Genetta*, Herpestidae, miombo woodland, *Rhynchogale melleri*, Viverridae, wildlife survey

## Distribution, utilisation de l'habitat et patrons d'activité des petits carnivores nocturnes dans la Vallée de Luangwa Nord, en Zambie

## Résumé

La diversité, la distribution, l'utilisation de l'habitat et les patrons nocturnes d'activité des petits carnivores ont été étudiés dans une partie protégée de la Vallée de Luangwa Nord, en Zambie, lors de trois périodes: 1) saison sèche (septembre–novembre) 2003, 2) saison sèche (septembre–novembre) 2004, et 3) saison humide (mai–juin) 2005. Durant la première saison, l'étude a été menée dans sept types d'habitats et était basée sur l'observation directe et l'utilisation de pièges photographiques, alors que pendant les deuxième et troisième saisons seuls des pièges-photos ont été utilisés dans deux habitats forestiers. Les appareils photographiques, associés à des leurres odorants, opéraient chaque nuit de 17h30–05h30. Durant la première saison, des observations directes d'animaux ont été faites lors d'inventaires effectués en voiture le long de 2'500 km (100 heures à la lumière du jour) et 150 km (8 heures pendant la nuit) de pistes en terre. L'étude a permis de détecter 13 espèces de carnivores. Les pièges-photos ont opéré durant l'équivalent de 690 nuits de piégeage, fournissant 315 clichés dont 62% d'entre eux contenaient un animal. Des animaux photographiés ($n$ = 194), 68% ($n$ = 131) étaient des carnivores appartenant à 11 espèces réparties en cinq familles taxonomiques: Mustelidae, Herpestidae, Hyaenidae, Viverridae, Felidae. Les viverridés représentaient presque la moitié (46%) de tous les carnivores photographiés, suivis par les mangoustes (35%), les hyènes (13%), les mustélidés (4%) et les félins (2%). Aucun canidé n'a été photographié malgré la confirmation de leur présence dans la zone d'étude. En raison des températures extrêmes durant la journée, le fonctionnement du senseur des appareils photographiques a été restreint aux périodes nocturnes, si bien que les espèces diurnes étaient sous-représentées. Les différences observées au niveau de l'heure des visites des pièges-photos suggèrent des différences interspécifiques dans les patrons d'activité. Lors des seconde et troisième périodes d'études combinées, les pièges-photos ont permis d'obtenir 674 photographies de cinq espèces de carnivores dans les deux habitats forestiers. Les mangoustes (Mangouste à queue touffue *Bdeogale crassicauda* et Mangouste de Meller *Rhynchogale melleri*) ont été photographiés le plus souvent (83%), suivis par les viverridés (genettes *Genetta*, 9%), Civette africaine *Civettictis civetta*, 7%) et les mustélidés (Ratel *Mellivora capensis*, <1%). A l'intérieur des deux habitats forestiers, la distribution des carnivores ainsi que l'heure d'occurence et le nombre de visites ont varié de manière saisonnière. Les niveaux de visite les plus élevés ont été observés dans le miombo collinéen durant la saison humide. Les variations dans les taux de visite durant la nuit suggèrent que les études nocturnes au phare (une méthode populaire pour recenser les carnivores nocturnes rarement conduite de façon uniforme durant la nuit) peuvent biaiser la détection et ainsi les évaluations du statut de certaines espèces.

*Mots clés*: *Bdeogale crassicauda*, forêt de miombo, *Genetta*, inventaire faunistique, mangoustes, piège-photographique, *Rhynchogale melleri*, viverridés

## Introduction

Many African small carnivore species are inconspicuous nocturnal forest dwellers (Ewer 1973, Smithers 1983) that are difficult to detect: as a consequence, little is known about them. Nevertheless, forest carnivores are of interest both from an academic standpoint and in light of global trends prioritising resource extraction and use without adequate consideration of environmental impacts (Greene 1988). It is often assumed that by virtue of their size, small carnivores are less prone to direct persecution than are the larger species. However, illegal trade in bush meat and skins (e.g. Colyn *et al*. 1988, Ray *et al*. 2002, Golden 2009, Shepherd & Shepherd 2010, Dolch 2011), land conversion and deforestation are all current threats to at least some small African carnivore species (Crooks 2002, Kauffman *et al*. 2007, Dunham & Gaubert 2008). The extent to which human practices threaten regional populations of small carnivores is only beginning to be investigated (Colón 2002, Crooks 2002, Azlan 2003, Kauffman *et al*. 2007, Cheyne *et al*. 2010a, Mathai *et al*. 2010, Wilting *et al*. 2010). The paucity of baseline data about many small carnivore species hinders assessment of impacts and development of appropriate conservation strategies (Greene 1988, Ray *et al*. 2002).

Camera-traps are growing in popularity as an invaluable tool for detecting secretive species (e.g. Foresman & Pearson 1998, Cutler & Swann 1999), replacing more invasive types of research such as radio-collaring. Increasingly, camera-traps are documenting first records of little-known carnivores in little-known ecosystems (Brink *et al*. 2002, Goldman & Winther-Hansen 2003, Rovero *et al*. 2006, Charoo *et al*. 2010, Cheyne *et al*. 2010b, Jenks *et al*. 2010, Moqanaki *et al*. 2010), and may clarify species abundance (Gerber *et al*. 2010). For example, Bushy-tailed Mongoose *Bdeogale crassicauda*, a species previously considered rare (Taylor 1987), was among the most frequently camera-trapped species at several localities in Tanzania's Eastern Arc Mountains (De Luca & Mpunga 2005). Camera-traps can also be used to identify individuals (Karanth & Nichols 1998, Sequin Larrucea *et al*. 2007), and to quantify activity patterns (Sequin Larrucea *et al*. 2007) or behaviour (Picman & Schriml 1994). For species about which almost nothing is known, even short-term camera-trapping studies (Charoo *et al*. 2010, Cheyne *et al*. 2010b) or data accrued incidentally (González-Maya *et al*. 2009) can contribute significant insight concerning group size, activity pattern, habitat use and geographic range.

Zambia's Luangwa Valley has a high species richness (Pomeroy 1993, Barnes 1998, BirdLife International 2000, WWF-SARPO 2003) and lies adjacent to areas of known high species endemism, e.g. Bangweulu swamp (Zambia), Nyika plateau (Malawi), the Southern Highlands (Tanzania) and the Albertine Rift (Democratic Republic of Congo) (White 1983). As a transverse offshoot of the greater African Rift Valley system, the Luangwa Valley is known to contain many endemic forms (Ansell 1960, 1978). Twenty-two species of carnivores have been reported from this region (Table 1), within six families: dogs (Canidae), mustelids (Mustelidae), mongooses (Herpestidae), hyaenas (Hyaenidae), civets and genets (Viverridae) and cats (Felidae) (Kingdon 1977, 1997, Ansell 1978, Skinner & Smithers 1990).

The Luangwa Valley is experiencing rapid human population growth and rural expansion (Chenje & Johnson 1994) resulting in environmental change (Stuart *et al*. 1990, Dalal-Clayton & Child 2003, WWF-SARPO 2003). Apart from a few studies that focused on larger species (Yamazaki 1996, Yamazaki & Bwalya 1999, Anderson *et al*. 2011), the ecology of Luangwa Valley's small carnivore community is unknown. The Luangwa Valley is just one of many areas in Africa lacking a long-term monitoring programme focused on small carnivore conservation. The present study therefore surveyed carnivores by camera-traps and direct observations in the dry and wet seasons of 2003–2005. It took place in an area of protected, intact habitat with minimal human disturbance. Thus, its results provide a starting point for future studies, especially in other regions within and beyond the Luangwa Valley that are experiencing rapid human population growth, rural expansion and resultant anthropogenic change.

## Methods

*Study area*

The study took place in the North Luangwa National Park (11°47′S, 32°10′E), Luangwa Valley, north-eastern Zambia, south-central Africa (Fig. 1). The Luangwa Valley is a transverse extension of the greater African Rift Valley system, bordered northwest by the Muchinga Escarpment and southeast by Malawi's Nyika Plateau. To the northeast lie Tanzania's Eastern Arc Mountains. The Luangwa River arises from the Mafinga Mountains at about 2,400 m a.s.l. It is fed by the perennial Mwaleshi River that originates in the Muchinga Escarpment, and by several other rivers that flow seasonally from the escarpment and plateau. The broad, silt-laden Luangwa River cuts a sandy swath through the Valley bottom on its way to join the Zambezi River in the south.

Vegetation throughout the region is predominantly Mopane *Colophospermum mopane* woodland and miombo *Brachystegia* woodland (MTENR 2005). On a more localised scale, different vegetation types occur patchily throughout the Luangwa Valley, especially in relation to elevational changes and topographic microclimates (Smith 1998) (Fig. 2).

During the single long rainy season from December to April, the Luangwa River reaches full flood. Using each month's average daily mean, the coolest temperatures (10 °C) occur in June and July, after the rains. From that point, temperatures rise steadily, peaking in October at 37 °C. Outlying water sources have dried up by that time, so herbivores and carnivores alike congregate along the rivers to await the onset of the rains in late November.

*Sampling methodology*

Part I. All surveys in 2003 were conducted during the dry season (September–November). Surveys consisted of direct searches for animals during daylight driving circuits and

**Table 1.** Number of camera-trap and direct-observation records of each carnivore species* in North Luangwa National Park, Zambia, during 2003–2005.

| Species | Number of records | | | |
|---|---|---|---|---|
| | Direct observation (daytime) | Direct observation (night-time) | Camera-trap Phase I | Camera-trap Phase II |
| Canidae | | | | |
| Side-striped Jackal *Canis adustus* | 0 | 0 | 0 | 0 |
| African Wild Dog *Lycaon pictus* | 0 | 0 | 0 | 0 |
| Mustelidae | | | | |
| Honey Badger *Mellivora capensis* | 0 | 0 | 5 | 2 |
| African Clawless Otter *Aonyx capensis* | 0 | 0 | 0 | 0 |
| Herpestidae | | | | |
| Egyptian Mongoose *Herpestes ichneumon* | 0 | 0 | 0 | 0 |
| Common Slender Mongoose *Herpestes sanguineus* | 11 | 0 | 0 | 0 |
| Common Dwarf Mongoose *Helogale parvula* | 2 | 0 | 0 | 0 |
| Banded Mongoose *Mungos mungo* | 1 | 0 | 0 | 0 |
| Marsh Mongoose *Atilax paludinosus* | 0 | 0 | 0 | 0 |
| White-tailed Mongoose *Ichneumia albicauda* | 0 | 0 | 8 | 0 |
| Meller's Mongoose *Rhynchogale melleri* | 0 | 1 | 13 | 162 |
| Bushy-tailed Mongoose *Bdeogale crassicauda* | 0 | 0 | 21 | 287 |
| Unidentified Meller's/Bushy-tailed Mongoose | 0 | 0 | 3 | 114 |
| Hyaenidae | | | | |
| Spotted Hyaena *Crocuta crocuta* | 2 | 5 | 17 | 0 |
| Viverridae | | | | |
| Genet *Genetta* | 0 | 2 | 16 | 62 |
| African Civet *Civettictis civetta* | 0 | 0 | 45 | 47 |
| Felidae | | | | |
| Wild Cat *Felis sylvestris* | 0 | 0 | 0 | 0 |
| Serval *Felis serval* | 0 | 0 | 0 | 0 |
| Caracal *Felis caracal* | 0 | 0 | 1 | 0 |
| Leopard *Panthera pardus* | 0 | 1 | 1 | 0 |
| Lion *Panthera leo* | 4 | 1 | 1 | 0 |
| Cheetah *Acinonyx jubatus* | 0 | 0 | 0 | 0 |
| **Total** | **20** | **10** | **131** | **674** |

*All species potentially present, based on historical information, are listed. Four genets are known from Zambia: Miombo Genet *G. angolensis*, South African Small-spotted Genet *G. felina*, Common Small-spotted Genet *G. genetta* and Rusty-spotted Genet *G. maculata* (Gaubert *et al*. 2005); the historical records from the Luangwa Valley, of 'Blotched Genet *Genetta tigrina*' and 'Servaline (or Pardine) Genet *Genetta servalina*', would need re-evaluation in the light of taxonomic and nomenclatural change.

night drives using spotlights (both at a speed of 25 km/hr), and camera-trapping at scented lures. Camera-trap stations were situated along transects in each of seven habitat types that spanned an elevational gradient from the Luangwa River in the Valley floor (600 m) to near the top of the Muchinga Escarpment (1,177 m). Seven habitats defined based on predominant vegetation type (Fig. 2) were surveyed: 1) Escarpment Forest (dry, evergreen), 2) Hill Miombo, 3) Wooded Grassland Mosaic, 4) Valley Riverine Complex (dry), 5) Valley Riverine Complex (perennial stream), 6) *Combretum*–*Terminalia* Woodland and 7) Secondary Annual Grassland (Fig. 1).

Part II. Two habitats (Escarpment Forest and Hill Miombo) were intensively camera-trapped during a three-month dry season (September–November 2004) and a two-month wet season (May–June 2005). The time- and date-stamped photographs were used to examine seasonal differences in species composition and visitation (activity) patterns within and between the two forest habitats.

*Camera-trap stations*

Camera-trap stations were located 10–50 m from roads, 0.5–1.0 km apart, and at least 1.0 km from transitions to other habitats. In Part I, ten camera-traps were set for 8–11 days along a transect within a homogenous habitat type, then moved to a new transect-line in a different habitat. During Part II, five camera-traps were operated at evenly spaced static locations in each of the two forested habitats for the entire dry (2004) and wet (2005) sampling period (Fig. 1). A 'trap-night' was the equivalent of one camera set for one night (i.e. a 12-hr period).

Each camera-trap station consisted of a remotely activated 35 mm instamatic camera with electronic flash (Trailmaster TM35-1) coupled to a motion/heat detector (Trailmaster TM550) (Trailmaster Inc., Lenexa, Kansas). The camera was set to be triggered by animals within 20 m and a 150° radius of the camera. In addition, a 5-min delay was set to avoid repeatedly photographing an individual lingering at a scent station. More than 85% of the time-consecutive photographs separated by 10 minutes or more contained different species. An

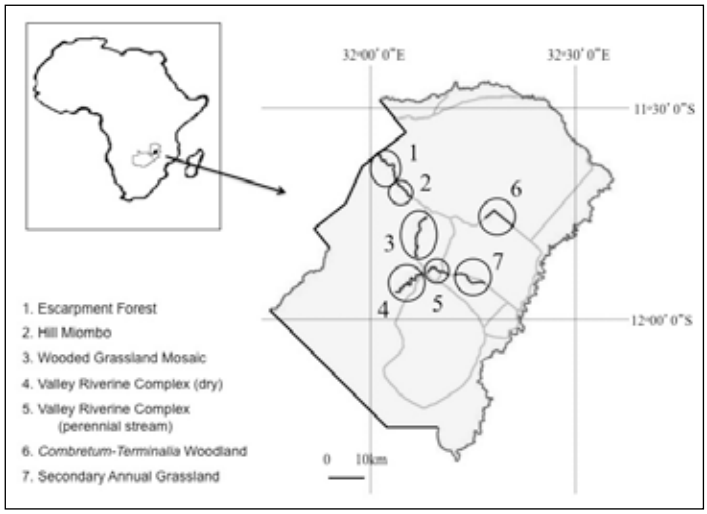


**Fig. 1.** North Luangwa National Park, Zambia, showing camera-trapping transect locations and associated habitat types. Park borders designated by irregular lines are rivers. Interior grey lines are dirt roads. Transects 1–7 were sampled during the dry season 2003. Transects 1–2 were resampled during the dry season 2004 and the wet season 2005.

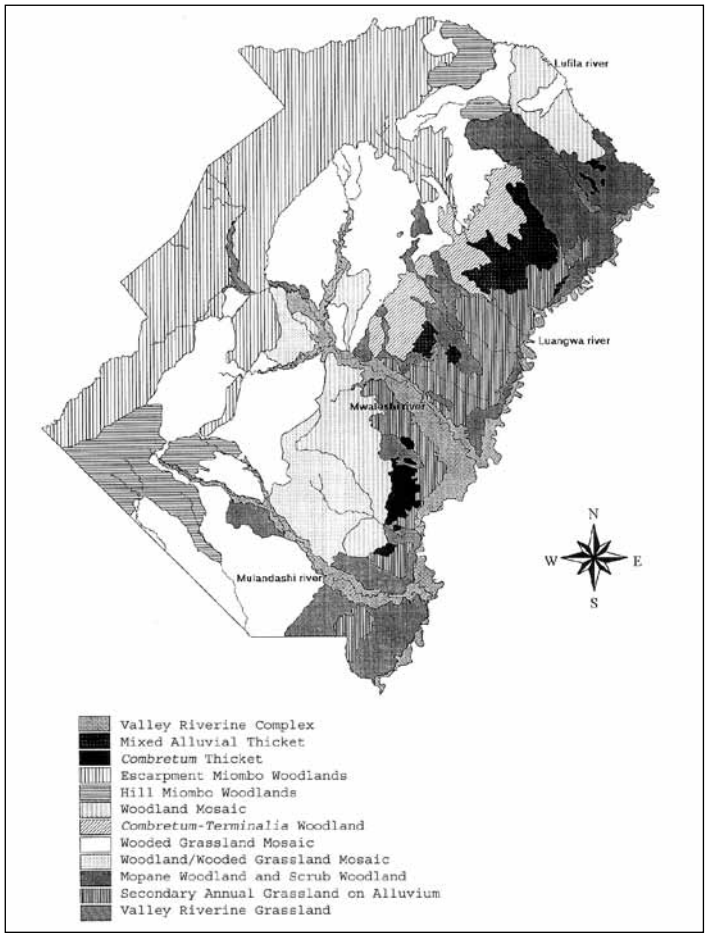


**Fig. 2.** Vegetation map of North Luangwa National Park, Zambia.

additional time of 5 minutes was added to create a 15-minute latency period between notionally independent 'visits'. Thus, a photograph of a species taken at least 15 minutes after the preceding one was counted as a new 'visit'.

Camera-trap systems were secured to trees at a height of 1.5 m and aimed towards a scent lure of minute amounts (<¼ teaspoon) of rotten meat juice and honey/jam juice applied with a spray bottle to a rock or tree-trunk at ground level. The lures produced a scent but did not constitute a significant amount of food even for a small carnivore, as evinced by the short (<10-min) duration of most visits. This combination of scents was selected in efforts to attract carnivorous, frugivorous and omnivorous species. Scents were refreshed daily. Cameras were checked each day around midday and film and batteries replaced as needed.

Exposed frames were examined, visitation times tallied, and animals identified to species when possible. Bushy-tailed Mongoose and Meller's Mongoose *Rhynchogale melleri* are similar enough on film as to hinder reliable distinction, so an 'unidentified mongoose' category was included when recording number of visits, and results of activity patterns for these mongoose species were combined. Similarly, four species of genet *Genetta* with relatively small external morphological differences inhabit Zambia (Table 1), so genet photographs were identified only to genus. Time-stamp photographs were used to analyse visitation times (activity patterns) by taxon.

## Results

*Part I. 2003 dry season*

During the 2003 dry season, daylight driving surveys along 2,500 km of dirt track during 100 hours provided 20 direct observations of carnivores, and night-time surveys along 150 km of dirt track during 8 hours generated 10 observations. In total, eight species of carnivores were detected during driving surveys (Table 1).

Camera-traps were deployed along 65 km of roads and rivers through seven habitat types during 690 trap-nights (80–110 trap-nights per habitat) (Table 2). The total number of visits varied by habitat type (mean = 46 visitors per habitat, range 26–69) (Table 2). Escarpment Forest and Secondary Annual Grassland had the highest visitation, Valley Riverine Complex (dry) and *Combretum–Terminalia* Woodland the lowest. Of the 315 camera-trap photographs, 194 (62%) contained an animal. Of the animals photographed, 131 (68%) were carnivores, of 11 species.

Combined, all survey methods detected 13 carnivore species from five families (Tables 1–2). The remaining photographs ($n$ = 63) featured non-carnivore species, most commonly Bush Duiker *Sylvicapra grimmia*, also Aardvark *Orycteropus afer*, African Elephant *Loxodonta africana*, Plains Zebra *Equus quagga*, Bush Pig *Potamochoerus larvatus*, Cape Buffalo *Syncerus caffer* and Impala *Aepyceros melampus*.

Dry season visitation patterns varied widely between habitat types, however two general patterns emerged (Fig. 3). Within the Escarpment Forest and Secondary Annual Grasslands, visitation was relatively uniform throughout the nocturnal hours with only minor peaks in activity in the early- and midnight hours, respectively. In contrast, within all other habitats sampled, highest levels of visitation occurred in the early evening, immediately or shortly after dark. Of the latter group, most showed a gradual tapering off over the course of the night, although a small secondary peak in activity just prior to

**Table 2.** Habitat features, camera-trapping effort and number of visits for each transect during Part I (dry season 2003) of this study in North Luangwa National Park, Zambia.

| Transect | Habitat Type | Elevation range[1] (m) | Number of camera-trap-nights | Number of visits |
|---|---|---|---|---|
| 1 | Escarpment Forest | 1,177–1,026 | 100 | 69 |
| 2 | Hill Miombo | 975–758 | 90 | 50 |
| 3 | Wooded Grassland Mosaic | 717–643 | 110 | 42 |
| 4 | Valley Riverine Complex (dry) | 640–629 | 80 | 26 |
| 5 | Valley Riverine Complex (perennial stream) | 636–608 | 100 | 43 |
| 6 | *Combretum–Terminalia* Woodland | 658–687 | 100 | 27 |
| 7 | Secondary Annual Grassland | 599–630 | 110 | 58 |

[1] The lowest and highest points in the transect.

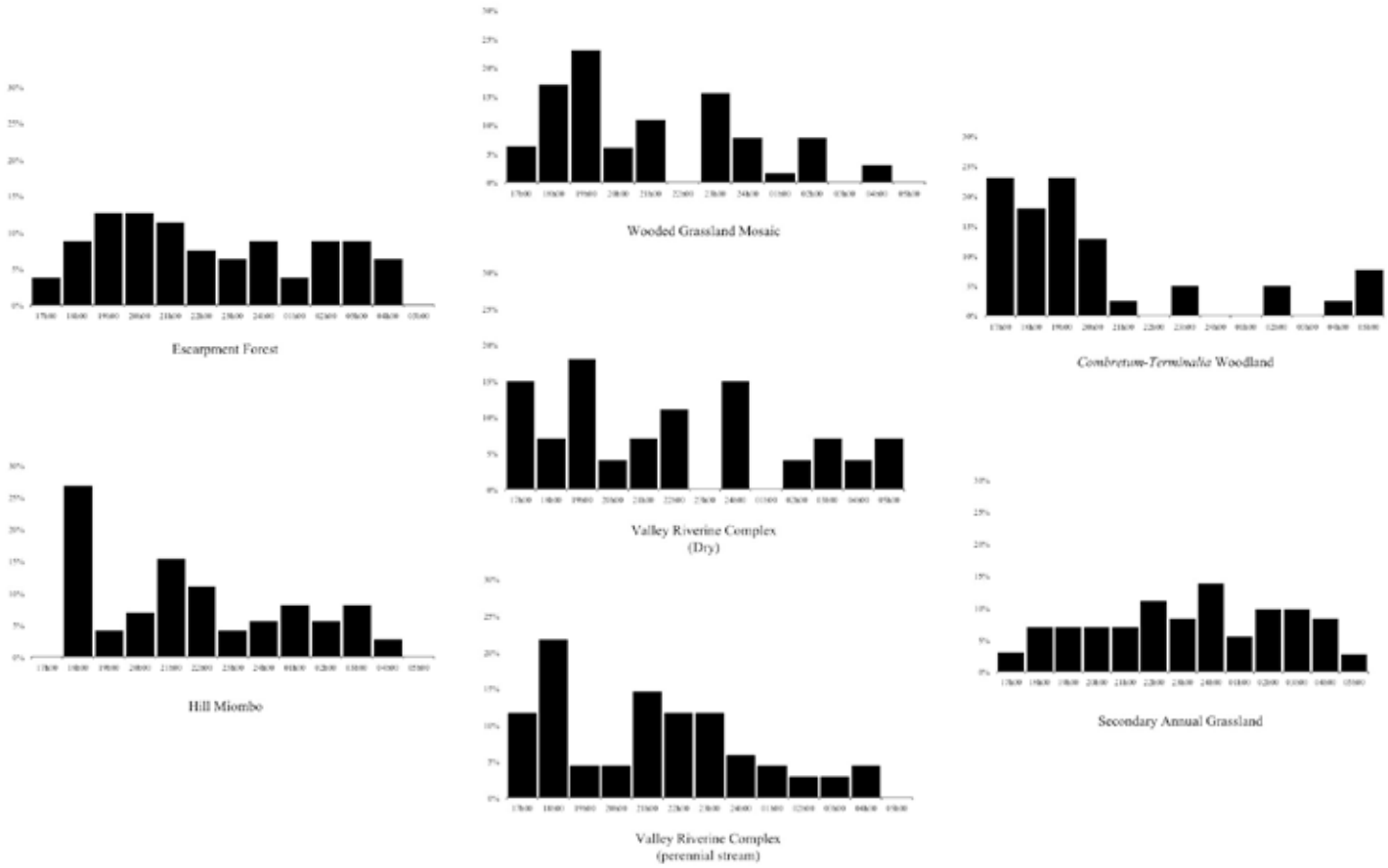


**Fig. 3.** Patterns of nocturnal carnivore visits to camera-trap stations in each of seven habitat types sampled during the dry season 2003 in North Luangwa National Park, Zambia. For each habitat, results shown are for all carnivore species combined.

dawn was not uncommon (Fig. 3). Differences in activity patterns were attributed to variable species composition among the different habitat types.

*Part II. Species composition in two forest habitats*

Of 392 visits recorded to the Escarpment Forest camera-traps, the most frequently photographed visitors were Meller's Mongoose and Bushy-tailed Mongoose combined (Table 3). These were also the most-photographed visitors in Hill Miombo. However, a larger percentage of the 282 total visits in Hill Miombo comprised other species, including genets and African Civet *Civettictis civetta* (Table 3). Genets were recorded more often in the wet season than in the dry, in the Hill Miombo 17× so, in the Escarpment Forest 2.5× so. Civets were photographed in both forest types during the dry season, but only in the Hill Miombo during the wet, where they were recorded 7× more often than during the dry. Ratels *Mellivora capensis* were detected very rarely in the Hill Miombo, and not at all in Escarpment Forest (Table 3).

*Seasonal variation in visiting patterns*

Within each of the two forest habitats, wet- and dry-season visiting patterns were compared (Fig. 4).

Meller's and Bushy-tailed Mongooses combined showed relatively uniform nocturnal visit patterns, becoming active shortly after dusk (18h00–19h00) and visiting often until tapering off just before dawn (Fig. 4). In both forest types, visits were much more frequent during the wet season than in the dry.

**Table 3.** Occurrence of small carnivores on photographs in each of two forest habitats in North Luangwa National Park, Zambia, dry season 2004 and wet season 2005.

| Species | Number of visits | | | |
|---|---|---|---|---|
| | Escarpment Forest | | Hill Miombo | |
| | Dry | Wet | Dry | Wet |
| *Rhynchogale melleri* | 33 | 76 | 9 | 44 |
| *Bdeogale crassicauda* | 50 | 138 | 11 | 88 |
| Unidentified *Rhynchogale/Bdeogale* | 10 | 55 | 7 | 42 |
| *Genetta* | 7 | 18 | 2 | 35 |
| *Civettictis civetta* | 5 | 0 | 5 | 37 |
| *Mellivora capensis* | 0 | 0 | 1 | 1 |
| **Total** | 105 | 287 | 35 | 247 |

Additionally, during the wet season in Hill Miombo, mongooses showed a sharp peak in visits around 21h00 (Fig. 4).

Genets were active early in the evening, visiting already at dusk when camera-traps began operating, and continuing throughout the night. Visiting distinctly peaked at 20h00–21h00 and at 02h00–03h00. Genets made more visits in both habitats during the wet than in the dry season (Fig. 4). In both habitats, the largest peaks in visiting were consistently around 20h00 and 02h00, although during the wet season genets visited in the Hill Miombo during other times as well.

African Civet showed polymodal nocturnal visiting during the dry season, beginning only after total darkness (19h00–20h00) with secondary peaks at 00h00–01h00 and 03h00–04h00, tapering off abruptly in the hours before dawn. During the wet season, Civets visited earlier in the evening than in the dry season and visited throughout the night hours with the exception of a lull around 21h00 (Fig. 4).

All species showed the highest visitation levels in the Hill Miombo during the wet season, when they remained relatively active throughout the night. Throughout the year, both genets and African Civet showed nightly lulls following polymodal peaks of activity.

## Discussion

Remote cameras proved effective in detecting nocturnal small carnivores in the Luangwa Valley, in particular viverrids and mongooses in densely vegetated habitats. Scent stations worked well to attract hyaenas and mustelids within camera range, but few pictures of cats, and none of canids were obtained. Methodology was similar across all habitats, thus potential biasing effects, e.g. camera-avoidance by species or individuals, or the effects of roads, were relatively constant. Overall, 60% of carnivore species previously reported from the region were detected by camera-traps and driving surveys combined over a 2-month dry season.

Time constraints on camera operation precluded detection

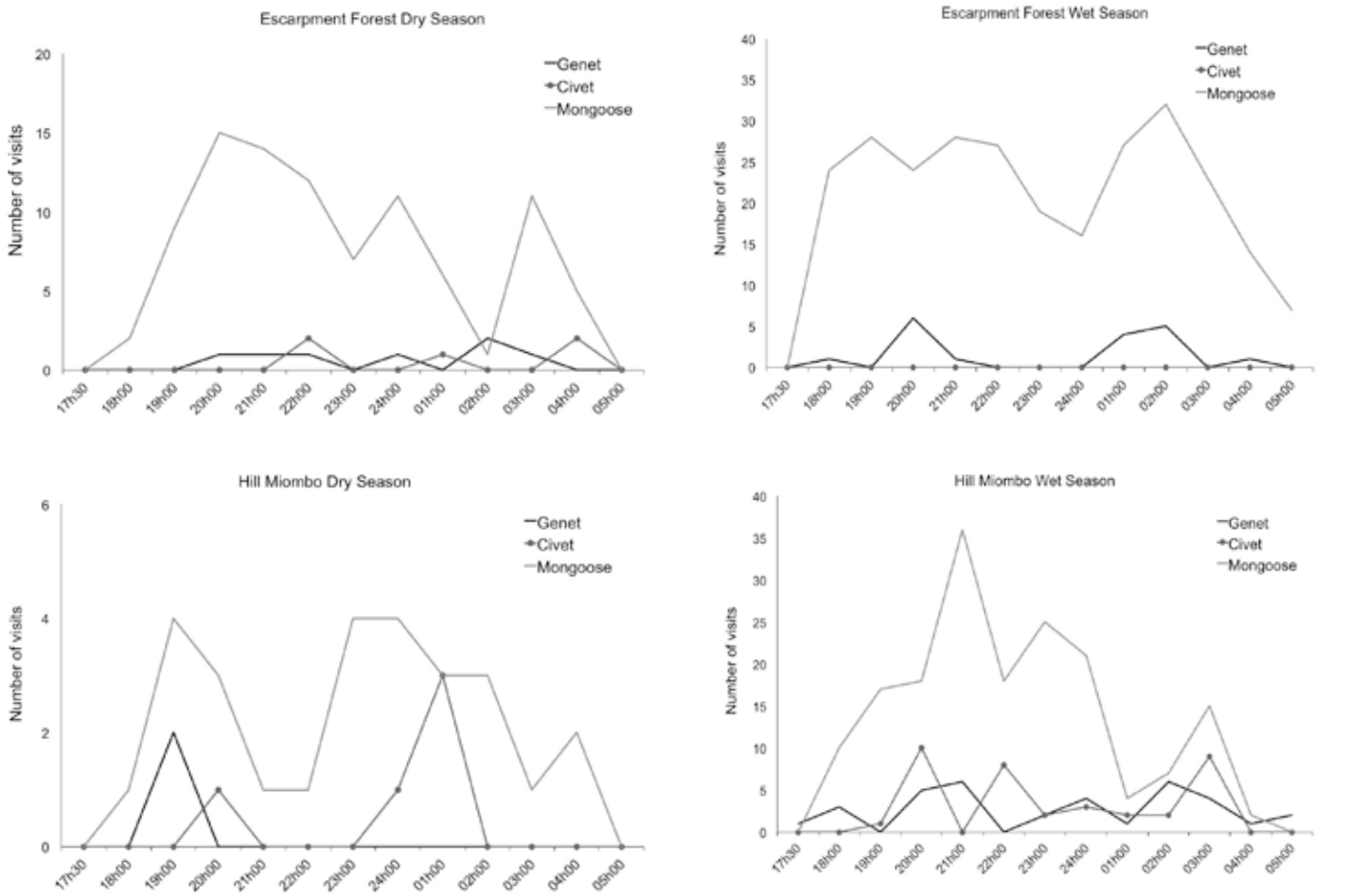


**Fig. 4.** Comparison of nocturnal visits to camera-traps during dry and wet seasons for all small carnivore species photographed within each of two forest habitats in North Luangwa National Park, Zambia.

of species active only by day. However, this does not explain the paucity of visits by larger ground-dwelling carnivores active at night, i.e. Lion *Panthera leo*, Leopard *Panthera pardus* and Side-striped Jackal *Canis adustus*. The Luangwa Valley holds about 500–600 Lions (PAW own data) and high densities of Leopards (Ansell 1960, Nowell & Jackson 1996). Cat presence was evidently not accurately represented by camera-traps, perhaps reflecting low appeal of the scents used. In contrast, African Wild Dogs *Lycaon pictus* are relatively few, and Side-striped Jackals have declined drastically over the past 30 years (A. Carr verbally 2005), so the lack of canid detections perhaps reflects their local rarity. The cause of Jackal decline is unknown. It might relate to disease transfer from Domestic Dogs *Canis familiaris*, which have increased dramatically in the Luangwa Valley during the past 10+ years (PAW own obs.).

Those species detected varied in the amount and pattern of visitation by habitat type. Camera stations were set >5 km from the nearest human dwellings, rendering activity patterns unlikely to be influenced by people as might be expected of small carnivores for example given the opportunity of scavenging on camp-site scraps. Excepting this study's night-surveys, park roads were closed to traffic after dark. Furthermore, scent lures were presented systematically, so any effects they may have had on carnivore visitation patterns should be uniform across all sampling stations. Differences in overall visitation patterns between habitats were attributed to species composition, although lunar phase may have also influenced predator movements (Waser 1980). Time-stamped photographs provided activity patterns for each species (for mongooses and genets, for aggregates of species). Consideration of species-specific activity times is important in designing spotlight surveys, because survey times may bias detection and abundance estimates if they are routinely conducted during a period of low activity for a particular species. However, activity patterns of partly arboreal and scansorial species may not be adequately represented when relying on camera-traps that detect ground-level movements.

Further dissection of mongoose and genet visitation data might detect differences in activity patterns between sympatric species. More detailed analyses of species activity times might lend evidence of temporal niche partitioning (Pianka 1969) as a mechanism reducing competition between the Luangwa Valley's sympatric carnivores. Temporal partitioning can facilitate coxistence among similar-sized sympatric carnivores (Ray 1997, Fedriani *et al*. 1999, Karanth & Sunquist 2000). However, Waser (1980) commented that overlap in both preferred vegetation types and foraging times within small nocturnal carnivore communities was not unusual. Likewise, the large overlaps of foraging times among the small carnivores inhabiting the Luangwa Valley's forests were possibly facilitated by the use of different types or sizes of prey (see Bothma *et al*. 1984, Sunquist *et al*. 1989, Karanth & Sunquist 2000, Walker *et al*. 2007).

Luangwa Valley's forests provide a year-round home to several species of nocturnal small carnivores, at least Bushy-tailed Mongoose, Meller's Mongoose, genets and African Civet. In the north of its range, Bushy-tailed Mongoose co-occurs with genets, White-tailed Mongoose *Ichneumia albicauda* and Zorilla *Ictonyx striatus* (Sale & Taylor 1970), in coastal forests with African Civet (Taylor 1986), and in Tanzania's Eastern Arc Mountains, with many nocturnal small carnivores including Marsh Mongoose *Atilax paludinosus*, Meller's Mongoose, Jackson's Mongoose *Bdeogale jacksoni*, White-tailed Mongoose, Servaline Genet *Genetta servalina*, Rusty-spotted Genet, Common Small-spotted Genet, African Civet, African Palm Civet *Nandinia binotata* and Ratel (De Luca & Mpunga 2005). The present study confirmed Bushy-tailed Mongoose co-occurrence with African Civet and genets in its western-central range, and is one of very few documented associations of it with Meller's Mongoose (see De Luca & Mpunga 2005).

While Bushy-tailed Mongoose was observed directly only once, it was among the most frequently photographed species in both the Escarpment Forest and Hill Miombo Forest communities. Similarly, it was the most frequently camera-trapped carnivore in the montane and lowland forests of Tanzania's Eastern Arc Mountains (De Luca & Mpunga 2005, Hoffman 2008), and uses a wide variety of other habitat types (Taylor 1987). The even lesser-known Meller's Mongoose is usually associated with woodland (Kingdon 1997), but has been photographed in montane bamboo forest and open wooded grassland in Tanzania at an altitude of 1,850 m (De Luca & Mpunga 2005). The present study recorded Meller's Mongoose in an altitudinal range of 750–1,175 m in Luangwa Valley, within that reported by Kingdon (1997).

Both Bushy-tailed and Meller's Mongooses are generally perceived as uncommon, yet in this study were frequently camera-trapped. This adds to the small carnivore conservation importance of Miombo Woodlands, which are among the earth's most biologically valuable and diverse ecoregions (Rodgers *et al*. 1996, Olson & Dinerstein 1998) with a plant community of particular importance to humans and other animals (Frost 1996, Barnes 1998, Williams *et al*. 2007, Munishi *et al*. 2010). Throughout Africa, Miombo Woodlands are heavily used for resource extraction by humans (Misana *et al*. 1996, Mapaure & Campbell 2002), but well-managed forests can support many small carnivores of many species (Wilting *et al*. 2010). Changes in carnivore community structure can have profound impacts on ecosystem dynamics (Terborgh 1988, Crooks & Soulé 1999), so studies examining species composition in relation to habitat perturbations help detect and document changes, and design regionally-effective conservation strategies (Kauffman *et al*. 2007, Mathai *et al*. 2010).

*Future studies*

Further analysis of this study's photographs will allow more positive identifications among similar-looking species (genets, and Bushy-tailed and Meller's Mongooses), and thus more detailed information on species within each sampled habitat. Re-evaluation of species-level visitation data may suggest differences in activity patterns that indicate temporal niche partitioning. This could help explain how similarly-sized mongooses and genets, respectively, reduce competition, especially during the dry season when resources are less abundant. GIS mapping of species locations will be used to analyse carnivores' microhabitat use. Camera-trapping throughout the 24-hr period would allow closer to complete documentation of the Luangwa Valley's small carnivore community. Surveying sites under different land-use regimes would clarify impacts of anthropogenic perturbations on the Luangwa Valley's carnivore

species. For species with individually unique coat patterns (African Civet, genets, Spotted Hyaena), photographic capture–recapture may provide insights on short- and longer-term spatial-use patterns and on density. For species not individually recognisable, occupancy surveys (MacKenzie *et al*. 2002) can estimate abundance more reliably than 'Relative Abundance Indices', by incorporating detection probabilities (MacKenzie *et al*. 2002, Linkie *et al*. 2007, Ancrenaz *et al*. 2012).

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**Center for Tropical Research,**
**University of California,**
**Los Angeles, 90095 U.S.A.**
**E-mail: paw@carnivoreconservation.com**