Ecology and Conservation of the African Golden Cat *Caracal aurata*

By

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Abstract

The African golden cat Caracal aurata, hitherto almost unstudied, is Africa's only forest-dependent felid. As such, it has the potential to act as both an indicator and flagship species for Africa's rainforests, which face threats from rapid development, exploitation, deforestation, human population increase, and bushmeat hunting. I collected camera trap and scat data over four years (2010 – 2013) in the central African country of Gabon to assess the impact of these threats on golden cat populations, as well as gain insight into the behavioural ecology of the species. I used spatially-explicit capture-recapture models to estimate population density of golden cats across five sites differing in human-land use, including two protected areas, two logging concessions, and a site with subsistence bushmeat hunting. Density was highest at the undisturbed protected site (16.23 individuals per 100 km2) and lowest at the hunting site (3.8 individuals per 100 km2), with evidence of the latter being a result of wire snare use. The logging concessions supported important populations of golden cats (10.18 - 12.84 individuals per 100 km2), suggesting that areas under concessions can be included within the conservation estate, provided they are operated under a sound management plan.

Golden cats occur in sympatry with leopards Panthera pardus in most of their range and there is evidence that leopards compete with, and prey on, golden cats, potentially limiting golden cat populations. In areas of sympatry, golden cat activity was cathemeral, but differed significantly in areas where leopards have been extirpated by people, displaying mostly nocturno-crepuscular activity. This provides evidence of behavioural plasticity in response to differing guild structure, supporting the mesopredator release hypothesis that mid-ranking predators respond to the removal of apex predators. Such behavioural shifts likely facilitate resource acquisition and avoidance of other threats, such as humans.

Where the two species co-occur, their shared use of trails leads to high spatial overlap. However, at the finer spatio-temporal scale, golden cats generally avoided camera trap stations until at least one day after a leopard had gone past. Food niche overlap between the two species was low (0.18, where 0 is no overlap and 1 is complete overlap), with golden cats and leopards mostly consuming rodents and ungulates, respectively. I conclude that mechanisms of co-existence between the two felids include fine-scale reactive avoidance by golden cats, and food niche segregation. This research reveals that co-existence between competing species can happen at a fine-scale, and that broad-scale displacement of mesopredators need not occur. Mesopredators may adapt to human-induced changes in dominant species' ecology and behaviour in order to persist in the face of disturbance.

Preface

The fieldwork described in this thesis was carried out by the author in central Gabon from June 2010 until November 2013, through the School of Life Sciences, University of KwaZulu-Natal, Westville campus. Supervision was provided by Prof. Rob Slotow, Prof. David Macdonald and Dr. Luke Hunter. Additional data was provided from studies in Uganda for use in comparative analyses.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution with the exception of chapter 4. The chapter 4 concept was originally developed as a diploma project of B. Mugerwa (Postgraduate Diploma in International Wildlife Conservation Practice at the University of Oxford), that was supervised by myself and with a large part of data used being from the data I collected. Following the submission of the diploma project, I then re-analysed the original data after adding in additional data, additional analyses, and revised the concept and redrafted the text for submission as part of this thesis.

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Declaration 1 - Plagiarism

I, Laila Bahaa-el-din, declare that

1) The research reported in this thesis, except where otherwise indicated, is my original research.

2) This thesis has not been submitted for any degree or examination at any other university.

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Declaration 2 - Publications

Publication 1 (Chapter 2)

Bahaa-el-din, L., Henschel, P., Butynski, T. M., Macdonald, D. W., Mills, D., Slotow, R., & Hunter, L. (2015). The African golden cat *Caracal aurata*: Africa's least-known felid. *Mammal Review*, *45*(1): 63-77.

Author contributions:

LB collected and processed the data, and designed and wrote the paper. DM collected data; PH, TMB, DWM, DM, RS & LH provided valuable comments on the manuscript.

Publication 2 (Chapter 3)

Bahaa-el-din, L., Sollmann, R., Hunter, L., Slotow, R., Macdonald, D.W. & Henschel, P. (in review). The effects of human-land use on Africa's only forest dependent cat: the African golden cat. Submitted to *Biological Conservation.*

Author contributions:

LB collected data, processed and analysed the data, and designed and wrote the paper. R Sollmann provided data analysis support and comments on the manuscript. LH, DWM, R Slotow & PH provided valuable comments on the manuscript.

Publication 3 (Chapter 4)

Bahaa-el-din, L., Mugerwa, B. Mills, D. Henschel, P., Hunter, L., Slotow, R. Hockemba, M.B., Astares, C. & Macdonald, D. (in review). Behavioural plasticity in a forest-adapted felid; African golden cats adjust their activity to the presence of leopards and humans. Submitted to *Behavioural Ecology.*

Author contributions:

LB collected data, processed and analysed the data, and co-designed and wrote the paper. BM and DM collected data from additional sites. LB, BM & DM co-designed the paper as part of BM's Diploma project. MBH collected data. PH, LH, RS, CA & DWM provided valuable comments on the manuscript.

Publication 4 (Chapter 5)

Bahaa-el-din, L., Henschel, P., Caragiulo, A. Sollmann, R., Hutterer, R., Slotow, R., Macdonald, D.W. & Hunter, L. (in prep.). Co-existence of the two African rainforest felids under increasing disturbance from land-use. To be submitted to *Journal of Animal Ecology.*

Author contributions:

LB collected data, processed and analysed the data, and designed and wrote the paper. AC carried out the genetic analysis of the faecal samples. RH assisted with identification of small mammal remains in faecal samples. R Sollmann provided data analysis support and comments on the manuscript. PH, R Slotow, DWM & LH provided valuable comments on the manuscript.

Publication 5 (Appendix 1)

Bahaa-el-din, L., Mills, D., Hunter, L., & Henschel, P. (2015). *Caracal aurata*. The IUCN Red List of Threatened Species 2015. (http://www.iucnredlist.org/details/18306/0).

Author contributions:

LB collected data, assimilated information and updated the assessment. DM carried out range mapping and, alongside LH & PH, provided ideas and valuable comments on the content.

Publication 6 (Appendix 2)

Bahaa-el-din, L., Henschel, P., Aba'a, R., Abernethy, K., Bohm, T., Bout, N., Coad, L.M., Head, J., Inoue, E., Lahm, S., Lee, M., Maisels, F., Rabanal, L., Starkey, M., Taylor, G., Vanthomme, H., Nakashima, Y., Hunter, L. (2013). Notes on the distribution and status of small carnivores in Gabon. *Small Carnivore Conservation* 48 (2013): 19-29.

Author contributions:

LB & PH collected data, processed and analysed data, and designed and wrote the paper. LC collected, processed and analysed the bushmeat data. RA, KA, TB, NB, JH, EI, SM, ML, FM, LR, MS, GT, HV & YN collected data. LH provided valuable comments on the manuscript.

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David Mills, Badru Mugerwa, Alex Braczkowski, Julien Fattebert, Jeremy Cusack, Rob Thomson and Gail Potgieter contributed to the preparation of manuscripts, whether through assistance with the monumental task of data entry, the identification of golden cat individuals, reviewing drafts or contributing R code. Rahel Sollmann hosted me at North Carolina State University and was of integral support for my statistical modelling, and Paul Johnson was always ready with answers to my statistical queries. Anthony Caragiulo and his colleagues at the American Museum of Natural History carried out genetic analysis of the scats I collected – thank you! And to top it off, Rainer Hutterer hosted me at the Zoologisches Forschungsmuseum Alexander Koenig in Bonn and carried out the small mammal identification.

When I embarked on this PhD, I saw it as a mountain I would have to climb alone. I had no idea, then, that this period of my life would be one of meeting so many incredible people, of making firm friendships, and establishing collaborations that I hope will last long into the future. I would get soppy if I started mentioning everyone individually, but I'm hoping to get the chance to tell each of you in person how you've contributed to what has been a very happy time for me. I even lucked out and acquired a surrogate family (the truly wonderful Adendorffs) during writing up in Durban. And that brings me to my actual family, who I'm grateful to not just for their support during this (lengthy) PhD process, but for a lifetime of love and care, and for accepting that my career choice may well mean that I end up on their doorstep many times over the course of my lifetime, asking for food and shelter.

Finally, I would like to dedicate this thesis to Peter and Adrienne Farrell Jackson: my beloved grandparents, my inspiration.

1. General Introduction

1.1 Background

The world is undergoing an extinction crisis whereby human activities are causing the widespread and rapid loss of wildlife populations and species (Ceballos & Ehrlich 2002). Tropical forests, which contain at least two-thirds of the world's terrestrial biodiversity, are among the most threatened ecosystems (Bradshaw et al. 2008). Africa is likely undergoing the fastest change of any continent in recorded history (Laurance et al. 2015), and its rainforests are predicted to go through imminent and severe changes due to increases in mining (Edwards et al. 2014), logging, and plantations (particularly for palm oil; Wich et al. 2014). The human population in Africa's rainforest regions is growing at the fastest rate in the world (FAO 2011), putting further pressure on the forests as they are exploited and cleared to make space for people. The only source of subsistence for many people living in these forests is wild caught meat (bushmeat), and large areas of forest are now depleted or empty of wildlife (Redford 1992, Wilkie et al. 2011, Abernethy et al. 2013).

Yet many species within Africa's rainforests remain unstudied and the extent of the threat to their populations unknown. One such species is the African golden cat Caracal aurata. Flagship species (often charismatic mammals) can be used as symbols for threatened ecosystems (Heywood 1995). As Africa's only forest-dependent felid (Nowell & Jackson 1996), the golden cat has the potential to act as a flagship species for the African rainforest, capitalising on the public's disproportionate affection for felids (Macdonald et al. 2015), to raise funds and awareness, and inspire conservation action.

The golden cat occupies a top position in the food chain and occurs at relatively low densities (Bahaa-el-din et al. 2015a), making it susceptible to extinction (sensu Purvis et al. 2000), and there is evidence that the species is particularly sensitive to human disturbance such as bushmeat hunting (golden cats appear to go locally extinct before other mammals such as chimpanzees Pan troglodytes; Bahaa-el-din et al. 2015b). These characteristics make it a good indicator species for the African rainforest mammal community as its presence and population density can be used as an indication of the community's status (sensu Landres et al. 1988). However, a thorough understanding of the species' ecology and conservation are required for it to be an effective indicator species (Landres et al. 1988). Gaining this understanding can allow us to draw attention to these forests, while guiding appropriate conservation planning to secure the long-term persistence of golden cats and sympatric species, such as critically endangered western gorillas Gorilla gorilla, and endangered leopards Panthera pardus, chimpanzees, forest elephants Loxodonta Africana, among many others.

Golden cat populations are considered to be decreasing, and the species is classified as Vulnerable on the IUCN Red List (Bahaa-el-din et al. 2015b; Appendix 1). This is primarily due to widespread deforestation (leading to habitat loss and fragmentation) and the hunting of wild animals for meat (leading to direct mortality and loss of prey; Nowell & Jackson 1996). Its dependence on tropical forest habitat, and our poor knowledge of the species' conservation biology and status make it one of the most vulnerable carnivore species in Africa (Ray et al. 2005). Urgent monitoring is required in order to make informed decisions for conservation management (sensu Nichols & Williams 2006). To be effective, this monitoring should include specific questions within the context of management, and results should be made widely accessible to policymakers (Gibbs et al. 1999). Estimating demographic parameters, such as species population density and distribution, and changes in these parameters over space and/or time, forms the backbone of wildlife monitoring (Pollock et al. 2012).

Central to current conservation research is the concept that species cannot be studied in isolation. Failure to consider and account for interactions among species (within networks) when implementing conservation can lead to counterproductive outcomes (Tylianakis et al. 2010, Soulé et al. 2005). Linnell & Strand (2000) also highlight the importance of understanding carnivore community interactions for conservation planning. This is because species occur within food webs, governed by trophic-cascades where top-down and bottom-up processes affect whole ecosystems (Hunter & Price 1992). Top-down processes begin with large carnivores as they exert pressure on species occupying lower trophic levels, often limiting potentially overabundant herbivore and smaller carnivore species and increasing overall species diversity (Miller et al. 2001, Terborgh 2010). However, large carnivores are decreasing in numbers and going extinct across the world as a result of persecution by humans (Ripple et al. 2014, Gittleman et al. 2001), with potential cascading effects throughout the food-web (Terborgh 2010).

As one of only two large carnivores (alongside the leopard) to occur in much of the African rainforest (Bahaa-el-din et al. 2015a), the golden cat may play an important ecological role in controlling prey and small carnivore populations (sensu Terborgh 2010). In addition, this relatively simple (two-species) large carnivore community allows us to explore some ecological questions made complicated where more species occur, such as in the Neotropical and Asian forests, as well as in the African savannahs (Macdonald et al. 2010).

Previous dietary studies found high food niche overlap between golden cats and leopards (Ososky 1998, Ray & Sunquist 2001), and Henschel et al. (2005) found golden cat remains in 2.5% of leopard scats, indicating that direct interference competition may occur. Leopards are known to exhibit this interference behaviour within other systems, and Palomares and Caro (1999) found them to be responsible for the most intra-guild predation among felid species. Golden cats could therefore be expected to function within a "landscape of fear" (Laundrés et al. 2001), avoiding spatial and temporal overlap with leopards. Where leopards no longer occur as a result of extirpation by humans (e.g. in parts of Uganda; Butynski 1984, Struhsaker 1997), golden cats shift to the top position in the food chain. This shift can result in the "release" of golden cats from the "landscape of fear", a phenomenon referred to as mesopredator release (mesopredators are mid-ranking predators within a food-web; Prugh et al. 2009). Research into the mesopredator release hypothesis has largely focused on the effects of large predator extirpation on mesopredator abundance (Prugh et al. 2009). However, behaviour of mesopredators may also be affected, with potential cascading effects to other species (Prugh et al. 2009). The nature of such behavioural changes is useful to understand when considering conservation intervention, such as carnivore re-introduction or control.

Because golden cats are subordinate to leopards in most of their range, it is imperative that their behavioural ecology be examined within this community context in order to avoid counterproductive conservation actions (sensu Linnell & Strand 2000, Tylianakis et al. 2010). Interference competition can have varying consequences for mesopredators. For example, large-scale displacement of subordinate species via exclusion from the landscape can result in reduced access to resources and population suppression, such as for wild dogs Lycaon pictus being displaced by lions Panthera leo (Swanson et al. 2014). Finer-scale spatial displacement can also occur, such as harbour seals Phoca vitulina underutilising a rich prey resource in deep strata to avoid predation by Pacific sleeper sharks Somniosus pacificus (Frid et al. 2008). On the other hand, mesopredators may show little spatial displacement but use fine-scale spatio-temporal avoidance to minimise antagonistic encounters, such as cheetahs Acinonyx jubatus reactively avoiding lions (Broekhuis et al. 2013, Swanson 2014). Finally, food partitioning may also mediate co-existence between carnivores, as recorded for jaguars Panthera onca and pumas Puma concolor in Venezuela (Scognamillo et al. 2003).

Species often display phenotypic plasticity that allows them to adapt under varying environments, changing their behaviour and/or food niche to maximise survival and reproduction (Agrawal 2001). Such changes affect the nature of species interactions, not only through direct effects on individual species, but through changes in one species driving (additional) changes in species that it interacts with (Agrawal 2001). Anthropogenic change to an ecosystem may therefore further complicate carnivore interactions, potentially altering competitive and predatory relationships (Ritchie & Johnson 2009). For example, food niche overlap between omnivorous tortoises and carnivorous vipers in the rainforest of West Africa was found to be lower in a pristine habitat than an altered one (Luiselli 2006). We might therefore expect the competitive relationship between golden cats and leopards to be affected by the widespread anthropogenic disturbance taking place in the African rainforest.

Conserving large carnivores often poses a great challenge. Not only do they occur at naturally low densities and have large home ranges, their predatory nature also makes them unfavourable to communities living alongside them (Linnell et al. 2001, Inskip & Zimmermann 2009). Predation on livestock as well as the threat posed to humans by large carnivores can result in conflict situations between local people who bear the brunt of living with large carnivores, and those trying to conserve them. The result is often the persecution of large carnivores, leading to local extinctions (Dickman 2010). Assessing the attitudes of people living alongside carnivores is a key step in conservation planning (Romañach et al. 2007, Dickman 2010).

1.2. Thesis structure

In light of the above threats, a greater understanding of the ecology and conservation needs of the golden cat can provide an important basis for the conservation of Africa's rainforest wildlife. This should include insight into the interactions between golden cats and leopards and the effects of human disturbance on those interactions. In order to achieve this, I set out with the aim of understanding the ecology and conservation of the African golden cat. I do this by using up-to-date methods to answer key questions that further our understanding of the species. I place these questions within broader contexts relevant to a wide variety of species and ecosystems. I present each chapter as a manuscript for publication, and some level of repetition is therefore unavoidable. The structure of my thesis is as follows:

Chapter 2: The African golden cat: Caracal aurata

Thought to be naturally rare, the golden cat is almost unstudied (Ray et al. 2005, Brodie et al. 2009) because of the unlikelihood of encountering it. Anecdotal reports and single observations have been published (e.g., Boy 2003, Aronsen 2010, Sheil 2011), but only diet has been assessed empirically (Hart et al. 1996, Ososky 1998, Ray & Sunquist 2001). My first aim, therefore, is to collate all published information on the golden cat into a thorough review in order to separate fact from fiction, and to identify gaps in knowledge. This includes a review of scientific and grey literature, as well as preliminary findings from my research in Gabon and parallel research in Uganda.

Chapter 3: Effects of human land-use on Africa's only forest-dependent felid: the African golden cat Caracal aurata

I monitored golden cats under varying forms of human land-use assumed to represent a disturbance gradient corresponding with the threats mentioned above. I use population density as the basis for assessment, first to obtain a baseline population estimate from a pristine area, and then to compare this with areas under different land-uses as part of a natural experiment. My aim is to understand the impacts of land-uses on golden cat density and make management recommendations in order minimise the potential threat to golden cats posed by human activities across golden cat range.

Chapter 4: African golden cat behavioural plasticity: temporal shifts in response to leopards and humans

I use data from several sites in Gabon and the Republic of Congo where golden cats co-exist with leopards, and data from several sites in Uganda where leopards have been extirpated, to compare golden cat activity at sites where it is the mid-ranking mesopredator and sites where it has been "released" from the controlling presence of leopards. I compare overall temporal activity between sites with the aim of finding out whether golden cat behaviour changes in response to differences in guild structure. I also include human and prey activity to explore potential explanations for activity shifts.

Chapter 5: Co-existence of the two African rainforest felids under increasing disturbance from land-use

I explore the competitive relationship between golden cats and leopards through an assessment of overlap and avoidance in space, time, and food niche. My aim is to gain insight into the mechanisms of co-existence between golden cats and leopards and to examine how these mechanisms are affected by human interference in the system.

Chapter 6: General conclusions

I conclude by bringing together all the findings of my research within the wider context of wildlife research and conservation. I also introduce some findings from additional data on local people's perceptions with the aim of establishing whether conflict with humans poses a threat to golden cats.

1.3. General methodology

This thesis is a collection of independent papers, and the study sites and methodology are described within each paper. To summarise, I collected data at six sites in the central African country of Gabon between 2010 and 2013. I used remotely triggered camera traps to collect data on abundance, and spatial and temporal activity of golden cats, as well as data on leopards and prey species. I collected golden cat and leopard scat samples to assess their diets and food niche overlap. I also make use of camera data collected as part of a parallel study on African golden cats in Uganda being undertaken by David Mills (Mills et al. 2012), and data from two sites (one in Uganda and one in the Republic of Congo) which form part of a global tropical monitoring project carried out by the TEAM network (http://www.teamnetwork.org).

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2. The African golden cat *Caracal aurata*: Africa's least-known felid

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Cover image: An African golden cat, © Laila Bahaa-el-din
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2.1 Abstract

The African golden cat Caracal aurata is endemic to tropical Africa. It is one of the world's least-studied felids and is considered rare in most of its geographic range. The status of the African golden cat in the wild has never been rigorously assessed, but the species is increasingly threatened by habitat degradation, loss and fragmentation, and by unsustainable hunting. We describe the African golden cat and review its taxonomy, distribution, ecology, behaviour, threats and conservation status. The information presented here is based on the literature and on new data from the first two intensive field studies on the species (underway in Gabon and Uganda). The golden cat is phenotypically variable. Within the two main colour morphs, golden/reddish-brown and grey, there is wide variation and intergradation. Both of these morphs occur throughout the species' range. Melanistic and chocolate-brown morphs also occur but are uncommon. Recent genetic analysis indicates that the golden cat is closely related to the caracal Caracal caracal, and it has, therefore, been changed from the genus Profelis to Caracal. The golden cat is predominantly terrestrial and cathemeral. Its diet consists mainly of rodents and small ungulates. Field studies in Gabon and Uganda have established that golden cats can be locally common. They are prone to capture by wire snares, however, and are absent in forests hunted at commercial scales. Species-focused camera trap surveys are effective for collecting distribution, abundance, population structure, ecological and behavioural data on golden cats.

2.2 Introduction

The African golden cat Caracal aurata (hereafter referred to as 'golden cat') is a medium-sized felid endemic to tropical Africa, with a confirmed historic distribution from SW Senegal in the west to at least central Kenya in the east (Ray & Butynski 2013). It is typically the second largest carnivore present within this habitat (Bahaa-el-din et al. 2011), though in areas where leopards Panthera pardus have been extirpated, the golden cat is now the 'top carnivore' (e.g. in Kibale National Park, SW Uganda; Mills et al. 2012). The golden cat is one of the least-known carnivores in Africa (Ray et al. 2005), and one of the least-studied felids worldwide (Brodie 2009). This species is a forest specialist and is, therefore, vulnerable to forest degradation, loss, and fragmentation (Nowell & Jackson 1996). The golden cat is also threatened by unsustainable hunting for bushmeat (Nowell & Jackson 1996, Robinson & Bennett 2000).

Despite these threats, there has been no detailed field research on golden cats until recently. The advent of motion-activated camera traps has resulted in several recent publications on golden cats based on opportunistic camera trap photographs, as well as more species-focused studies (e.g. Aronsen 2010, Bahaa-el-din et al. 2011, Sheil 2011, Mills et al. 2012, Mugerwa et al. 2013, Sheil & Mugerwa 2013).

We aim to collate information about the golden cat in order to identify key knowledge gaps, thereby creating a foundation for future research that will guide conservation planning for this species. We build on the recently published species account in the Mammals of Africa (Ray &

Butynski 2013) by providing additional information including new field data from Gabon and Uganda. We describe the golden cat and review its taxonomy, habitat, distribution, ecology, behaviour, reproduction, threats, conservation status, and present opportunities for research and for the implementation of evidence-based conservation measures.

2.3 Methods

2.3.1 Literature review

We located published papers concerning the golden cat through an ISI Web of Science (Thompson Scientific) search; 'grey' literature (consisting of unpublished reports) was found by using Google Web and Google Scholar searches. We used the following search: African golden cat, Profelis aurata, Caracal aurata, and Felis aurata. We supplemented papers and reports with unpublished information obtained from colleagues who have extensive field experience within the geographic range of the golden cat.

2.3.2 Camera trapping

Where it increases our understanding of the golden cat, we include preliminary results from (independent) camera- trapping studies in Gabon and Uganda (in the west and east of the golden cat's range, respectively). We surveyed three sites in central Gabon between June 2010 and November 2012 as part of an on-going study on the impact of anthropogenic disturbance on golden cats. This region is mostly covered by mature lowland semi-evergreen moist forest and contains two large national parks (Lopé, 4910 km2; Ivindo, 3000 km2); most of the remainder of the region is under logging concessions (WRI 2009). For a detailed description of the geography, climate, flora and fauna of this region, see Vande Weghe (2006, 2011). Our three sites represent a gradient of disturbance, from a pristine primary forest to a logging concession certified as sustainable by the Forest Stewardship Council (FSC; http:// www.fsc.org).

We also surveyed three sites as part of an on-going golden cat study in northern and central Kibale National Park (ca. 766 km2), SW Uganda (hereafter referred to as 'Kibale'), from September 2010 to January 2012. These sites are in areas used for research and tourism. Kibale is a mid-altitude moist evergreen forest located along the Albertine (Western) Rift. The vegetation over much of Kibale is relatively undisturbed forest, whereas several areas of indigenous forest are still recovering: in the north, from selective logging that took place during 1966–1975 (Struhsaker 1997), and in the south, from illegal agricultural encroachment that occurred prior to eviction in 1992 (Chapman & Lambert 2000). Today, Kibale consists of a mosaic of primary and secondary forest, colonizing bush and forest, tall grassland, swamp, and exotic pine and cypress plantations. For a detailed description of the climate, flora, fauna, ecology and history of Kibale, see Struhsaker (1997, 2010) and Chapman and Lambert (2000). Though connected to the woodlands and savannahs of Queen Elizabeth National Park to the south, Kibale is effectively isolated from other forests by large areas of intensive agriculture.

We designed our studies in both Gabon and Uganda to maximize captures of golden cat images. At each of the six sites, we installed 24 – 46 camera trap stations (with two cameras at each station) within an area of 20 – 42km2. Camera trap stations were 600 – 1000 m apart; cameras were 25 – 30 cm off the ground and 1.5 – 2.5 m back from the edge of the trail. At each station, one camera was placed on each side of the trail. Cameras were left active for 55 – 90 days; batteries were checked every 10 – 15 days.

2.4 Review

2.4.1 Description

The golden cat is a medium-sized, strongly built felid. Adult males weigh 8.0 – 14.0 kg, and adult females weigh 6.2 – 8.2 kg. Head–body length for adult males ranges from 62 to 94 cm and for adult females from 63 to 75 cm. The tail is less than half of the head–body length (25–37 cm for adult males and 28 – 30 cm for adult females; Ray & Butynski 2013).

The golden cat has a relatively small, round head with a short face and heavy muzzle. The face has distinctive pale patches on the cheeks and around the eyes and mouth. The ears are small and rounded, lack tufts, and are entirely black on the back. The fur between the shoulders and crown grows forward; a single or double whorl marks where the fur changes direction (van Mensch & van Bree 1969). For a more detailed description, see Ray and Butynski (2013).

Golden cats occur predominantly in two colour forms: golden/reddish-brown and grey, with some intergradation and variation between them (Fig. 2.1). Melanistic and chocolate-brown individuals are uncommon (van Mensch & van Bree 1969, Ray & Butynski 2013). Fur on the chin, throat, chest and abdomen is typically cream or white in non-melanistic individuals. The tail has a dark line that runs down the middle of the upper side, a dark tip, and is often banded.

Examination of skins and camera trap photographs suggests that the ratio of golden/reddish-brown to grey individuals is about equal throughout the species' geographic range, varying only slightly by locality (Table 2.1). Melanistic golden cats are present in the Virunga-Bwindi region [where the borders of Uganda, Rwanda and Democratic Republic of Congo (DRC) meet] (Monfort 1992, Boy 2003; Fig. 2.1). Intermediate forms between the golden/reddish-brown and the grey morphs are known from several localities (Allen 1924, van Mensch & van Bree 1969). In Uganda, a grey individual was photographed with a reddish tint on the shoulders. A captive grey individual in Gabon had a similar reddish tint on the forehead and cheeks (Bahaa-el-din 2012).

Figure 2.1. Camera trap photographs of (clockwise from bottom left): golden, reddish-brown, grey and black (melanistic) African golden cats. Golden and reddish-brown are usually considered as one morph (golden/reddish-brown). The photographs of golden and reddish-brown individuals demonstrate the considerable variation within the golden/reddish-brown morph.

Table 2.1. Percentages, by country, of golden/reddish-brown, grey and melanistic African golden cats based on skins (van Mensch & van Bree 1969; *n* = 186; sample size by country is not available) and based on camera trap photographs (this study; individual *n* = 50).

		Percentage of colour morph in sample			
Country	Sample size	Golden/ reddish-brown	Grey	Melanistic	Source
Liberia	-	36	59	5	van Mensch & van Bree 1969
Gabon	-	50	50	0	van Mensch & van Bree 1969
Gabon	27	56	44	0	This study
DRC	-	58	35	6	van Mensch & van Bree 1969
Uganda	23	48	52	0	This study

The skin of a grey individual with a red tail was interpreted by Elliot (1883) as being in the process of changing colour. However, van Mensch and van Bree (1969) suggested that the tail might belong to a different skin. Recent publications (e.g. Boy 2003, Aronsen 2010) perpetuate the suggestion that golden cats change colour over time. Although there is one record of a captive individual that changed colour from reddish to grey (Pocock 1907), this animal died soon after, perhaps suggesting a pathological case (van Mensch & van Bree 1969).

Golden cats vary widely in the degree of spotting on the pelage (Fig. 2.2), and spotting is more extensive in western populations. Differences in the degree of spotting have led to the description of two subspecies; van Mensch and van Bree (1969) suggested a western subspecies Profelis aurata celidogaster west of the Cross River of Nigeria and Cameroon, and an eastern subspecies Profelis aurata aurata east of the Congo River; the area in between these rivers is described as having intermediate forms. Profelis aurata celidogaster is described as having a dark mid-dorsal line, a distinctly or indistinctly banded tail, and bold spots all over the body. Profelis aurata aurata is described as having no dark mid-dorsal line, indistinct or no bands on the tail, and spots restricted to the flanks and belly (van Mensch & van Bree 1969).

The subspecies delineation has not been validated by molecular or additional morphological data, and remains open to question. Photographs from camera traps of 27 individuals reveal a wide range in the type and extent of spotting in Gabon, including large spots over the entire flank, few spots on the flank, and no spots on the flank. All individuals photographed had spots on the belly and inner legs. In 23 individuals photographed in Uganda, spots were typically restricted to the belly and inner legs (Fig. 2.2).

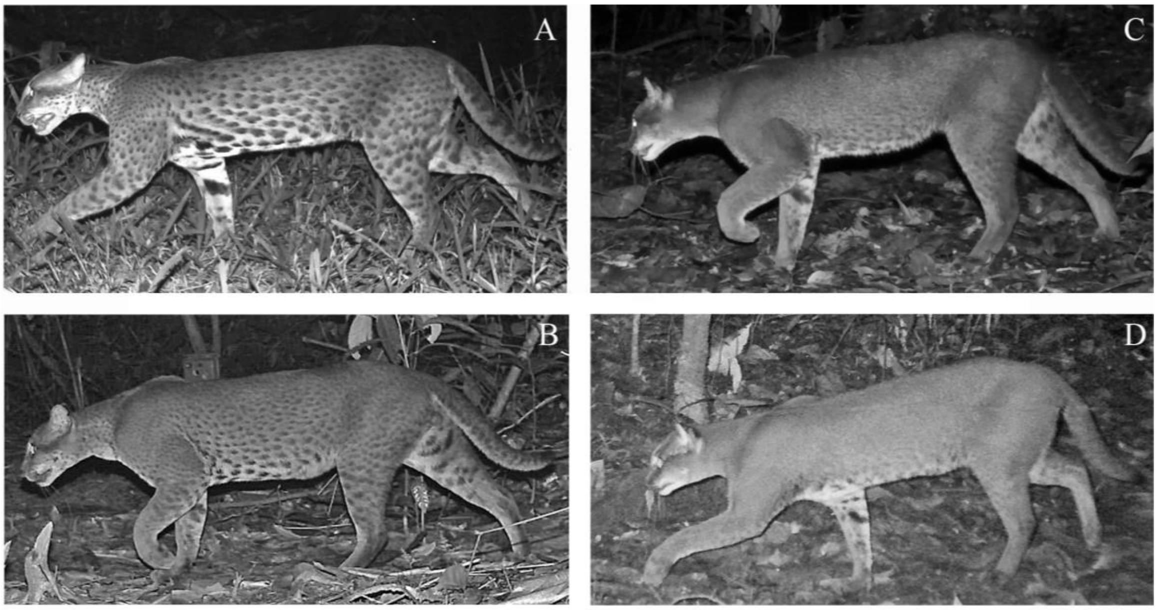

Figure. 2.2. Camera trap photographs of African golden cats from central Gabon (a–c), showing the range of types and extent of spotting that occur in individuals from the west of the species' geographic range. Spots are, typically, restricted to the belly and inner legs of golden cats from Kibale, SW Uganda, (d) and from other sites east of the Congo River.

Over a small portion of their geographic range, golden cats are sympatric with caracals Caracal caracal, servals Leptailurus serval and wild cats Felis silvestris, particularly in woodland and gallery forests on the northern, eastern and southern fringes of the main West-Central African forest block (e.g. in the Chinko/Mbari Basin of the Central African Republic [CAR]; Hickisch & Aebischer 2013). In the forest/savannah mosaics of the western Congo Basin, servals and golden cats co-occur (e.g. Henschel et al. 2014). Butynski et al. (2012) provide details on how to differentiate among the four felid species in the field and emphasize that the ears (pattern, colour, size and shape) and tail (pattern, colour and carriage) are the most useful diagnostic field traits. Tail length, and tail length relative to head-body length, are not diagnostic (Butynski et al. 2012).

Accurate knowledge of the occurrence of the golden cat is imperative for research and conservation decision-making. Identification of this species, particularly outside of its confirmed range, should therefore be done cautiously using the most diagnostic traits, with an emphasis on ear features rather than on the commonly used features of colour and tail length.

2.4.2 Taxonomy

The presence of both golden/reddish-brown and grey morphs confused early taxonomists: Temminck (1827) described the African golden cat as two species. This taxonomy stood until Pocock (1907) ascertained that the two forms represented sympatric colour morphs. These morphs do not represent sexual, geographic or seasonal varieties (e.g. Allen 1924).

Early taxonomists regarded the African golden cat and Asiatic golden cat Catopuma temminckii as closely related due to similarities in appearance, and grouped them together in Felis (Temminck 1827) or Profelis (Pocock 1917). Hemmer (1974) placed them in different genera (Profelis for the African species and Catopuma for the Asiatic species). Recent molecular data reveal that these two species are not closely related and that their phenotypic and morphological similarities are the result of convergent evolution (Johnson et al. 2006). The African golden cat is, instead, closely related to the caracal and the serval. Therefore, Johnson et al. (2006) placed the African golden cat in the genus Caracal. Caracal diverged from other felids c. 8.5 million years ago (MYA; Janczewski et al. 1995, Pecon-Slattery & O’Brien 1998). The serval then diverged c. 5.6 MYA, and the golden cat and caracal diverged c. 1.9 MYA (Johnson et al. 2006).

Morphologically, golden cat and caracal skulls do not differ in size or basic design (Sicuro & Oliveira 2011); both have enlarged external pterygoid crests (A. Kitchener, pers. comm.). These similarities of the skull lend strong support to the taxonomy of Johnson et al. (2006). The Cat Classification Task Force, using a strict set of principles and criteria (Breitenmoser et al. 2011), supports the new taxonomy, as does the International Union for Conservation of Nature’s Species Survival Commission (IUCN/SSC) Cat Specialist Group. Therefore, the 2014 IUCN

Red List refers to the African golden cat as Caracal aurata. We follow this taxonomy in this review but note that some authors publishing since 2006 continue to use Profelis aurata.

2.4.3 Habitat

The golden cat is endemic to tropical Africa in two disjunct populations; in both, it is typically associated with moist forests (Fig. 2.3). This species is found in lowland, mid-altitude (transition), montane, bamboo and subalpine forests, as well as in alpine moorland, wooded savannah, savannah/forest mosaics, gallery forest and riverine forest (Schouteden 1948, Rahm & Christiaensen 1963, van Mensch & van Bree 1969, Kingdon 1977, Nowell & Jackson 1996, Grubb et al. 1998, Andama 2000, Brugière 2001). The golden cat occurs from near sea level up to 3600m (Guggisberg 1975), where mean annual rainfall is between 1200 mm and 2400 mm (Butynski et al. 2012).

Golden cats are tolerant of logged forest, where thick understory vegetation and higher rodent densities follow exploitation (Kingdon 1977). We photographed golden cats in primary forest, secondary forest and recently logged forest. In Lopé National Park, Gabon, the species was observed in forest/savannah mosaics. In Batéké Plateau National Park, Gabon, golden cats were seen crossing 500 m wide savannah patches, and in gallery forest that is <1 km wide and 20 km from continuous forest (P. Aczel, pers. comm.).

2.4.4 Distribution

The most northerly record for the golden cat is Bakor Forest, SW Senegal (Gaillard 1969), from where the range extends south-eastwards across the Upper Guinean coastal moist forests of Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana and W Togo (Fig. 2.3). No records exist from the Dahomey Gap of Benin or western and central Nigeria (Happold 1987). The golden cat is present in Lower Guinean moist forests in SE Nigeria, southwards through Cameroon, Gabon, Republic of Congo and N Angola, and eastwards through S CAR, DRC, S Sudan and Uganda (Pocock 1907, van Mensch & van Bree 1969, Kingdon 1977, Grubb et al. 1998). The most easterly confirmed records are two skins from Mau Forest, SW Kenya (Toschi 1946). There are many reported sightings farther east across the Eastern (Gregory) Rift Valley (Boy 2003) to the Arabuko-Sokoke Forest on the coast of Kenya (Virani 1993), but none of these has been confirmed by either specimens or photographs (Butynski et al. 2012). While suitable habitat appears to exist for golden cats at many sites in Tanzania, there are no verified records from that country (Butynski et al. 2012). The golden cat's use of riverine and gallery forests extends its distribution beyond the immediate tropical forest zone (Kingdon 1977): records exist from the more open habitats of Guinea (Brugière 2001) and CAR (Hickisch & Aebischer 2013).

Figure 2.3 depicts the golden cat's 'Extent of Occurrence' (the geographic area encompassing all known or inferred sites of occurrence; IUCN 2001), which does not exclude areas within the range that do not have suitable habitat, or from which the species may be extirpated. The 'Area of Occupancy' (the area that is known to be presently occupied; IUCN 2001) is a more useful representation of occurrence for conservation planning, but too few reliable occurrence records exist from throughout the golden cat's range to produce an accurate range map reflecting the species' current distribution. Ground-truthing needs to take place in those parts of the range where the golden cat's occurrence is uncertain, such as along the fringes of the known range, particularly in parts of West Africa and in Kenya. A lack of field evidence for the species' occurrence in recent decades suggests that the golden cat may no longer be present in the former western extreme of its range, in SW Senegal, where forest habitat formerly harbouring the species has been lost.

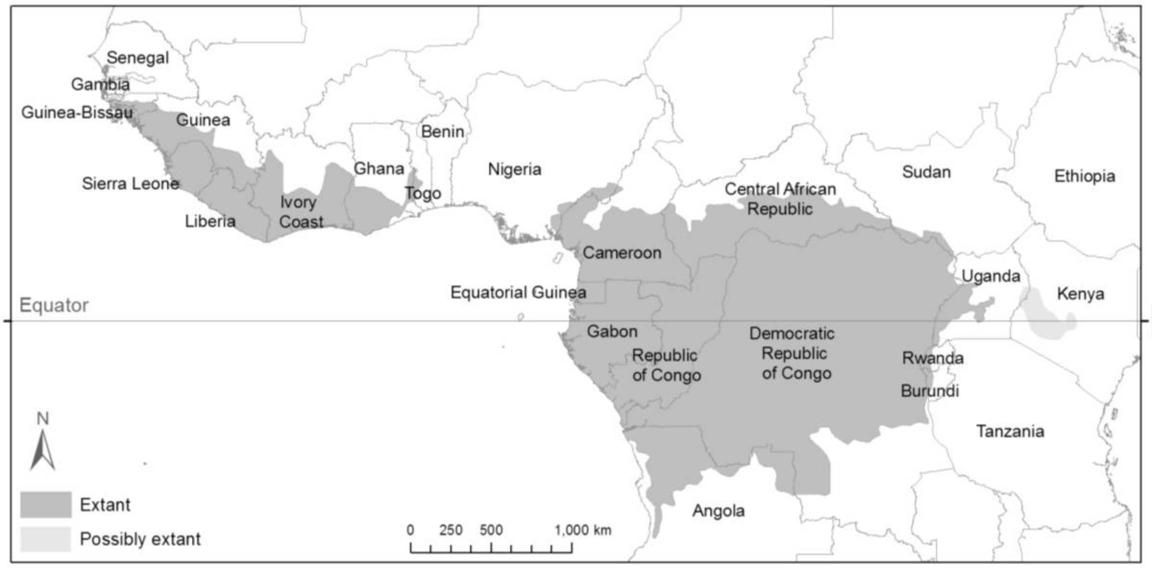

Figure. 2.3. Geographic range of the African golden cat, mapped according to verified occurrence records and suitable forest habitat (Bahaa-el-din et al. 2015).

2.4.5 Feeding ecology

The golden cat hunts on the ground by using a typical felid stalk-and-rush technique, as filmed in the wild (http:// www.panthera.org/african-golden-cat) and observed in captivity (Bahaa-el-din 2012). Captive golden cats secure prey with their claws and deliver a rapid bite to the back of the neck (Kingdon 1977). The Mbuti people in NE DRC believe that this species hunts on the ground and that it does not readily catch arboreal monkeys (Carpaneto & Germi 1989).

Studies on the diet of the golden cat indicate that in Ituri Forest, DRC (Hart et al. 1996), in Nouabale-Ndoki National Park, Republic of Congo (Ososky 1998), and in Dzanga- Sangha Reserve, CAR (Ray & Sunquist 2001), rodents are the most frequent prey, representing 62–70% of prey items. Small ungulates, particularly the blue duiker Philantomba monticola, are next most frequent. Shrews, birds and primates are also eaten. Research has shown that while golden cats and leopards partition their food by prey size (Hart et al. 1996, Ososky 1998), food niche overlap is high (Ososky 1998, Ray & Sunquist 2001). The golden cat's diet consists of a subset of the leopard's highly varied diet at the smaller end of the prey size scale (Ososky 1998). In all three studies, the blue duiker was important prey for both species.

In Bwindi Impenetrable National Park, SW Uganda (hereafter referred to as 'Bwindi'), where leopards were extirpated in about 1972 (Butynski 1984), the diet of the golden cat consists mostly of duikers (52%). Rodents, birds and eggs, monkeys and bushpigs Potamochoerus larvatus are also eaten (Andama 2000). This may indicate that the golden cat hunts larger prey, particularly duikers, in the absence of leopards; however, caution should be exercised in the interpretation of these results in the absence of information on the size or age of the prey; remains might come from infants and juveniles of the larger species.

The frequency of occurrence of prey species remains found in golden cat scats, as determined in four studies, is presented in Table 2.2. Multiple prey species may occur in the same scat, so total frequencies of occurrence do not add up to 100%. We therefore standardized the data for ease of comparison by dividing the percentage of occurrence for each species or species group by the total occurrence and multiplying by 100. In cases where small mammal species were not grouped by weight in the original literature, we grouped them using the weights for adults given by Kingdon et al. (2013). Minor errors may have been introduced by summing percentage of occurrences to group the species, but this was unavoidable without the original data.

In all four dietary studies summarized in Table 2.2, golden cat and leopard scats were separated based on scat diameter and bone fragment size. Ray and Sunquist (2001) used thin-layer chromatography of bile acids to distinguish felid scats from those of other carnivores but could not differentiate between the scats of leopards and golden cats by using this technique (Ray & Sunquist 2001). They also applied size criteria to distinguish leopard and golden cat scats.

Farrell et al. (2000) raise concerns about relying on scat size and presence of field signs to assign species. They found significant overlap in scat size between puma Puma concolor and ocelot Leopardus pardalis, two Neotropical felids with similar size and weight differences to leopard and golden cat. They stressed the need for genetic analyses to confirm species, and to avoid high error rates and concomitant misrepresentations of predator diets. Molecular testing of scat origin should, therefore, be a prerequisite for future dietary studies on the golden cat.

Table 2.2. Corrected frequency of occurrence of prey species in the diet of the African golden cat at four sites, as determined from scats.

Prey type/species	**Ituri, DRC (n = 60)**	**Ndoki, Rep. of Congo (n = 36)**	**Dzanga, CAR (n = 17)**	**Bwindi, Uganda (n = 42)**
Source	Hart et al. 1996	Ososky 1998	Ray & Sunquist 2001	Andama 2001
Ungulates				
Neotragus batesi	4	*	*	*
Philantomba monticola	15	16	22	
Cephalophus dorsalis	1			*
Cephalophus callipygus	*		16	*
Duiker spp.				54
Potamochoerus larvatus	*	*	*	6
Total ungulates	20	16	38	60
Primates				
Cercopithecus sp.?	3			
Cercopithecus cephus	*		6	*
Galagoides demidoff		3		
Total primates	3.0	3	6	10
Rodents				
Protoxerus stangeri	5			
Cricetomys emini	3	13	11	
Atherurus africanus		9	11	
Sciuridae	6	22	7	
Rodents <100g	16	16	11	
Rodents 100-300g	15	3		
Rodents 300-500g	5			
Unknown small rodents		6		
Total rodents	50	69	40	14 (rodents/shrews)
Total Shrews/Insectivora	7	9	6	
Other mammal				
Manis tricuspis		3		
Unknown very small <100g	1			
Unknown small 100-300g	2			
Unknown size	5		11	
Total other mammals	8	3	11	0
Birds				
Unknown passerine	7			
Unknown medium bird	3			
Unknown phasianidae	1			
Total birds	11	0	0	12
Eggs				2
Unidentified animal remains				3

*Species does not occur at this site, based on known distributions (IUCN Red List of Threatened Species).

Gallinaceous birds (e.g. francolins Francolinus spp. and guineafowls Guttera spp. and Numida spp.), being large and ground-dwelling, may be an important component of the golden cat's diet. These might be under-represented in the data if wild golden cats pluck feathers prior to eating, as observed in captivity (Blonk 1965). A captive golden cat was observed to catch very fast-moving balls in the air (Bahaa-el-din 2012), which suggests that golden cats may be able to catch birds on the wing, like caracals and servals. A camera trap video from our Gabon study shows a golden cat attempting, unsuccessfully, to catch a flying bat.

Primates, including galagos (Galagidae), comprise 3–10% of the golden cat's diet (Table 2.2). A golden cat was observed killing an adult Sykes's monkey Cercopithecus mitis on the ground in thick cover in the Aberdares Range, central Kenya, in 1981 (J. Rowling, in Boy 2003). M. Ghiglieri and L. Leland examined the fresh carcass of a c. 3-year-old, 3-kg, male eastern red colobus monkey Piliocolobus tephrosceles that was almost certainly killed by a golden cat in Kibale. The colobus had four puncture wounds on the front of the throat and one at the back of the skull. This monkey was apparently feeding on the ground on the dead wood of a stump when captured (Struhsaker 1981, 2010). A golden cat was filmed hunting red colobus monkeys that were feeding on the ground in Kibale (S. Angedakin, pers. comm.; http://www.panthera.org/african-golden-cat).

Struhsaker (1981) observed two instances in Kibale in which monkeys emitted alarm calls and followed golden cats from as close as 5 m overhead, for a distance of c. 25 m. Video footage shows monkeys emitting alarm calls as they surround a sleeping golden cat in a tree in Kalinzu Forest Reserve, Uganda (Y. Tashiro, pers. comm.; http://www.panthera.org/african-golden-cat). At Makokou, NE Gabon, there were several sightings of golden cats close to sleeping sites of northern talapoin monkeys Miopithecus ogouensis (Gautier-Hion 2013).

2.4.6 Abundance

As a result of the paucity of golden cat sightings and signs (e.g. tracks and scats), the species is regularly described as 'uncommon' or 'naturally rare' (Hart et al. 1996, Hunter & Barrett 2011). Additionally, golden cats comprise but a small proportion of the bushmeat catch: 0.8% in NE Gabon, 0.4% of carnivore carcasses in E Republic of Congo and 0.4% of captures in snares in Lobeké Forest, SE Cameroon (Ray et al. 2005). The large number of skins found in museums and among hunters may, however, indicate that golden cats are less rare than suggested (Malbrant & Maclatchy 1949, Rosevear 1974).

Carbone and Gittleman (2002) showed that carnivore body mass is inversely related to density. In a forest felid guild in Chiquibul Forest Reserve and National Park, Belize (cited by Davis 2009), jaguar Panthera onca (adult weight 36–100 kg) and puma (adult weight 23–80 kg) densities were at least three times lower than densities of ocelots (adult weight 7–19 kg). The African moist forest carnivore guild is structured differently, with fewer felids and a larger number of small carnivores. Nevertheless, we expect leopard (adult weight 17–90 kg; Hunter & Barrett 2011) densities to be substantially lower than those of golden cats (adult weight 6–14 kg; Ray & Butynski 2013) based on body size difference. Henschel et al. (2011) found leopards to occur at 4.6 and 12.1 individuals per 100 km2 at two remote forest sites in Gabon. We therefore hypothesize that golden cats occur at higher densities than leopards within suitable habitat.

Using spot patterns to identify individual golden cats photographed during our camera trap studies in Gabon, we identified a minimum of 6–11 individuals within each of three c. 20 km2 areas. This suggests that the low frequency of field sightings is due largely to secretive and cryptic behaviour and to dense vegetation, rather than to low densities.

2.4.7 Population structure

Camera trap and carcass data suggest that males are more susceptible to capture than females, perhaps indicating they make more use of roads and trails or travel greater distances to patrol larger territories. Among golden cat museum specimens of known sex, 25 (74%) are males and nine (26%) are females (Ray & Butynski 2013). Of 13 golden cats found in snares in Cameroon, 12 (92%) were males (T. Davenport & G. Ngandjui, pers. comm.). Of 27 golden cats identified from camera trap photographs in Gabon, 56% were males and 44% were females. Males were photographed more often (66% of 82 captures) than females (34%). Higher photo-capture rates for males are typical in camera trap studies on forest felids: studies on ocelots (Dillon & Kelly 2007), Sunda clouded leopards Neofelis diardi (Wilting et al. 2012) and jaguars (Sollmann et al. 2011) all produced at least four times more male than female captures. In contrast to carcass data from Cameroon and camera trap data from Gabon, more individual females (67%) than males (33%) were photo-captured in Kibale (n = 33). This rate changed only slightly when the number of photo-captures was considered (61% female and 39% male; n = 99). Further investigation will reveal whether this is a result of differences in study design, camera placement, movement patterns, population structure or some other factor(s).

There are few records of kittens and immature individuals from museums (E. Sarmiento, pers. comm.), snares (T. Davenport & G. Ngandjui, pers. comm.) or camera traps (this study). This low frequency suggests that young are well hidden and that the movement of kittens and juveniles is very limited.

2.4.8 Behaviour and spatial ecology

Though earlier naturalists described the golden cat as arboreal (Dekeyser 1945, Rosevear 1974, Haltenorth & Diller 1980), the species is certainly predominantly terrestrial as almost all confirmed sightings are of animals on the ground. During 91 person-years of field research on primates and birds in Kibale and Bwindi, T. Butynski, C. Chapman, L. Chapman, M. Ghiglieri,

J. Kalina, L. Leland, J. Mitani, T. Struhsaker and P. Waser encountered golden cats on 12 occasions; in all cases, the golden cat was on the ground, although in one case it fled into a tree. There is a video record from 2010 of a golden cat sleeping in a tree about 12 m off the ground in Kalinzu Forest Reserve, SW Uganda. Sykes's monkeys and red-tailed monkeys Cercopithecus ascanius surrounded the golden cat while alarm-calling. After several minutes, the golden cat descended to the ground and moved out of sight (Y. Tashiro, pers. comm.).

The golden cat is frequently described as primarily crepuscular or nocturnal (Rosevear 1974, Guggisberg 1975, Andama 2000, Ray & Butynski 2013), presumably timing activity to that of its prey species. Hayward and Slotow (2009), however, found no evidence that predators time their activity to coincide with their prey. Diurnal, crepuscular and nocturnal prey species all feature heavily in the golden cat's diet. In Gabon and Kibale, golden cats were photo-captured at all times of day and night and showed no strong affinity for either daytime or night-time hours (Fig. 2.4); they are therefore considered cathemeral. It may be that, like leopards (Henschel & Ray 2003), golden cats vary their temporal activity according to the level and type of human activity in the area. Their activity may also be timed to avoid competition with leopards in the same way that pumas avoid jaguars in the Bolivian Chaco through temporal partitioning (Romero-Munoz et al. 2010).

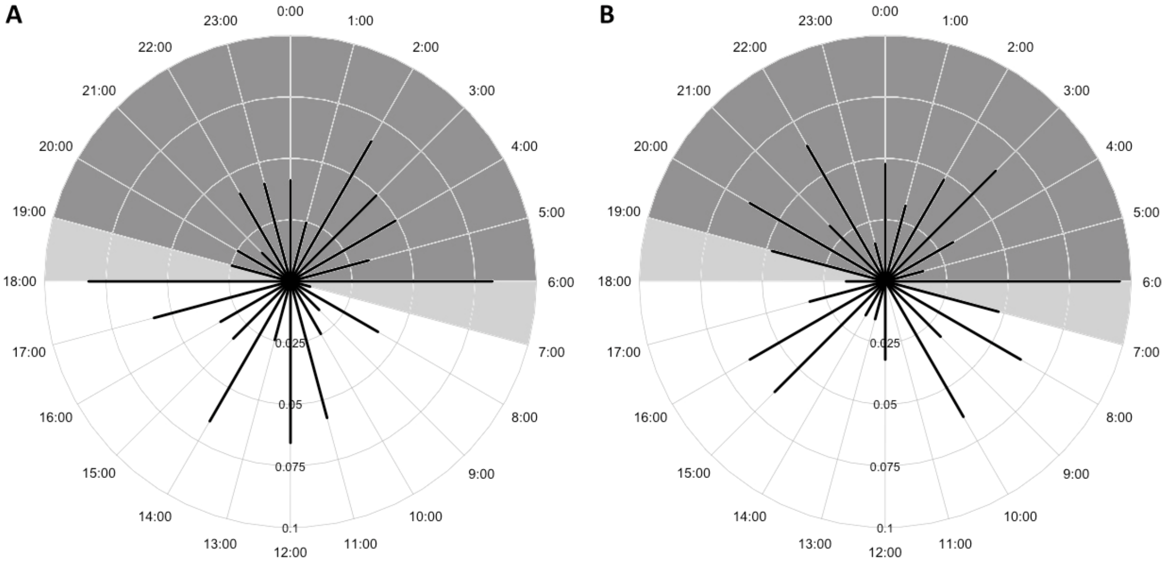

Figure. 2.4. Activity patterns of the African golden cat based on camera trap surveys at three sites in central Gabon (a) and at three sites in Kibale, SW Uganda (b), presented as proportions of the total number of photo-captures (Gabon, *n* = 122; Kibale, *n* = 63). Circular grid lines (*y*-axis) represent proportion thresholds, with 0 at the centre and 0.1 at the outer circle. Numbers around the outer circle (*x*-axis) correspond to time (h). Dark grey shading represents night-time and light grey represents twilight.

Like leopards living in forest where the undergrowth is dense (Henschel & Ray 2003), golden cats prefer to move along roads and well-used tracks. Photo-capture rates for golden cats in Gabon are much higher on abandoned logging roads and skidder tracks than along wildlife trails. In logged areas, scats are found almost exclusively on old roads and large trails. At a pristine site without human trails, photo-captures and sign were typically found along large trails created by forest elephants Loxodonta cyclotis. Preliminary findings from Gabon and Uganda suggest that golden cats avoid trails that are regularly used by humans.

Golden cats probably have a similar territorial tenure system to other solitary felids, in which adult males hold territories that encompass all or part of the home ranges of several adult females [e.g. puma (Seidensticker et al. 1973); leopard (Bertram 1979); jaguar (Rabinowitz & Nottingham 1986); tiger Panthera tigris (Sunquist 1981)]. Exposed scats along trails are a sign of marking behaviour and territoriality (Ray & Butynski 2013).

Tonkin and Kohler (1978) describe the vocal repertoire of captive golden cats as extensive; the principal vocalization is a strong, abrupt and husky ‘meow’. Typical felid sounds such as ‘hisses’, ‘snarls’ and ‘growls’ occur in captivity (Kingdon 1977). A low-volume, short (0.5s), rhythmical sound sequence, described as ‘gurgling’, is also produced (Peters 1984).

2.4.9 Reproduction

Little information is available on golden cat reproduction in the wild. There is one record of a golden cat with a nursing kitten in a hollow log in the Ituri Forest (Hart et al. 1996). Hunters in Lobeké Forest claim that kittens are delivered and cared for in tree holes that are often >5 m above ground (T. Davenport & G. Ngandjui, pers. comm.). A pregnant female with two foetuses in the final trimester was trapped in early September in Bwindi (Kingdon 1977).

Information on reproduction in captive individuals is also scarce as there are currently no African golden cats in registered zoos, and only one male in captivity of which we are aware (Bahaa-el-din 2012). The only published information comes from Tonkin and Kohler (1978), who report on a captive pair (siblings) that bred four times, producing two kittens each time. One set of kittens, born 75 days after the heat period, began to open their eyes at 2–3 days, and showed high mobility once their eyes fully opened at 6 days. One kitten stood for the first time at 10 days. Kittens were agile from day 16, and ate meat from day 40. Tonkin and Kohler (1978) remarked that development in this species seemed advanced compared with other small felids. A female first came into oestrus at 11 months while a male seemed to reach sexual maturity at about 18 months.

2.4.10 Threats and conservation

Several aspects of the golden cat's ecology make it vulnerable to extinction: a geographic range limited to tropical Africa, habitat specialization (dependence on forest) and a high trophic level making it susceptible to cumulative disturbances in the food chain (sensu Purvis et al. 2000). The golden cat has already been extirpated from large parts of its former range due to loss of habitat, particularly in West Africa, and its numbers have been reduced over much of the remaining habitat as a result of hunting (Ray et al. 2005). In 2005, it was estimated that 44% of the historic range had been lost (Ray et al. 2005). The golden cat is listed as 'Near Threatened' on the 2014 IUCN Red List based on assessments of habitat loss, hunting and loss of prey (Henschel et al. 2008)1.

An estimated 0.46% (15,350 km2) of West and Central Africa's forest was lost annually between 2000 and 2010 (FAO 2010). By 1992, as many as 17 tropical African countries had already lost more than 90% of their original forest cover (Sayer 1992). For the golden cat, this probably translated into a 90% loss of habitat in these countries. In the species' remaining range, the hunting of wild animals for protein (bushmeat) is accelerating rapidly due to an increasing human population, modernization of hunting techniques and remote areas becoming more accessible through roads and rail (Blake et al. 2007, Fa & Brown 2009). Bushmeat hunting is unsustainable when commercialized (Noss 1998, Muchaal & Ngandjui 1999) and may lead to a widespread phenomenon commonly referred to as the 'empty forest syndrome' (Sayer 1992, Wilkie et al. 2011). The main stronghold for the golden cat is the Congo Basin, considered to be the least accessible part of its range. Blake et al. (2007), however, found that over 64% of forest habitat in the Congo Basin is within 10 km of a road and is therefore exposed to hunting.

The bushmeat trade is having a serious impact on many of the golden cat's prey species, posing an indirect threat to the golden cat (Ray et al. 2005). For example, in Korup National Park, W Cameroon, the forest is intact, but commercial bushmeat hunting is intensive (Fa et al. 2006). A thorough camera trap study carried out in Korup (2011 – 2013) produced no golden cat or leopard captures (TEAM, http://www.teamnetwork.org).

In Gabon, golden cats comprise 0.12% of bushmeat market sales and 0.08% of village hunting off-take (Bahaa-el-din et al. 2013). Thirteen golden cats found in wire snares in Lobeké Forest over three months represented 0.4% of mammals caught (this was 0.6% of mammal biomass and 21% of carnivore biomass). Forty-seven per cent of the mammals captured were prey species of the golden cat (T. Davenport & G. Ngandjui, pers. comm.). Two of the four principal bushmeat species in Dzanga-Sangha Reserve are among the main prey of golden cats (Ray 2001). Forest leopards occur at lower densities near settlements as a result of competition with

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[1] Since the publication of this chapter in Mammal Review, the Red List status of the golden cat has been updated to 'Vulnerable' (Bahaa-el-din et al. 2015; Appendix 1).

humans for prey, and are entirely absent in forests where hunting occurs at a commercial scale (Henschel et al. 2011). Golden cats may be similarly affected by reductions in their prey base from bushmeat hunting.

Golden cats appear to be extremely vulnerable to snaring, which is the most commonly used hunting method in African forests (Fa & Brown 2009). They are usually killed, but those that escape are left maimed (Fig. 2.5). Photo-captures indicate that one individual that lost part of his leg to a snare survived for at least 2 months.

Figure. 2.5. Camera trap photographs of snare-wounded African golden cats. (a) Back right leg is severed (central Gabon) and (b) Cat is scarred on the waist from a snare wound (Kibale, SW Uganda).

In Yaoundé (Cameroon), Kampala (Uganda) and Pointe- Noire (Republic of Congo), golden cat skins are sold alongside medicinal herbs and fetishes (Wilson 2001, T. Davenport & G. Ndanjui, pers. comm.). They are reportedly used for circumcision rites and for wrapping valuable objects (van Mensch & van Bree 1969), and as good luck charms when hunting (Guggisberg 1975). The golden cat is listed in CITES Appendix II. In addition, the hunting of this species is prohibited or regulated by national laws in about half the range countries (Nowell & Jackson 1996).

West and Central Africa have the fastest growing human population of any region in the world: a rate of 2.6% per year (FAO 2010). The resultant increase in demand for forest products, land, and meat, will further accelerate the loss of forest and the hunting of wild animals (Butynski 2001). Currently, 16% of the area covered by forest in West and Central Africa is designated for conservation; 29% of the area is designated for production of wood and non-wood forest products (FAO 2010). Golden cats are frequently captured by camera traps in logged forests. A key element for the conservation of this species is to ensure that commercial ventures (mainly logging, mineral extraction, agriculture) within forests operate under strict regulations that allow for the persistence of wildlife (Meijaard & Sheil 2008, Clark et al. 2009). This is often not the case, and these ventures typically greatly exacerbate the issue of bushmeat hunting by opening roads into remote areas and importing people (Wilkie et al. 2000).

If road-blocking and hunting regulations were obligatory and enforced, as is required for forest certification by the FSC, commercial logging ventures would have the potential to act as stewards of wildlife. This would more than double the area in which golden cats and other forest-dependent species are effectively protected (Clark et al. 2009, Putz et al. 2012). In Gabon, for example, 11% of the land is designated for protection, whereas 35% is designated for logging (Nasi et al. 2012). Of the land designated for logging, 34% is under some form of certified management (52% of which is FSC certified). In Cameroon, just 13% of the land designated for logging is certified (all by the FSC; Nasi et al. 2012). A key step in the conservation of golden cats is, therefore, to tackle the issue of non-certified logging (as well as the monitoring of certified logging) at government and forest management levels. This would help to create conservation strongholds and reduce the level of fragmentation through the creation of safe corridors between protected areas (Clark et al. 2009).

Political instability and corruption are prevalent in much of the golden cat’s geographic range and pose additional threats. In DRC, for example, large tracts of land were given to neighbouring countries to exploit for timber and other resources in exchange for military support to combat rebels (Vedder et al. 2001).

Inskip and Zimmermann (2009) categorized golden cats as having a low rate of conflict with humans, but in areas where they are perceived as conflict animals, they are likely to be persecuted (Ray et al. 2005). Kingdon (1977) and Davenport (1996) report that, in Uganda, golden cats kill livestock (e.g. poultry, goats and sheep). Such reports may, at least in part, result from confusion with other sympatric carnivore species (Ray & Butynski 2013). Most reports rely on retrospective accounts rather than direct observation. Many reports of predation are from isolated forests surrounded by high human population densities (>300 people/ km2) and intensive agriculture. On the border of Kibale, for example, all reported golden cat predation events occurred within the forest or in very close proximity to the hard forest edge (D. Mills, unpublished data). Preliminary findings from an attitudinal survey carried out in four villages in Gabon indicate that the golden cat is not perceived as a problem animal (L. Bahaa-el-din, unpublished data). Unlike other carnivore species included in this survey, the golden cat was not identified as a livestock predator. Though golden cats may occasionally kill livestock, their interface with people is narrow, and they are therefore unlikely to be significant conflict animals.

There is very little information available on natural sources of golden cat mortality. Golden cat remains were found in five of 197 leopard scats from Lopé National Park, indicating predation by leopards (Henschel et al. 2005).

2.5 Conclusion

2.5.1 Camera trapping synthesis and survey design recommendations

The African golden cat is the focus of our current camera trap studies in Gabon and Uganda. These studies demonstrate that camera trapping can produce adequate data to assess golden cat distribution, abundance, ecology, behaviour and threats. Camera trapping shows the golden cat to be cathemeral, rather than crepuscular or nocturnal as stated in the literature. Most significantly, camera traps detected golden cats more frequently than expected given the low number of sightings, and preliminary identification of individuals suggests that, in some areas, they may be more abundant than previously thought.

Based on the height of golden cats and their trail use patterns, we recommend that cameras be placed c. 25 cm above the ground and 1.5 – 2.0 m from the edge of abandoned logging roads, skidder tracks and large game trails, facing the track. This protocol appears to maximize photo-captures of golden cats. Spacing of 600 – 800 m between trapping stations will ensure recaptures of females at several stations, which may be desirable if density estimation is an aim. It is possible to counteract the small sample area created by such tight camera spacing by placing a subset of the cameras farther apart, to widen the survey area. Analysis of data from differently spaced camera traps has been made possible through the development of spatially explicit capture–recapture models (Borchers & Efford 2008). These models, however, require adequate movement data, both for males and females, through recaptures at different sites. For individual identification, it is advisable to use white-flash cameras that produce clear photographs, and to set the cameras to take several consecutive photographs.

2.5.2 Conservation and future research

The literature review and field studies presented here are intended to guide conservation planning for the golden cat. Use of wire snares can have significant direct and indirect impacts on golden cat populations and has caused extirpation from some areas. Tightening and enforcement of hunting regulations, particularly snaring bans, should be encouraged.

The presence of golden cats in active logging concessions is encouraging and highlights the importance of these areas for the conservation of the species. Requiring logging concessions to be certified helps to secure the conservation value of these areas. Considering that 29% of the forest area in West and Central Africa is designated for extraction while just 16% is designated for conservation (FAO 2010), governments should enforce strict regulations for the logging industry so that environmental degradation is minimized in and around exploited areas during and after extraction.

Our camera trap surveys were designed to assess golden cat occurrence and abundance within human land-use areas. Valuable additions to this work would be to conduct camera trap surveys in areas where occurrence is uncertain and to monitor sites in changing landscapes to assess population trends. As studies of the golden cat become more widespread, we encourage and invite collaboration to build a landscape-scale assessment of this little-known species.

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3. Effects of human land-use on Africa's only forest-dependent felid: the African golden cat *Caracal aurata*

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Cover image: Logging and bushmeat hunting are common human activities in the African rainforest, and affect golden cat populations. © Left: Tim Rayden; right: Laila Bahaa-el-din

3.1. Abstract

Africa's equatorial forests are threatened by widespread deforestation and bushmeat hunting, with both threats spreading into formerly remote areas due to rapid human population growth and large-scale expansions of commercial resource extraction such as logging and mining, as well as forest clearing for agriculture. Many globally threatened species are endemic to these forests, but the potential effects of these threats are not well understood. Using the case of the forest-dependent African golden cat, we assess the potential effects of disturbance including logging and hunting on African forest carnivores. We applied spatially-explicit capture-recapture models to camera trap data to estimate density across a human disturbance gradient at five sites in central Gabon. Estimates had wide confidence intervals, but there was a general trend towards decreasing density with increasing human disturbance. The density estimate was highest at an undisturbed site (16.23 individuals per 100 km2) and lowest at a village site with moderate levels of mostly subsistence bushmeat hunting (3.8 individuals per 100 km2). Logging concessions can support important densities of the species (10.18 and 12.84 individuals per 100 km2), with the slightly higher estimate of the two for the concession certified by the Forestry Stewardship Council (FSC) versus the non-certified concession. While protected intact forests are the main strongholds for golden cats, well-managed logging concessions may also play an important role in the conservation of golden cats and other threatened species.

3.2. Introduction

African rainforests are predicted to undergo major changes in the near future due to widespread development of mining, logging, and oil palm plantations, as well as clearing to make space for an increasing human population (FAO 2011, Edwards et al. 2014, Wich et al. 2014). Remaining forests occur mostly in West and Central Africa, where annual forest loss during 2000 – 2010 was 1.1% for West Africa and 0.3% for Central Africa, and that loss is increasing (FAO 2011). Forests in these economically poor regions are seen as a source for subsistence by rural communities and of commercial income by industry and governments. In Central Africa, where the bulk of Africa's tropical forest remains, 22.9% of forest area is designated for production, while only 3.7% is designated for biodiversity conservation (FAO 2011). Unselective hunting of wildlife for bushmeat is also ubiquitous in the region, with forests being emptied of their wildlife to provide protein for rural communities and trade to urban centres (see "empty forest syndrome"; Redford 1992, Wilkie et al. 2011, Abernethy et al. 2013). Human population growth rates in West and Central Africa are among the highest in the world (+2.6 per annum; FAO 2011), thereby increasing demand on forest products and land, and accelerating the rate of forest and wildlife loss.

The African golden cat Caracal aurata is Africa's only forest-dependent felid, being endemic to equatorial Africa (Bahaa-el-din et al. 2015a). Due to its forest-specialisation, threats to Africa's forests are likely to translate directly to threats to golden cat populations. This reliance on forest habitat and its position at the top of the food chain make it a promising candidate indicator species for long-term sustainability of the African forest ecosystems. The golden cat is elusive and has hitherto never been studied systematically. There is no baseline information on golden cat populations as a result, but it is widely reported as naturally rare (Hart et al. 1996, Hunter and Barrett 2011). The golden cat is currently classified as Vulnerable on the IUCN Red List based on an estimated 30% loss of range over the last 15 years (Bahaa-el-din et al. 2015b). However, due to the paucity of data, assessments have relied mostly on inferences based on general trends in forest loss and bushmeat hunting. There are neither data on population size, nor an assessment of the impact of human activities on golden cat populations.

The relatively recent advent of remotely-triggered camera traps has allowed for the non-invasive study of elusive species such as forest felids (e.g. Maffei & Noss 2008, Wilting et al. 2012, Mohamed et al. 2013). Further advances in spatially-explicit capture-recapture analysis (SECR or SCR; Efford 2004, Royle and Young 2008) permit more robust estimation of felid population density. SECR models incorporate the spatial information of captures, and use it to account for animal movement about their home ranges when modelling detection probability. They permit estimation of density for an explicitly defined area by using the location of traps relative to the location of animals, and are not biased by ad-hoc approaches to estimating the size of the sampled area, as traditional non-spatial capture-recapture models are. We use SECR models to produce the first density estimates of African golden cats. We applied this method across a gradient of human land-uses to assess potential impacts on golden cat populations, thereby remedying the lack of baseline population information on golden cats while using the species as an indicator for the effects of logging and hunting on forest wildlife.

Prior studies on leopards Panthera pardus in Gabon established adverse effects of bushmeat hunting and logging on the occurrence and abundance of this species (Henschel et al. 2011). We predict that golden cats are likewise negatively affected by hunting and logging and that within logging concessions, Forest Stewardship Council (FSC) certified concessions hold higher densities of golden cats than non-certified ones due to FSC requirements to follow regulations on anti-poaching and reducing structural damage to the forest.

3.3. Methods

3.3.1. Study area

The study was conducted at five sites (each of ca. 20km2) in central Gabon, where human population density is low (1.5-2.0 inhabitants/km2), and more than 95% of the region is covered by mature lowland semi-evergreen rainforest (Henschel et al. 2011). The terrain is undulating with elevations ranging between 100 and 1000 meters. Lopé National Park and Ivindo National Park are located within this forest landscape, while much of the forests outside these parks consist of logging concessions (Fig. 3.1). The climate within this area is equatorial with two rainy seasons and two dry seasons and average yearly precipitation of 1300 – 2000 mm (Vande Weghe 2006, Vande Weghe 2011).

3.3.2. Camera trapping and data preparation

Within our study area, we selected 5 sites along a gradient of human land-use types (Table 3.1, Fig. 3.1) to assess variation in golden cat density in response to anthropogenic impacts. At each site, we started with a reconnaissance period where we recorded golden cat sign and trail type (see below) by GPS (Garmin eTrex Legend HCx). We based placement of 38 – 41 camera trap stations per site on field sign and trails, mapped using ESRI's ArcGIS software (version 9.3), in order to maximise golden cat captures. We placed cameras on a variety of existing trails, including logging roads, skidder trails, elephant trails and smaller game trails (Fig. 3.2).

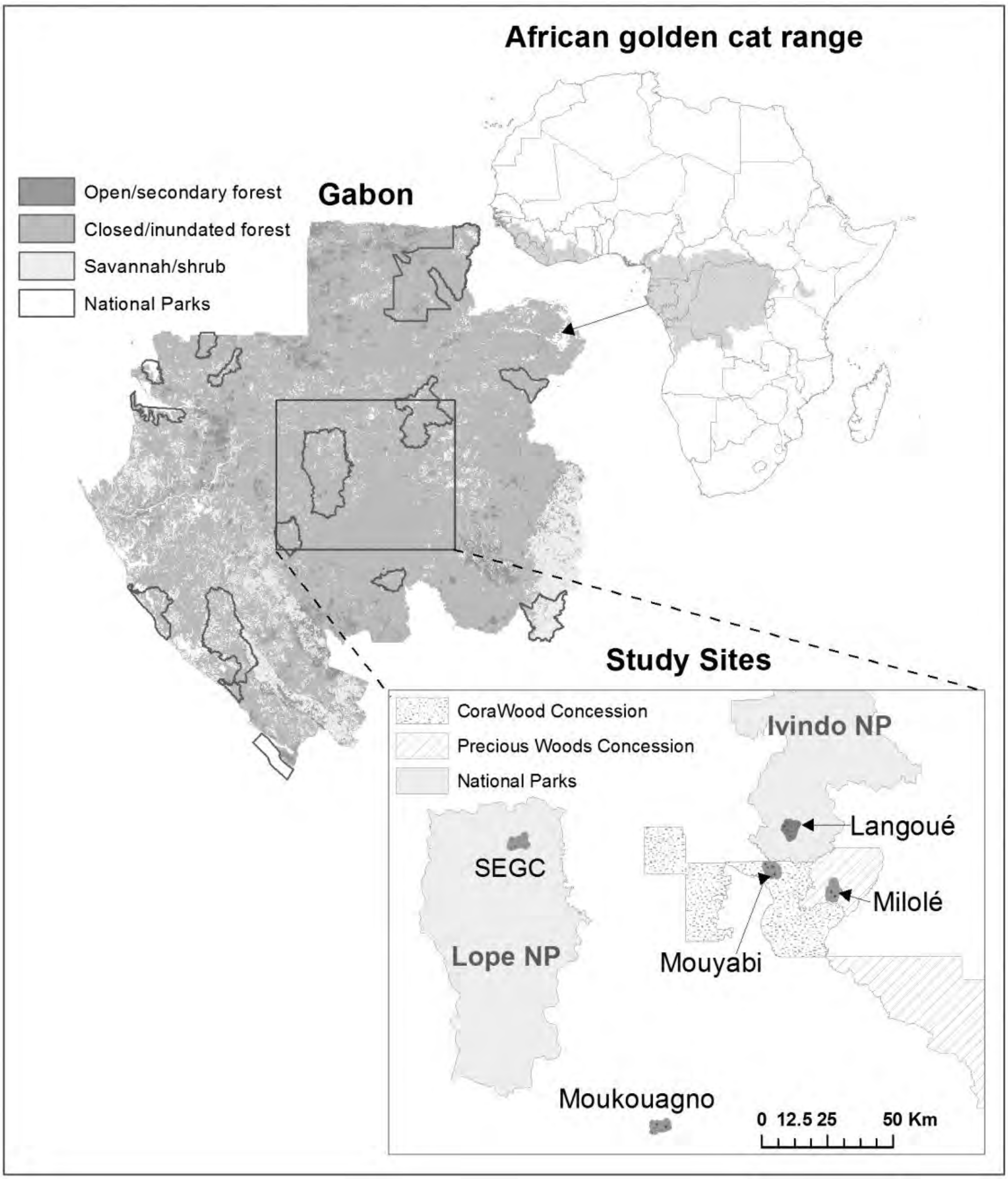

Figure 3.1. African golden cat range, with an inset of Gabon's habitat and parks, and further inset of study sites.

We placed stations 600 – 800 m apart based on finding during a pilot study that 1 km spacing did not allow for many individual recaptures of females (Bahaa-el-din et al. 2011). Each station consisted of two cameras facing each other with a slight offset to avoid flash interference. We used 40 – 70 Panthera camera traps (models v3 & v4; panthera.org), supplemented with 6 – 20 ScoutGuard (model SG565F; Boly Media Communications (Asia) Co., Ltd.) and 4 – 24 DeerCam (model 200 with 35 mm film; Non Typical Inc., Park Falls, Wisconsin, USA). Most camera stations included one Panthera camera trap, placed opposite a ScoutGuard or DeerCam. We placed cameras on trees, about 25 cm above the trail, and checked units every 10 – 20 days to change batteries and download photos (or change 35 mm films, in the case of the DeerCam units). Where possible, we timed survey periods to coincide with the long dry season of June – September but surveys at Langoué, CoraWood and SEGC overlapped with the start of the rainy season. We aimed to have traps active simultaneously for at least 50 days per site, and extended the study period in areas where we had a low number of captures in order to increase the chance of being able to apply SECR models.

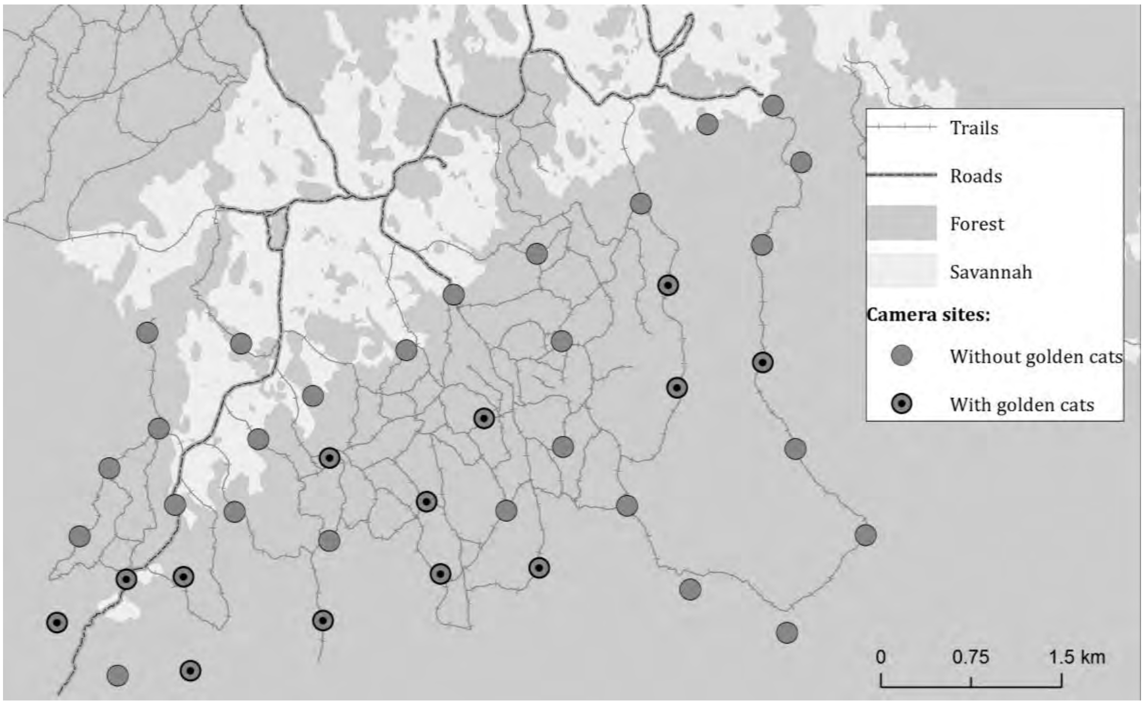

Figure 3.2. Trapping grid at the *Station D'Etudes des Gorilles et Chimpanzes* (SEGC), Lopé National Park, as an example of grid layout.

Table 3.1. Details of our five study sites in central Gabon

Site name	**Management**	**Trapping location range**	**Elevation range (m)**	**Forest description**	**Disturbance history**	**Period**	**Survey duration (days)**
Langoué, Ivindo NP	National Park	0°8'-0°12'S, 12°31'-12°34'E	380-581	Mature semi-evergreen rainforest	Pristine forest, with no evident past disturbance	Sep – Nov 2011	55
Station D'Etudes des Gorilles et Chimpanzes (**SEGC**), Lopé NP	National Park	0°11'-0°14'S, 11°34'-11°38'E	216-583	Colonising, post-logging secondary forest along savannah edge	Logged in 1970s	Sep – Dec 2013	102
Milolé, PreciousWoods Concession	Logging concession (FSC-certified)	0°20'-0°24'S, 12°40'-12°42'E	229-323	Mature semi-evergreen rainforest, with post-logging secondary forest	Logged 2 years prior	June – Aug 2011	54
Mouyabi, CoraWood Concession	Logging concession (not-certified)	0°17'-0°20'S, 12°27'-12°30'E	349-533	Mature semi-evergreen rainforest, with post-logging secondary forest	Logged 2 years prior	Aug – Oct 2012	79
Moukagno	Village hunting area (ca. 21 households)	1°10'-1°12'S, 12°3'-12°7' E	461-711	Mature semi-evergreen rainforest, with post-logging secondary forest	Hunting, logged in 1990s	May – Aug 2013	89

*FSC = Forestry Stewardship Council

Golden cats have unique markings on their coats, making it possible to identify individuals of the species (Fig. 3.3). However, these markings are often restricted to the underside and inside of limbs, which renders identification difficult from camera trap photographs. We therefore identified photographs of golden cats independently using three observers (Kelly et al. 2008), all experienced in the identification of felids. We included photographs in the analysis that were identified as the same individual by at least two out of the three observers. To ensure temporal independence of captures, we used an independence threshold of one hour and excluded all but one capture of the same individual taken at the same camera station within an hour (Tobler et al. 2008).

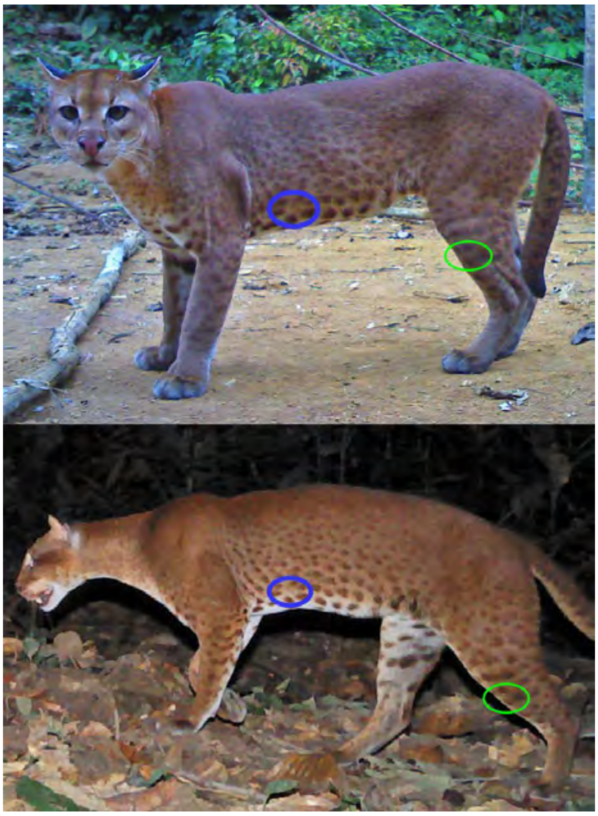

Figure 3.3. Coat markings on African golden cats allow individuals of the species to be identified: a prerequisite for the capture-recapture models that we used. Markings within colour-coded circles correspond to each other.

Leopards are presumably the main natural competitors for golden cats (Hart et al. 1996, Ray & Sunquist 2001), and are known to occasionally prey on them (Henschel et al. 2005). We therefore included leopard capture rate as a station-level covariate that may influence detection, to test if golden cats avoid trails frequented by leopards (Table 3.2). We also included prey photographic rate to assess whether golden cat detection is positively correlated with that of their prey. We selected main prey species based on dietary studies (Hart et al. 1996, Ososky 1998, Ray & Sunquist 2001), but were restricted to those species readily caught on camera traps (therefore excluding small rodents). We included blue duiker Philantomba monticola, giant pouched rat Cricetomys gambianus and African brush-tailed porcupine Atherurus africanus.

Prior studies on Neotropical forest felids found that species detection probability at camera stations can also depend on trail width (e.g. Harmsen et al. 2010) and vegetation (e.g. Kelly & Holub 2008), so we measured trail width and herbaceous understory density at each camera station. We measured trail width in millimetres between the two cameras. To assess herbaceous understory density, we counted stems in four 1m2 plots, 5 m from the trail in the cardinal directions and averaged results to obtain one value for each station. In cases where rivers or trails interfered with cardinal directions, we adjusted directions by 45^0. We calculated leopard photographic rate as the number of independent photographs of leopards for each camera station out of the total number of trapping days at each station.

Table 3.2. The mean and standard errors (SE) of the camera site variables in each study area.

	Trail Width (mm)		Vegetation (# of stems)		Leopard (photographic rate)		Golden cat prey (photographic rate)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Langoué	501.3	20.8	24.5	1.7	0.9	0.3	20.9	2.9
SEGC	844.0	314.0	46.2	20.2	2.7	2.6	17.8	3.2
Milolé	921.9	178.3	23.3	1.5	1.0	0.3	26.3	3.5
Mouyabi	1778.0	222.0	46.4	2.7	2.4	0.6	16.4	2.7
Moukagno	1371.0	173.7.0	42.7	4.4	0.6	0.2	10.5	2.6

3.3.3. Data analysis

We used the package "secr" (Efford 2015) in the programme R (R Core Team 2014) to run maximum-likelihood spatially-explicit capture-recapture models. These models describe detection probability of an individual at a given trap as a function of the distance of that trap to the individual's activity (or home range) centre. The location of that centre is estimated based on the spatial locations of captures of an individual. The decline in detection with increasing distance to the centre is assumed to follow a detection function. We used a half-normal detection function, which is governed by two detection parameters: g0, the baseline trap encounter rate at a hypothetical trap located at an activity centre, and σ, the scale parameter of the function, which is related to how far animals move. We ran multi-session models, with each study site as a "session". This allowed us to obtain estimates for the sites that had lower numbers of captures by sharing detection parameters across sites where appropriate, but providing independent density estimates for each site. Accounting for differences in detection probability and movement between the sexes improves density estimates in some felids (Sollmann et al. 2011). We therefore dealt with males and females as two "groups" within the same models to test whether accounting for these sex-specific parameters is important for golden cats. We used "count" as detector type to allow for multiple captures of the same individual at the same camera station per occasion. We accounted for days when cameras were not functioning by including a binary matrix of active-inactive days as a measure of effort.

We first ran basic models on each site separately and found that the baseline detection probability g0 was similar across protected sites and similar across non-protected sites. In the multi-session model, we therefore modelled g0 as a function of protection status. The scale parameter σ was similar across all sites, thus we modelled σ as constant. We used a buffer width of 5000 m, a little over three times σ; increasing the buffer above this had no effect on density estimates.

We first compared a basic model with site-specific densities and constant detection parameters with a model using protection status as a session covariate on g0. We compared models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). The model including protection status had a lower AIC than the basic model, and we therefore used this as our baseline model and built on it, with a group covariate (sex) on both detection parameters, and with station level covariates on g0 (trail width, ground vegetation density, leopard photographic rate and main prey photographic rate).

3.4. Results

We photographed golden cats a total of 203 times across the 5 sites, representing 36 identified individuals (Table 3.3). Of these, 86.2 % were identified by at least two out of the three observers and were used in analysis (Table 3.3). Of the captures that were not identified as a particular individual by all three observers, 50 captures (out of 78) had at least one observer that did not attempt to identify the individual due to poor photograph quality or bad angle.

Our most supported model by AIC included protection status (beta coefficient: -0.75 ± 0.27 SE) and leopard photographic rate as covariates on g0 (beta coefficient: 0.16 ± 0.02 SE; Table 3.4). The baseline detection probability, g0, was higher for non-protected than protected sites (Fig. 3.4). The effect of leopard capture rate was positive, indicating that detecting golden cats was positively associated with the number of leopard photographs at a given camera station. Trail width, ground vegetation density and prey photographic rate as covariates on detection also received more AIC support compared with the basic model (beta coefficients: 0.36 ± 0.07 SE for trail width; 0.24 ± 0.08 SE for vegetation; -0.01 ± 0.005 for prey photographic rate). The basic model and models incorporating sex in the functions of g0 and/or σ were least supported.

Notwithstanding the overlap in 95% confidence intervals between site estimates of density (Fig. 3.5), there was a general trend towards lower population density with increased human disturbance. Langoué, the undisturbed site, had the highest density estimate (16.2 individuals per 100 km^2). Milolé and Mouyabi, two logging concessions, had the next highest density estimates (12.8 and 10.1 individuals per 100 km^2 respectively), with Milolé (the FSC-certified concession) having a slightly higher estimate. SEGC, a protected site within a forest-savannah mosaic, had a substantially lower estimate (6.2 individuals per 100 km^2), while Moukagno, the village hunting site, had the lowest estimate (3.8 individuals per 100 km^2; Fig. 3.5).

Table 3.3. Details relating to African golden cat captures for each site, including individuals identified, rates of identification and movement.

Site name	Trap days	Golden cat captures	# capture stations out of total stations	# individuals identified	# recaptures	# male & female individuals (# captures)	% captures used for analysis*	Mean maximum distance moved (km)**
Langoué, Ivindo NP	1899	37	$\frac{22}{38}$	9	28	5 (18) & 4 (12)	81.1	2.48
SEGC, Lopé NP	2885	24	$\frac{13}{40}$	5	19	3 (11) & 2 (6)	70.8	1.79
Milolé, Precious Woods	1956	48	$\frac{19}{40}$	10	38	6 (28) & 4 (10)	77.1	2.47
Mouyabi, CoraWood	2911	77	$\frac{25}{41}$	9	68	4 (36) & 5 (38)	96.1	2.62
Moukagno	2859	17	$\frac{9}{40}$	3	14	2 (14) & 1 (3)	100	2.86

*Only photo captures that were identified as the same individual by at least two out of three observers during double-blind identification were used for analysis

** Excluding individuals that were only photo-captured at one site

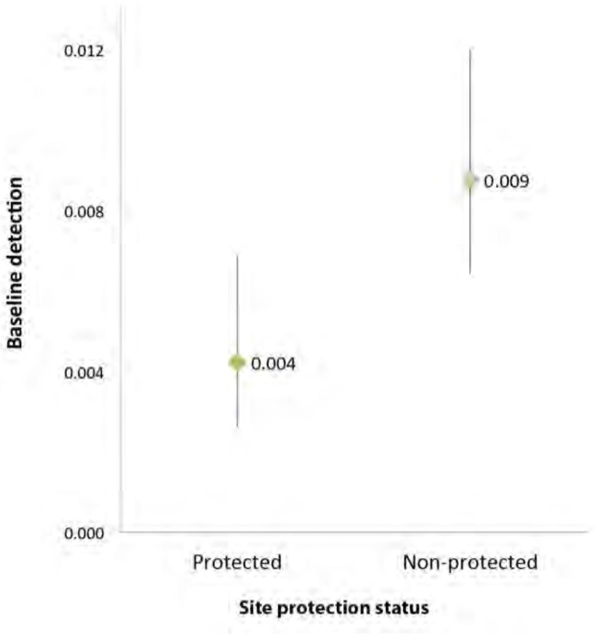

Figure 3.4. Baseline detection probability (*g0*) at protected and non-protected sites (per camera station, per day), with 95% confidence intervals.

Table 3.4. Summary of density estimation models run in the "secr" package (Efford, 2015) in R, and their corresponding AIC values. *Parameters: D = Density estimate, g0 = baseline detection, sigma = scale parameter. **Covariates: "Protection" = the protection status of the site, "Leopard" = leopard photographic rate, "Trail" = trail width, and "Veg" = ground vegetation density, "sex" = individual gender.

Model (detection function = halfnormal)	Para-meters	loglike-lihood	AICc	dAICc	AICc wt
D(Site), g0(Protection + Leopard), sigma(.)	9	-1114.78	2254.48	0.00	1
D(Site), g0(Protection + Trail), sigma(.)	9	-1125.74	2276.40	21.92	0
D(Site), g0(Protection + Prey), sigma(.)	9	-1134.04	2293.01	38.53	0
D(Site), g0(Protection + Veg), sigma(.)	9	-1134.70	2294.33	39.85	0
D(Site), g0(Protection), sigma(.)	8	-1138.99	2299.31	44.83	0
D(Site), g0(Protection + Sex), sigma(Sex)	10	-1138.91	2306.61	52.13	0
D(Site), g0(.),sigma(.)	7	-1144.36	2306.71	52.23	0
D(Site), g0(Sex), sigma(.)	8	-1144.01	2309.34	54.86	0
D(Site), g0(.), sigma(Sex)	8	-1144.07	2309.48	55.00	0
D(Site + Sex), g0(Protection + Sex), sigma(Sex)	11	-1138.88	2310.77	56.29	0

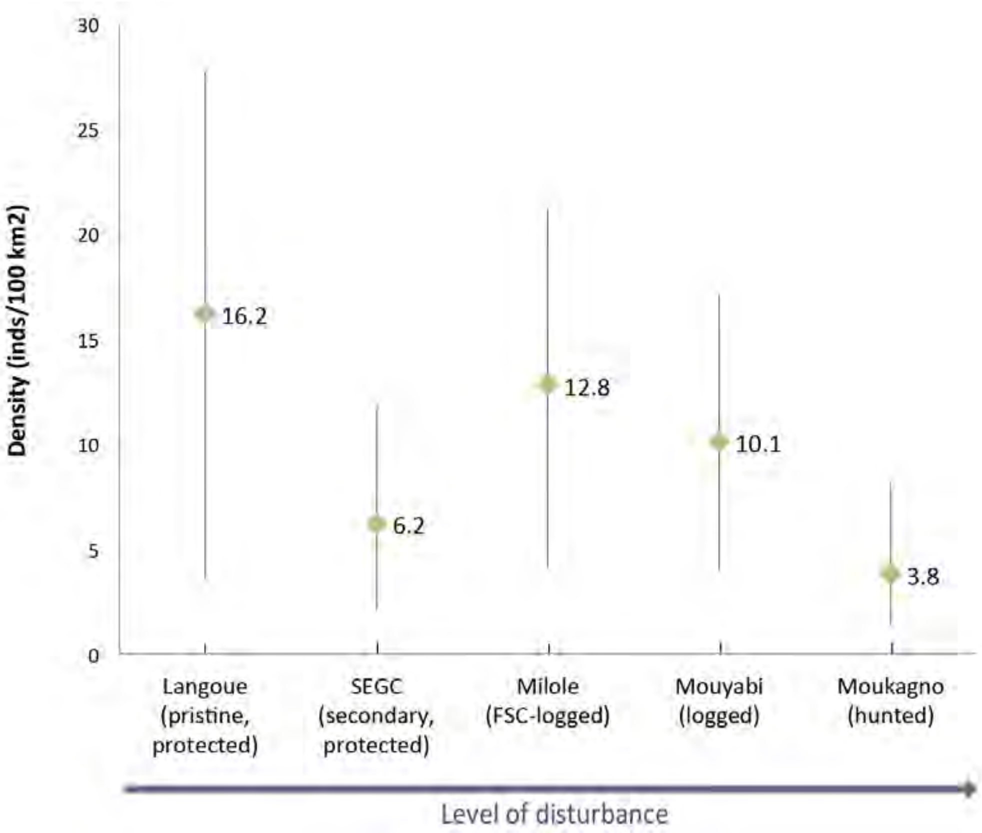

Figure 3.5. Density estimates (as number of individuals per 100 km^2) and 95% confidence intervals from spatial capture-recapture for each survey site.

3.5. Discussion

Our results provide the first density estimates of golden cats, and also show how density varies along a human land-use gradient in Gabon. Golden cats reached their highest density in a pristine forest site with no recent history of either deforestation or hunting. This estimate of 16.2 individuals per 100 km2 (inds/100 km2) is similar to density estimates for other similar-sized forest felids, indicating that in pristine forest habitat, the species is not naturally rare as previously thought (Hart et al. 1996, Hunter and Barrett 2011). For comparison, the leopard cat Prionailurus bengalensis in Malaysia reaches densities of up to 16.5 inds/100km2 (SECR results from camera traps; Mohamed et al. 2013). Ocelot Leopardus pardalis density in Belize was estimated at 11.2-12.5 inds/100 km2 using home-range radius from radio telemetry and at 25.9 inds/100 km2 using non-spatial capture-recapture from camera trap data (Dillon and Kelly 2008); the latter method has been shown to over-estimate density (Obbard et al. 2010).

While little is known about golden cats in disturbed areas, it has been suggested that they can adapt well to logged forests (Kingdon 1977). Mongo et al. (2012) showed greater relative density of the principal golden cat prey (rodents; Hart et al. 1996) in secondary forest compared to primary forest in the Democratic Republic of Congo, and golden cats may therefore benefit from a larger prey base within the secondary forest generated after logging. Our estimates of density in the two logging concessions (Milolé and Mouyabi) were the 2nd and 3rd highest amongst our study sites, confirming that golden cats can reach important densities in forests structurally impacted by commercial timber exploitation.

Within these two logged sites, we found that density was higher for the FSC-certified concession (in Milolé). FSC certification requires that the logging company minimises its impacts through strict regulations on extraction and site management, including a ban on hunting within the concession area. While the second logging concession (in Mouyabi) was not FSC-certified, it did operate under a management plan (a contract with the government to operate under sustainable practices). van Kreveld and Roerhorst (2009) found that apes, including gorillas, chimpanzees and bonobos, benefit from FSC-certification due to the FSC requirements to block and guard roads to reduce poaching, as well as protect fruiting trees. It is likely that many species benefit in a similar way. Forest management in logging concessions may therefore also play an important role in maintaining critical habitat for golden cats. This is especially relevant given the high rate of forest set aside for production in Central Africa relative to that set aside for protection (22.9 % for production versus 3.7 % protected; FAO, 2011).

Our results support the inclusion of logging concessions within the conservation estate as a means to expand the area within which endangered species are protected (Clark et al. 2009). It should be noted that we carried out our research in Gabon, a country unique to the region in having almost all its logging concessions operating under approved management plans (Nasi et al. 2012), 23% of which are FSC-certified (Table 3.5). Within the Congo Basin, considered the stronghold for golden cats (Bahaa-el-din et al., 2015a), just 90 out of 293 concessions were operating under a management plan in 2010, while 95 more were designing their plans (Nasi et al. 2012). Just 9% of these concessions in the Congo Basin were certified as of October 2015 (Table 3.5). Further investigation into the impacts of logging and certification on golden cats and other forest-dependent species should be pursued as a potential strategy for conservation planning. It would also be worthwhile to carry out similar studies comparing certified companies with companies not operating under a management plan, to assess the impacts under varying management strategies.

We note that intact primary forests are important for some specialised species, and may also be important as population sources from which disturbed areas can be repopulated (Clark et al. 2009). Both logging concessions included in this study were within 10 km of a national park boundary and it is as yet unclear how disturbance would affect an isolated golden cat population away from a large source population within a protected area.

We recorded the lowest density estimate (3.8 individuals per 100 km2) in the Moukagno village hunting area. Villagers reported the killing of at least four golden cats by wire snares during the two-month survey (Bahaa-el-din, unpubl. data). Such high offtake within an area with such low population density may indicate that the hunting area acts as a population sink (Pulliam 1988). Indeed, the village in question is remote, with uninhabited rainforest up to 25km to the north, 22km to the south and just one small village to the west, likely resulting in a large area for a source population. In contrast, in a more densely populated area to the east of Moukagno village, the hunting area of Dibouka hunting village was found to be devoid of golden cats, with no evidence of the species from camera traps (Henschel 2008) or bushmeat studies (Coad 2007). The same patterns were observed in a prior study on the impacts of human disturbance on leopards in Gabon, which showed that leopards were absent in the heavily hunted area of Dibouka village, occurred in low densities in Moukagno, and reached the highest densities in the sites least affected by hunting, irrespective of their logging history (Henschel et al. 2011). Our findings for the golden cat also match those of Brodie et al. (2015) who found that hunting poses a greater threat to forest mammals in Borneo than does selective logging. Abernethy et al. (2013) reviewed the impacts of various human activities on forest mammals and also found that bushmeat hunting poses the greatest threat to wildlife in Central Africa.

While gun-hunters in Moukagno spoke of rarely encountering or hunting a golden cat (one in 10 years for one hunter and none in eight years for another hunter; Bahaa-el-din, unpubl. data), the high snare capture rate from Moukagno (four in two months) suggests that this hunting method is particularly threatening to golden cat populations. A bushmeat study in Cameroon also found high snare capture rates for golden cats, with 13 individuals caught in three months at four survey sites (Davenport, pers. comm.).

We estimated relatively low golden cat density in the SEGC area of Lopé National Park, despite it being in a protected area. This low density may be the result of competition with and/or predation pressure from leopards at this site. The study site is situated at the southern edge of an extensive forest-savannah mosaic (Fig. 3.2), which is known to support a high biomass of principal leopard prey species (cf. Henschel et al. 2005) about eight times greater than the contiguous forest further south (Tutin et al. 1997). The site likely hosts a very high leopard density, which is supported by our data which show that the photographic rate for leopards (Table 3.2), and also the number of individual leopards identified, was highest at SEGC among our study sites. While we found that golden cat detection at a camera station was influenced positively by the number of leopard photographs, indicating a positive association in trail use, a particularly high leopard density may have a negative impact on the golden cat population.

Our study also found a higher baseline detection probability of golden cats in non-protected versus protected areas. We believe this is because golden cats frequently travel along large trails. Logging activities that necessitate the opening of logging roads and skidder trails facilitate the movement of golden cats (and leopards). Camera traps placed along these trails have a higher capture probability than those placed on smaller trails. Thus, our capture rate was higher at the two logging concession sites, which had among the highest average trail width (Table 3.2), but these did not translate into higher density estimates. Accordingly, comparing relative capture rates, or relative abundance indices (RAIs), should be avoided (Sollmann et al. 2013), at least for felids and other species that preferentially utilise trails.

To conclude, the golden cat is a useful proxy for the effect of anthropogenic disturbance on vulnerable forest taxa. Our findings that golden cats can be found at relatively high densities within well-managed logging concessions suggests that these areas should be considered a priority for conservation efforts, including post-extraction management to avoid further human encroachment to newly accessible forests. While in Gabon and Republic of Congo an important proportion of logging companies already strive for FSC certification and sustainable logging practices, this is not yet the case in most other Congo Basin countries which also harbour populations of golden cats and other vulnerable rainforest taxa. Consumer countries could stipulate further expansions of certified logging concessions by directing demand, which would in turn lead to an improvement of the conservation status of Congo Basin mammal communities, as evidenced by our work. In addition, pristine areas remain strongholds for golden cats, and likely provide source populations to degraded and recovering areas, and protecting primary forests should therefore also be a priority.

Table 3.5. Land-use in Congo Basin countries: protection, logging and FSC certification

Countries	Land*	Designated for protection*		Designated for logging*		FSC certified**	
	Area (km^2)	Area (km^2)	% Area	Area (km^2)	% Area	Area (km^2)	% Logging
Cameroon	465,445	37,450	8.05	60,935	13.09	9,409	15.44
Central African Republic	620,152	76,743	12.37	34,293	5.53	0	0
Congo	342,766	35,993	10.5	147,127	42.93	24,432	16.61
Democratic Republic of Congo	2,328,225	261,063	11.21	248,276	10.66	0	0
Equatorial Guinea	26,730	5104	19.09	14,375	42.93	0	0
Gabon	262,538	28,620	10.96	90,375	34.6	20,625	22.82
Congo Basin	40,45,856	444,973	11	595,381	14.72	54,466	9.15

* Nasi et al., 2012, ** FSC, 2015 (there may be slight discrepancies due to the difference in source dates)

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4. African golden cat behavioural plasticity: temporal shifts in response to leopards and humans

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Cover image: An assessment of the temporal activity of the forest-adapted African golden cat in relation to leopards, humans and prey. © Laila Bahaa-el-din (Hunter photo: © Lauren Coad).

4.1 Abstract

The mesopredator release hypothesis predicts that the loss of apex predators drives changes in the density, distribution and behaviour of mesopredators, which, in turn, has cascading effects throughout the food-web. The medium-sized African golden cat Caracal aurata is sympatric with the larger leopard Panthera pardus across most of its range. There is competition for prey between both species, and leopards occasionally prey on golden cats. Local extirpation of leopards from regions of equatorial Africa has resulted in golden cats becoming the largest felid in those forest regions. We contrasted golden cat temporal activity using camera trap data from six localities with both golden cats and leopards, against four localities without leopards. We recorded golden cats on 550 independent occasions in 35,968 camera trap days. Golden cat temporal activity differed significantly between sites with and without leopards. Golden cats were cathemeral with no evident pattern in the presence of the more nocturnal leopards, but were predominantly nocturno-crepuscular at sites where leopards are extirpated. As a result of this difference, the extent of overlap in temporal activity between golden cats and their main prey species also differed, with increased or decreased overlap depending on the prey species. Golden cat prey activity did not differ between areas with and without leopards, suggesting a lack of temporal response to leopard extirpation lower down the food chain. Overlap between golden cats and predominantly diurnal humans reduced from 63% where leopards were present to 29% where there were no leopards, suggesting that the switch in activity facilitates human avoidance in the absence of leopards.

4.2 Introduction

Co-existence of sympatric carnivores has been associated with asymmetric interactions, where the smaller species suffer exclusion from preferred habitat, reduced population growth, intra-guild predation, and kleptoparasitism (Creel 2001, Macdonald et al. 2010a, Cozzi et al. 2012). Such interactions have resulted in niche separation, with smaller carnivores showing avoidance through differences in diet (Hayward & Kerley 2008), temporal activity (Hayward & Slotow 2009) and/or space use (Creel 2001, Swanson et al. 2014, du Preez et al. 2015).

Extirpation of top predators from ecosystems is therefore likely to have an effect on persisting mesopredators through a phenomenon referred to as the mesopredator release hypothesis (MRH) (Soulé et al. 1988, Courchamp et al. 1999, Brook et al. 2012). Mesopredators are any mid-ranking predator in a given food web, regardless of body size and taxonomy (Prugh et al. 2009). The MRH states that the removal of dominant predators from a system may result in increased abundance of mesopredators (Paine 1969, Soulé et al. 1988, Ripple et al. 2014). More recently, Prugh et al. (2009) and Brashares et al. (2010) have opted for a broader definition, encompassing changes in density, distribution and behaviour (dietary, temporal and spatial) of mesopredators following declines in density and distribution of top-ranked competitors.

Unprecedented loss of large predators from ecosystems (Estes et al. 2011, Ripple et al. 2014) has led to increased investigations into the MRH in recent years (e.g. Kasparian et al. 2002, Brashares et al. 2010, Terborgh 2010). However, studies have focused mainly on the trophic release of mesopredators (e.g. Moreno et al. 2006). Little attention has been given to exploring whether shifts in mesopredator temporal behaviour are associated with the absence of larger predators (but see Harrington et al. 2009). Such shifts may increase interactions with other predators and humans (Rasmussen & Macdonald 2011), and have implications for prey selection and acquisition (Brook et al. 2012), with potential cascading effects impacting entire ecosystems (Terborgh 2010).

We address this knowledge gap using the case of the African golden cat Caracal aurata (hereafter “golden cat”), a medium-sized felid (8 - 14 kg; Ray & Butynski 2013) that is endemic to the African equatorial forest belt (Fig. 4.1), and is the continent’s only obligate forest felid (Bahaa-el-din et al. 2015a). Across most of its range, the sole sympatric felid is the leopard Panthera pardus (21 - 59 kg) (Hunter et al. 2013). This small felid community of the African rainforest contrasts with the felid-rich tropical forests of Central/South America and Asia, as well as Africa’s savannahs, which typically have five or six felids present (Macdonald et al. 2010b). The simplicity of the African forest felid community is ideal for testing the MRH without the confounding effects of multiple species.

Africa’s forests are also host to a large diversity of non-feline carnivores, especially members of the Viverridae and Herpestidae (Do Linh San et al. 2013). These species, however, do not have high trophic overlap with golden cats (Ray & Sunquist 2001), and are themselves potentially golden cat prey. Servals Leptailurus serval and side-striped jackals Canis adustus occur in Bwindi Impenetrable National Park (hereafter “Bwindi”) (Mugerwa et al. 2013) and Kibale National Park in Uganda (hereafter “Kibale”), where our four study sites without leopards were located. However, at those sites they are only recorded in open habitat along the forest edge, and we therefore do not consider them as competitors with high potential to affect golden cat activity.

In areas of sympatry, golden cats and leopards are reported to have high trophic niche overlap (Ososky 1998, Ray & Sunquist 2001). Golden cat remains have been found in leopard scat (Hart et al. 1996, Henschel et al. 2005), which could be indicative of interference competition by leopards (sensu Palomares & Caro 1999, Donadio & Buskirk 2006), or reflect general traits of leopard predation on medium-sized felids and canids documented elsewhere (Hayward et al. 2006). The golden cat may thus face a trade-off between optimum prey acquisition and avoiding potentially fatal interactions with leopards, as has been reported for other mesopredators (Mukherjee et al. 2009, Bischof et al. 2014, du Preez et al. 2015).

The golden cat has become the largest extant felid in rainforest areas where leopards are locally extinct, such as in Bwindi (Mugerwa et al. 2013) and Kibale (Mills et al. 2012), where leopards were extirpated around the 1970s (Butynski 1984, Struhsaker 1997). The effects of leopard extirpation on golden cats have not yet been explored. Here, using camera trap data from ten sites across three countries, we explore the temporal aspect of mesopredator release by comparing golden cat temporal activity patterns (hereafter "activity") at sites with and without leopards. We hypothesise that golden cat temporal activity will no longer be constrained in the absence of leopards. We predict that golden cats avoid periods of high leopard activity at sites where the two species co-occur, and that their activity patterns have fewer constraints (i.e. are released), and, therefore, differ at sites where leopards no longer occur.

Human activity often exerts a strong influence on the activity patterns of wild animals (Kitchen et al. 2000, Rasmussen & Macdonald 2011, Valeix et al. 2012) in a similar way that prey respond to predators within a "landscape of fear" (Oriol-Cotterill et al. 2015). We therefore also explore the role of human activity patterns on golden cat activity. We predict that golden cats exhibit avoidance behaviour of humans, and that this is more pronounced in areas without leopards as a result of golden cats not being constrained by having to avoid leopards as well.

4.3 Methods

4.3.1 Study sites

We collected data at ten sites over the course of three camera trapping studies (Fig. 4.1, Table 4.1). Two studies specifically targeted golden cats during surveys at five sites in central Gabon and at three sites in Kibale. The third study took place at one site in Bwindi, and one site in Nouabalé-Ndoki National Park (NNNP), Republic of Congo, as part of the Tropical Ecology Assessment and Monitoring Network (TEAM, www.teamnetwork.org). All surveyed sites have an equatorial climate, with two rainy and one or two dry seasons per year.

4.3.2 Data collection

We designed our surveys in Gabon and Kibale to maximise photo-captures of golden cats by targeting areas where there was golden cat sign (tracks, scat) and trails that were likely to be regularly used by the species. TEAM maintains camera trap grids in 18 tropical rainforests around the world, two of which we include here, to monitor bird and mammal communities following a standardized protocol (TEAM 2009).

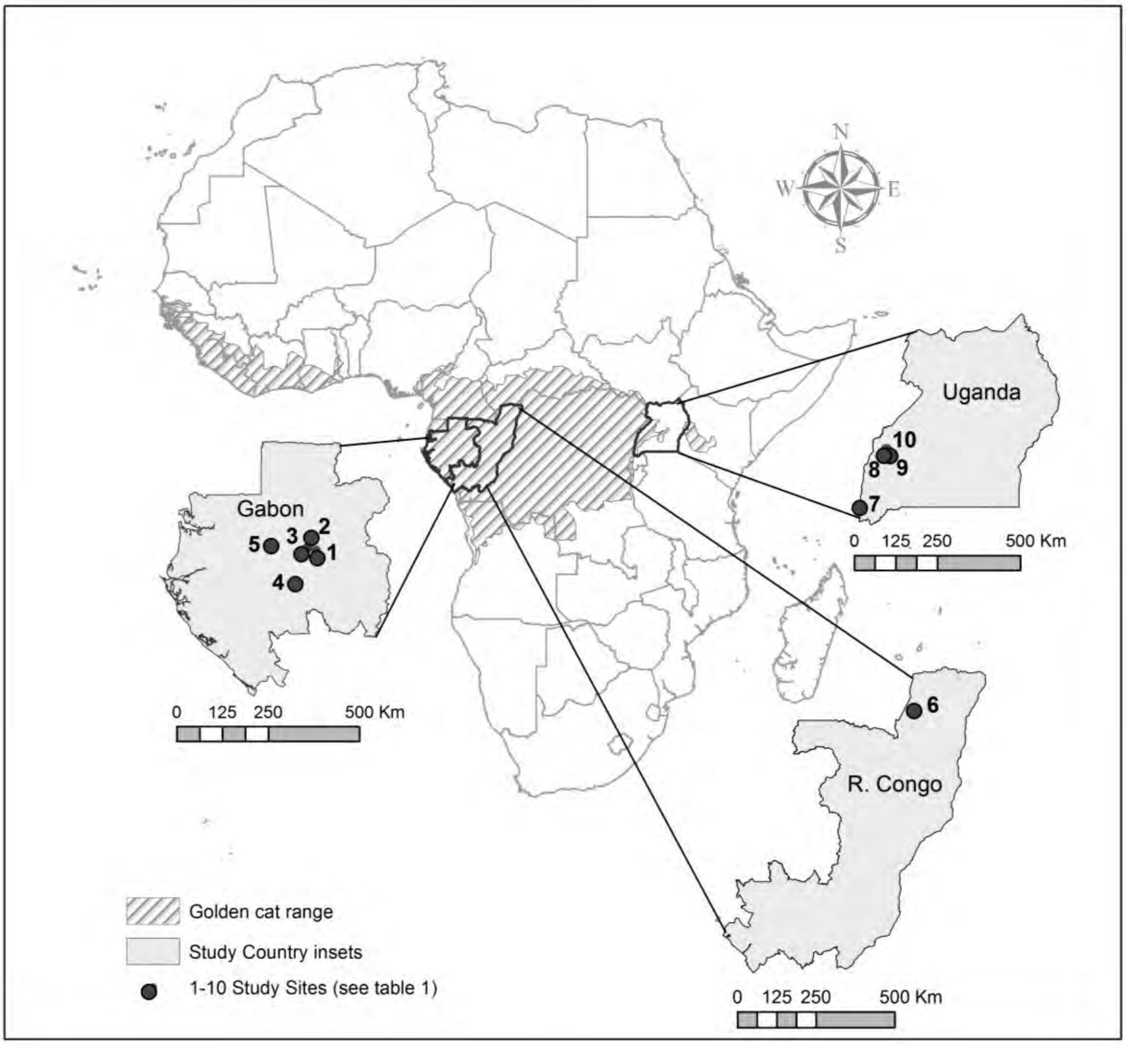


Figure 4.1. Map of Africa showing the geographical distribution of the African golden cat, with insets of the three study countries and locations of study sites (corresponding site details can be found in Table 4.1).

In Gabon, we used Panthera (Olliff et al. 2014), Scoutguard (HCO, USA) and DeerCam (Non-Typical Inc., USA) camera traps. We set them up in pairs (constituting "trap stations") for 2 – 4 months at 39 – 41 locations between 2011 and 2013. We placed trap stations 0.6 – 0.8 km apart and secured camera traps to trees, aimed at 25 cm above the trail. In Kibale, we set up Panthera, Stealthcam (LLC, USA), Camtrakker (CamTrak South Inc., USA) and DeerCam camera traps in pairs for 2 – 3 months at 27 – 49 trap stations between 2011 and 2014. We placed cameras on trees aimed at 25 cm above the trails, and trap stations 0.6 to 1 km apart. In Bwindi, we set up single Reconyx RM 45 camera traps (RECONYX, Inc. USA) at 60 randomly-selected trap sites during the dry season (May to June) between 2010 and 2013. We placed trap sites 1 km apart and we attached camera traps to trees up to a height of 50 cm from the ground. We used a similar protocol in NNNP, with 30 Reconyx RM 45 cameras set up between November and December and between February and March (also between 2010 and 2013), as part of on-going TEAM monitoring.

Table 4.1. Details of all study sites in Gabon, Republic of Congo and Uganda

Site #	Site name	Study, Country	Location	Elevation range (m)	Forest description	Disturbance history & hunting	Leopard
1	Milolé, PreciousWoods Logging Concession	Golden cat, Gabon	0°20'-0°24'S, 12°40'-12°42’E	229-323	Mature semi-evergreen rainforest, with secondary forest	Recently logged	Present
2	Langoué, Ivindo National Park	Golden cat, Gabon	0°8'-0°12'S, 12°31'-12°34'E	380-581	Mature semi-evergreen rainforest	Pristine with no known disturbance	Present
3	Mouyabi, CoraWood Logging Concession	Golden cat, Gabon	0°17'-0°20'S, 12°27'-12°30'E	349-533	Mature semi-evergreen rainforest, with secondary forest	Recently logged with some hunting	Present
4	Moukagno Village	Golden cat, Gabon	1°10'-1°12'S, 12°3'-12°7’E	461-711	Mature semi-evergreen rainforest	Hunting	Present
5	Station d'Etudes des Gorilles et Chimpanzés, Lopé National Park	Golden cat, Gabon	0°11'-0°14'S, 11°34'-11°38'E	216-583	Mature semi-evergreen rainforest, with post-logging secondary forest	Logged 40 years prior	Present
6	Nouabalé-Ndoki National Park	TEAM, Republic of Congo	2º31’-3º00’N, 16º35’-16º59’E	344-595	Mixed semi deciduous forest	Pristine with no known disturbance	Present
7	Bwindi Impenetrable National Park	TEAM, Uganda	0º53’-1º08’S, 29º35’-29º50’E	1060-2670	High elevation submontane forest[1]	Pit sawing & hunting/poaching[2]	Extinct
8	Kanyawara, Kibale National Park	Golden cat, Uganda	0°32'-0°36'N 30°21'-30°25'E	1425 - 1607	Mid elevation, moist deciduous with grass land forest[3]	Pit sawing & hunting/poaching[4]	Extinct
9	Kanyanchu, Kibale National Park	Golden cat, Uganda	0°26'-0°28'N, 30°23'-30°25'E	1207 - 1344	Mid elevation, moist deciduous with grass land forest[3]	Pit sawing & hunting/poaching[4]	Extinct
10	Sebitoli, Kibale National Park	Golden cat, Uganda	0°36'-0°40'N, 30°23'-30°27'E	1418 - 1496	Mid elevation, moist deciduous with grass land forest[3]	Logging, exotic tree plantation & hunting/poaching[4]	Extinct

[1] Langdale-Brown et al. (1964), [2] Butynski (1984), [3] Chapman & Lambert (2000), [4] Lwanga (2006).

4.3.3 Data preparation

We retained one capture (the first) per species per camera location per hour (assumed to be an independent event) for analysis to avoid amplifying activity rates of gregarious or locally active species (Tobler et al. 2008). We then calculated temporal activity of species as the proportion of independent detections occurring in each hour of the 24 h daily cycle.

We selected the principal golden cat prey species based on findings from dietary studies (Hart et al. 1996, Ososky 1998, Ray & Sunquist 2001), including only those species readily detectable by camera-trapping. These were the blue duiker Philantomba monticola, giant pouched rat Cricetomys gambianus and African brush-tailed porcupine Atherurus africanus. The blue duiker does not occur in Bwindi and the porcupine was not recorded in Kibale; these species were therefore not included in the analyses for these sites.

We also assessed human temporal activity from camera trap data. As with non-human species, we counted one capture per hour as an independent event and we included photographs of all people whether involved in legal (primarily research) activities or illegal (primarily poaching) activities.

4.3.4 Data analysis

4.3.4.1 Temporal activity modelling

We carried out all analyses in R (version 3.1.1; R Core Team 2014). We used a circular statistical framework to avoid picking an arbitrary time origin and to clearly illustrate that the difference between, say, 23.00 h and 1.00 h is the same as that between 1.00 h and 3.00 h (Ridout & Linkie 2009). Within this framework, we used linear regressions to model species' activity using the proportions of detections recorded for each hour slot over 24 h (Ross et al. 2013). We modelled temporal activity as a function of continuous trigonometric predictors describing one ($\mathrm{Sin}\Theta$, $\mathrm{Cos}\Theta$) and two ($\mathrm{Sin}2\Theta$, $\mathrm{Cos}2\Theta$) complete cycles in a 24 h period, where $\Theta = \pi t/24$ and t = time in hours (Ross et al. 2013). We graphed these results using the "plotrix" package (Lemon 2006).

To assess differences in golden cat temporal activity between sites with and without leopards, we pooled data from sites where leopards were present (NNNP and Gabon sites) and compared them with similarly pooled data from sites where leopards were absent (Bwindi and Kibale sites) in the same circular framework as above. In addition, we tested the following site variables to explore whether leopard presence versus absence best explains the difference in golden cat activity: individual site, whether humans hunt at the site, and distance to human settlement. We did this by including the site variables as predictors in the regression models, and then comparing the models using the Akaike Information Criterion (AIC; Burnham & Anderson 2002).

As golden cats appeared to become more nocturnal in the absence of leopards, we performed a t-test to test for differences in nocturnality (proportion of independent events occurring between the hours of 19.00 h and 6.00 h) between sites with and without leopards. We carried out the same test to assess whether extent of nocturnality differed between sites with and without human hunting. The latter was a binary variable (hunting or no hunting) based on our knowledge of activities in the study areas (Table 4.1).

4.3.4.2 Estimating temporal activity overlap between golden cats and leopards, prey, and humans

We converted time data from 24 h format to radians, and then to circular format by multiplying time as a decimal by 2π. We fitted non-parametric kernel density functions to estimate a coefficient of overlap (Δ) between the activity densities of pairwise species combinations (Ridout & Linkie 2009). The coefficient of overlap is the proportion under the curve created by two minimum density functions of the two species under comparison at each time point (Ridout & Linkie 2009). The coefficients of overlap range between 0 (no overlap) and 1 (complete overlap).

We followed Ridout & Linkie (2009) who used simulations and data on felids from Sumatra to compare the performance of different methods for estimating overlap. Based on their findings, we used estimators Δ-hat1 and Δ-hat4 for species with small (<50) and large (>50) sample sizes, respectively. We ran one thousand bootstrap permutations to generate confidence intervals to measure precision for the Kernel density overlap estimates. Schmid & Schmidt (2006) and Ridout & Linkie (2009) provide a detailed mathematical background on Kernel density estimation. We conducted the analyses using the R package "overlap" (version 0.2.3; Meredith & Ridout 2014).

4.4 Results

We photo-captured golden cats on 550 independent occasions out of a total of 35,968 camera trap days across all the study sites (see Table 4.2 for capture details for all species).

4.4.1. Activity patterns

Golden cat activity differed significantly between sites where leopards were present and absent (F9,230 = 4.26, p < 0.001). In fact, of the site variables tested, leopard presence/absence best explained the variation in golden cat activity between sites, as indicated by the lowest AIC value (Table 4.3). Other site variables, including individual site and the presence of human hunting, also had a significant effect on golden cat activity (F9,230 = 3.4, p < 0.001; F9,230 = 3.0, p < 0.05; respectively). Distance to human settlement did not have a significant effect on golden cat activity (F9,230 = 2.4, p = 0.12).

Table 4.2. Sampling effort (total number of days that camera traps were active) and number of independent events for considered species per study site.

	Leopard present sites							Leopard absent sites				
	Milolé	Langoué	Mouyabi	Moukagno	SEGC	NNNP	**Total**	Bwindi	Kanyawara	Kanyanchu	Sebitoli	**Total**
Sampling effort	1956	1899	2911	2859	2885	8033	**20543**	6164	3584	3440	2237	**15425**
Species events												
Golden cat	48	37	78	17	24	54	**258**	58	89	119	26	**292**
Leopard	21	16	63	19	94	68	**281**	NA	NA	NA	NA	**0**
Blue duiker	404	230	307	173	396	7267	**8777**	NA	237	122	125	**484**
Porcupine	157	44	136	159	93	187	**776**	26	NA	NA	NA	**26**
Giant rat	87	26	113	28	1	193	**448**	96	80	35	31	**242**
Human	217	166	276	1030	211	3	**1903**	182	1283	1148	120	**2733**

Table 4.3. Model selection using the Akaike Information Criterion (AIC) for regression analyses including trigonometric predictors and site variables. The * denotes the lowest AIC, and therefore model with most explanatory power.

A) Golden cat

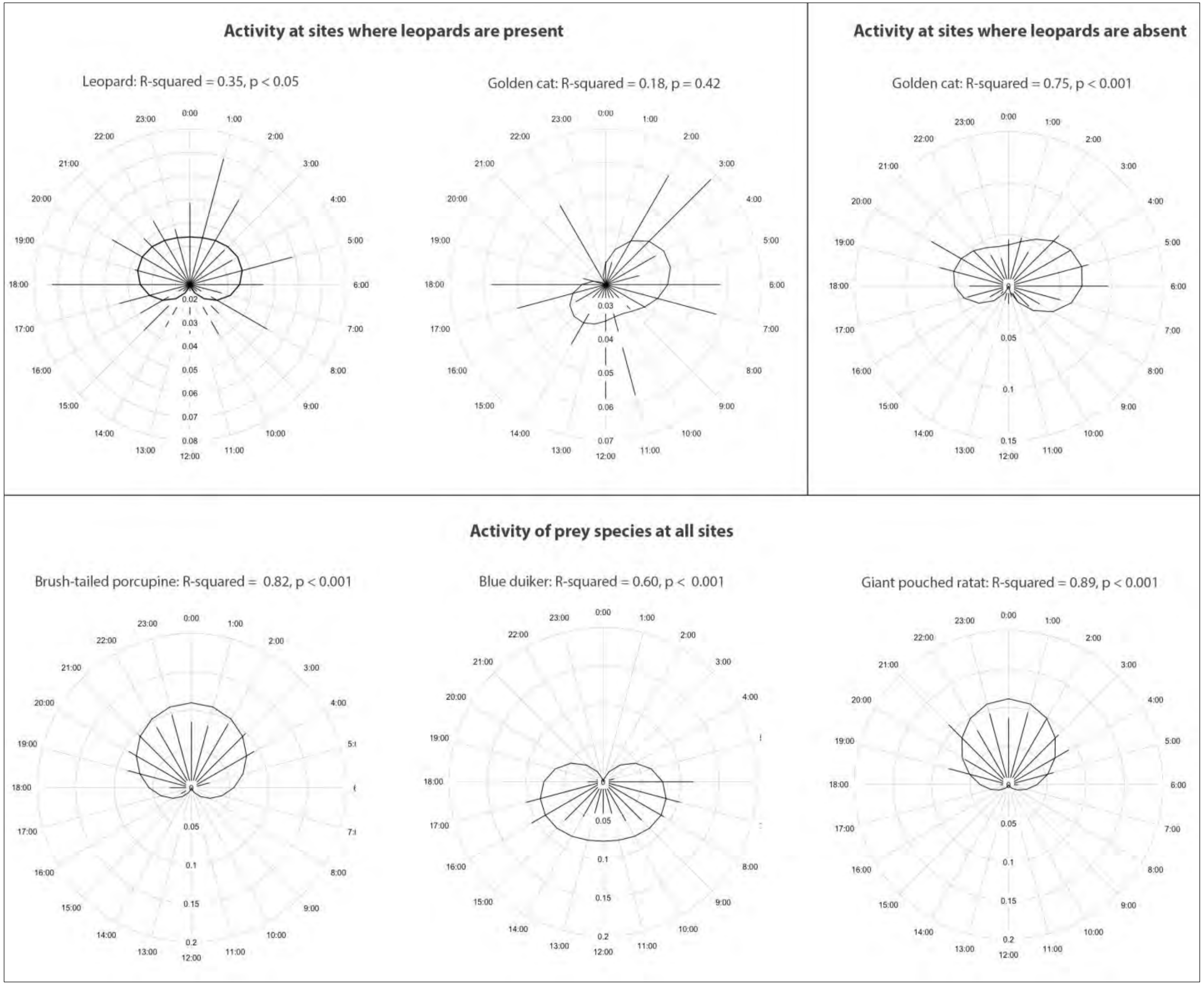
Site variable	**df**	**AIC**
Leopard presence/absence	11	-909.6*
Individual site	11	-902.3
Null (Time of day)	6	-900.1
Human hunting presence/absence	11	-899.6
Distance from site to human settlement	11	-894.3

B) Leopard

Site variable	**df**	**AIC**
Null (Time of day)	6	-521.2*
Human hunting presence/absence	11	-518.2
Individual site	11	-514.3
Distance from site to human settlement	11	-513.6

At sites where leopards were present, golden cats were cathemeral with no evidence for a particular pattern ($r2 = 0.17$, $p = 0.41$; Fig. 4.2). They were particularly active at dawn and in early morning hours, with some activity peaks during the day. Where leopards were absent, golden cats were predominantly nocturnal with significant crepuscular activity, particularly at dawn ($r2 = 0.67$, $p < 0.001$; Fig. 4.2). Overlap in golden cat activity between sites with leopards and without leopards was 0.79 (95% CI: 0.72 – 0.85) (Fig. 4.3). The proportion of nocturnality was significantly higher ($t6.7 = 2.5$, $p < 0.05$) at sites where leopards were absent (Fig. 4.4). The proportion of nocturnality was higher, but not significantly, at sites where human hunting occurred ($t7.3 = 1.0$, $p = 0.36$).

Leopards were mainly nocturnal ($r2 = 0.36$, $P < 0.01$; Fig. 5.2) and humans were strongly diurnal ($r2 = 0.97$, $p < 0.001$). At all sites where they occurred, the giant rat and porcupine were significantly nocturnal (giant rat: $r2 = 0.89$, $p < 0.001$; porcupine: $r2 = 0.82$, $p < 0.001$), while the blue duiker was significantly diurnal ($r2 = 0.60$, $p < 0.001$). There was no significant difference in the activity of any prey species between sites where leopards were present or absent.



Activity at sites where leopards are present

Leopard: R-squared = 0.35, p < 0.05

Golden cat: R-squared = 0.18, p = 0.42

Activity at sites where leopards are absent

Golden cat: R-squared = 0.75, p < 0.001

Activity of prey species at all sites

Brush-tailed porcupine: R-squared = 0.82, p < 0.001

Blue duiker: R-squared = 0.60, p < 0.001

Giant pouched ratat: R-squared = 0.89, p < 0.001

Figure 4.2. Temporal activity pattern of leopards, golden cats (with and without leopards present) and golden cat prey (shown as proportion of detections per hour plotted over 24h). Radial lines depict raw activity data. Curved polygons are the modelled activity patterns generated from regression models (with model results above each graph). Activity patterns are plotted hourly, where the proportion of detection events per hour is shown on axis at 12.00 h.

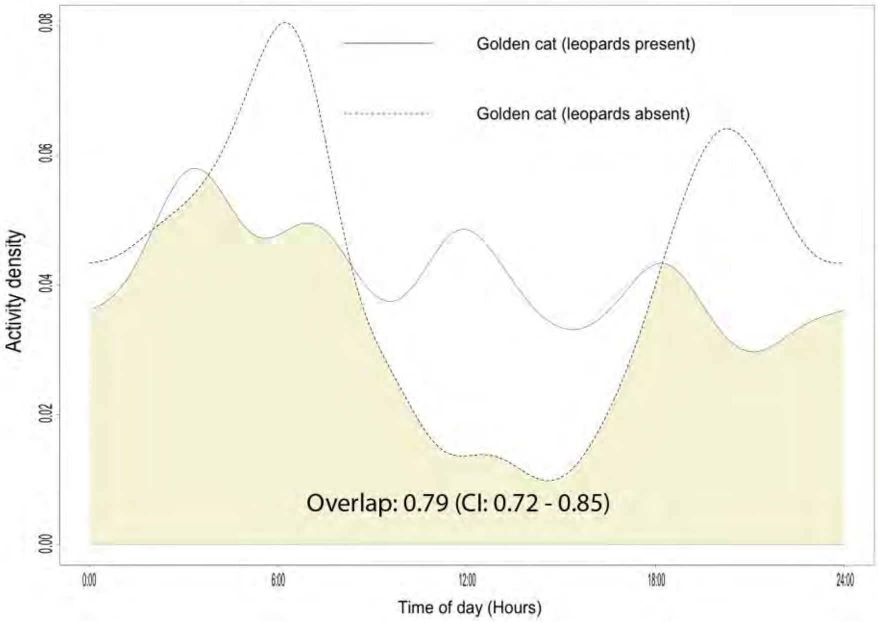


Figure 4.3. Estimated temporal activity overlap between golden cats at sites where leopards were present and sites where they were absent. The coefficient of overlap (corresponding to the shaded area) is included in the figure with 95% confidence intervals in brackets and is the area under the minimum of the two density estimates.

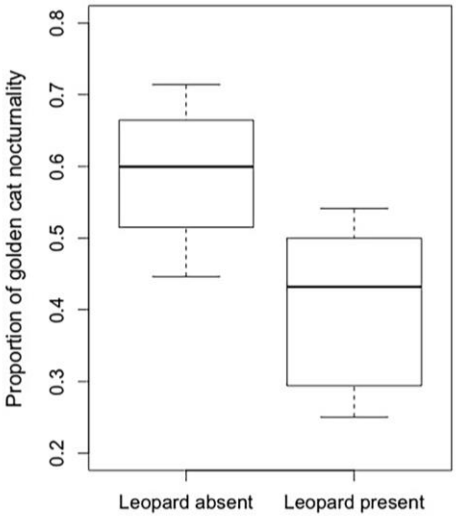


Figure 4.4. Difference in the proportion of independent captures of golden cats taken at night (between 19.00 and 6.00) between sites with and without leopards ($t_{6.7} = 2.5$, $p < 0.05$).

4.4.2 Temporal activity overlap

Where leopards occurred, there was 0.87 (95% CI: 0.80 - 0.93) overlap between golden cat and leopard activity when data from all sites were pooled. However, golden cats appeared to adjust their activity depending on leopard activity, such that overlap at each site individually was lower. For example, at the pristine site of Langoué where leopards showed greater diurnal activity, golden cats were more nocturno-crepuscular and overlap was 0.68 (95 % CI: 0.61 - 0.96). In contrast, golden cats were more diurnal at SEGC where leopards were nocturno-crepuscular, with an overlap of 0.71 (95% CI: 0.58 - 0.91) (Fig. 4.5). Results and graphs for all sites individually can be found in Supplementary Materials.

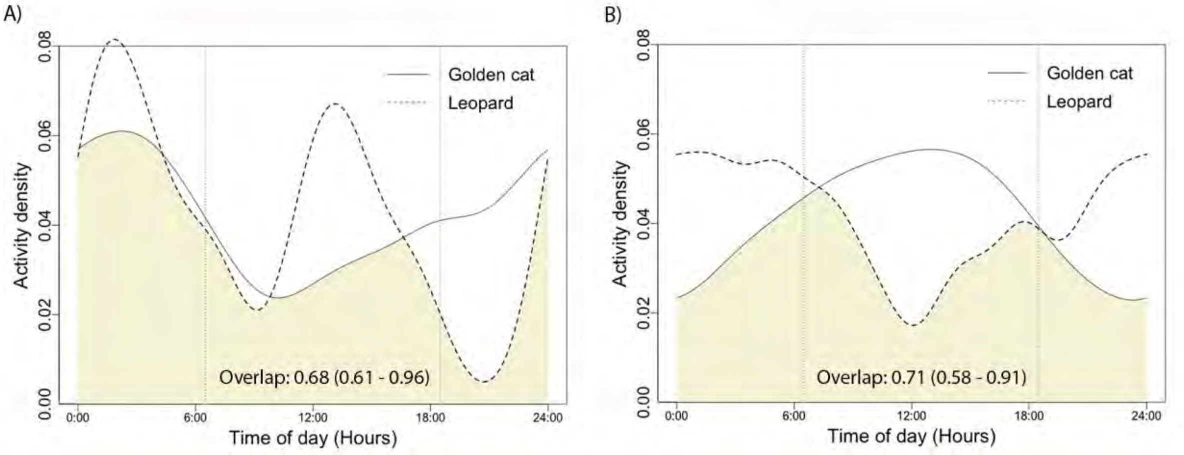


Figure 4.5. Estimated temporal activity overlap between golden cats and leopards at two sites in Gabon: A) Langoué and B) SEGC. The coefficient of overlap (corresponding to the shaded area) is included in the figure with 95% confidence intervals in brackets and is the area under the minimum of the two density estimates. The dotted vertical lines indicate sunrise and sunset times at the study site during the study period (www.aa.usno.navy/data/docs/RS_OneYear.php).

The extent of overlap between golden cats and humans more than halved in the absence of leopards (from 0.63 to 0.29; Fig. 4.6). Overlap between golden cats and their nocturnal prey species (brush-tailed porcupine and giant pouched rat) increased in the absence of leopards while overlap decreased with the diurnal blue duiker (Fig. 4.6).

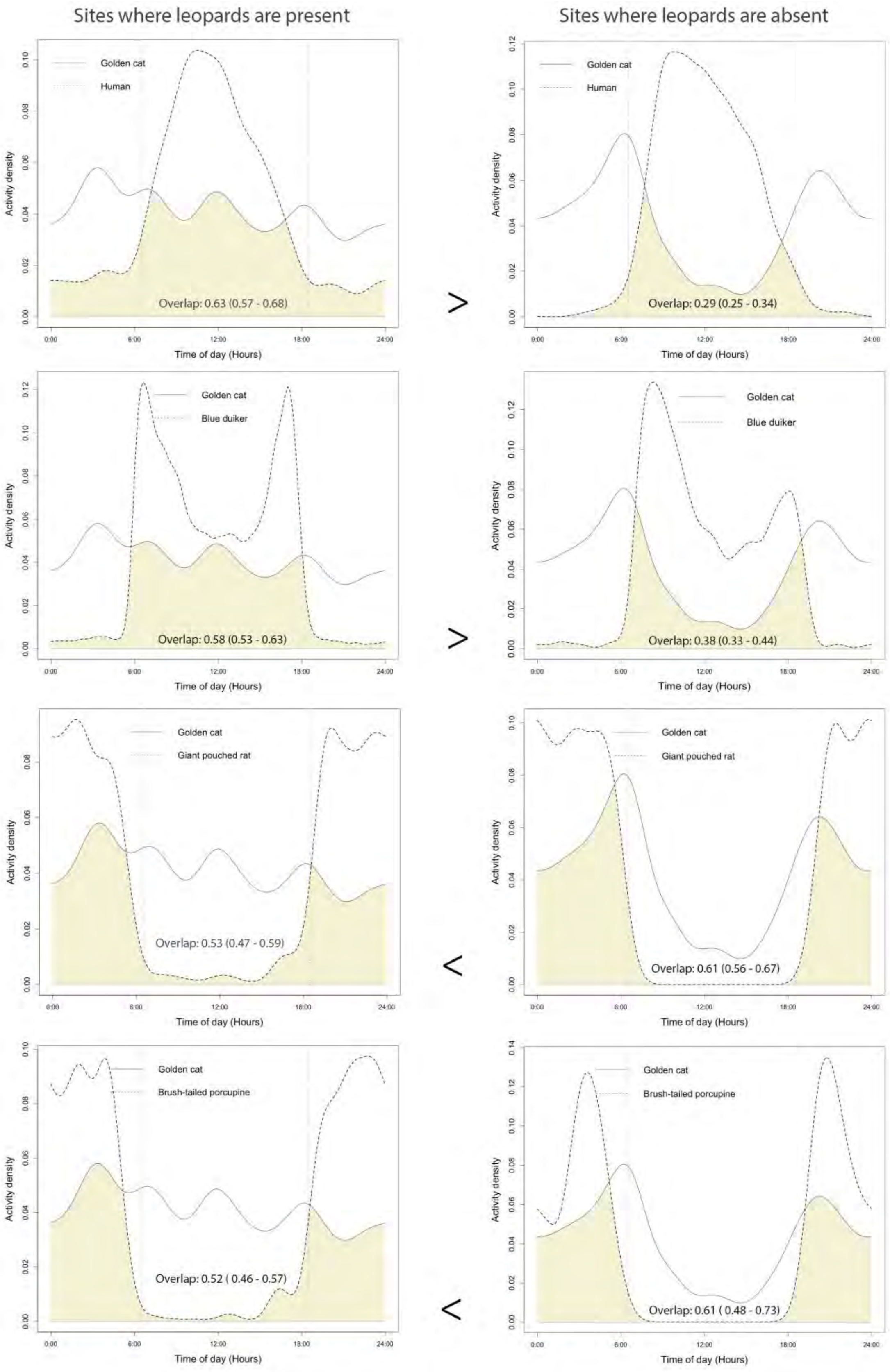


Figure 4.6. Estimated temporal activity overlap between golden cats, humans, and prey species in areas with and without leopards. The coefficient of overlap (the shaded area in the plots) is included in each figure with 95% confidence intervals. The dotted vertical lines represent sunrise and sunset.

4.5 Discussion

African golden cats were primarily cathemeral where they were sympatric with leopards and became nocturno-crepuscular in the absence of leopards. Leopards were largely nocturnal at our sites and cathemeralism may be a strategy by which golden cats minimise antagonistic encounters with the larger felid (sensu Harrington et al. 2009). This is corroborated by golden cat behaviour at individual sites, which revealed avoidance of peaks in leopard activity. As the only non-human predator recorded to prey upon golden cats, the leopard could be expected to be an important influence on golden cat behaviour. A similar relationship occurred in a simple predator guild in Australia where the feral cat Felis catus became most active during dusk at sites where its main predator, the dingo Canis lupus dingo, was abundant and most active at dawn (Kennedy et al. 2012).

Predators also synchronise their temporal activity with that of their prey (Sunquist and Sunquist 2002, Harmsen et al. 2011, Bischof et al. 2014), and changes in temporal activity may be an adaptive response in relation to prey acquisition as well as to predator avoidance (Kotler et al. 2010). The golden cat's cathemeral behaviour in the presence of leopards is likely fostered by its ability to exploit both diurnal and nocturnal prey. At sites where golden cats were more nocturnal, a decrease in overlap with blue duikers is compensated for by an increase in overlap with brush-tailed porcupines and giant pouched rats. Additionally, a decrease in overlap between golden cats and blue duikers at sites where leopards were absent does not necessarily indicate a reduction in that prey's availability. For example, overlap increased between golden cats and blue duikers at dawn and dusk, a period that may represent a period of higher blue duiker vulnerability to predation.

The influence of humans on golden cat activity further complicates interpretation. Shifts in temporal activity in response to high human activity have been recorded for other carnivores (Henschel and Ray 2003, Kusak et al. 2005, Theuerkauf et al. 2009, Rasmussen and Macdonald 2011, Valeix et al. 2012), although the interaction between human influence and that of other predators or competitors on this activity remains poorly known. Our data suggest that golden cats avoid periods of high human activity but that the presence of leopards drives increased overlap between golden cats and humans. However, it is impossible to separate the effects of leopard absence from increased human pressure as the former is caused by the latter and no sites were identified where golden cats were present and leopards absent, but where there was low human pressure (Table 4.1). Identifying such a site would be valuable to better elucidate these complex relationships.

Given the potentially complex avoidance strategies employed by mesopredators, there is a need for additional data on the mechanisms at work within this system. Research into the possibility of long-term spatial avoidance (du Preez et al. 2015), short-term, opportunistic spatio-temporal avoidance (Harmsen et al. 2009) and dietary shifts (Moreno et al. 2006) would allow us to shed more light on how mesopredators in general and golden cats in particular adapt to altered environments such as the extirpation of large predators. No wild golden cat has been radiocollared, and a well-planned telemetry study on the species would likely yield rich rewards on this topic, especially where the presence and absence of the leopard can be incorporated in the study design.

While we are cautious in attributing changes in golden cat activity entirely to mesopredator release, the absence of their main competitor/predator appears to facilitate a switch in activity, whether the switch is a strategy to become more cryptic and avoid humans, to optimise foraging, or a combination of both.

African golden cats have recently been assessed as Vulnerable on the IUCN Red List of Threatened Species due to rapid loss of forest habitat, as well as increasing bushmeat hunting pressure across their range (Bahaa-el-din et al. 2015b). Although the behavioural plasticity identified here may improve the species' ability to persist under changing environmental conditions, the greatest cause of mortality is the ubiquitous use of wire snares in the region (Bahaa-el-din et al. 2015b). Behavioural plasticity can do little to diminish this threat.

4.6 References

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4.7. Supplementary Materials

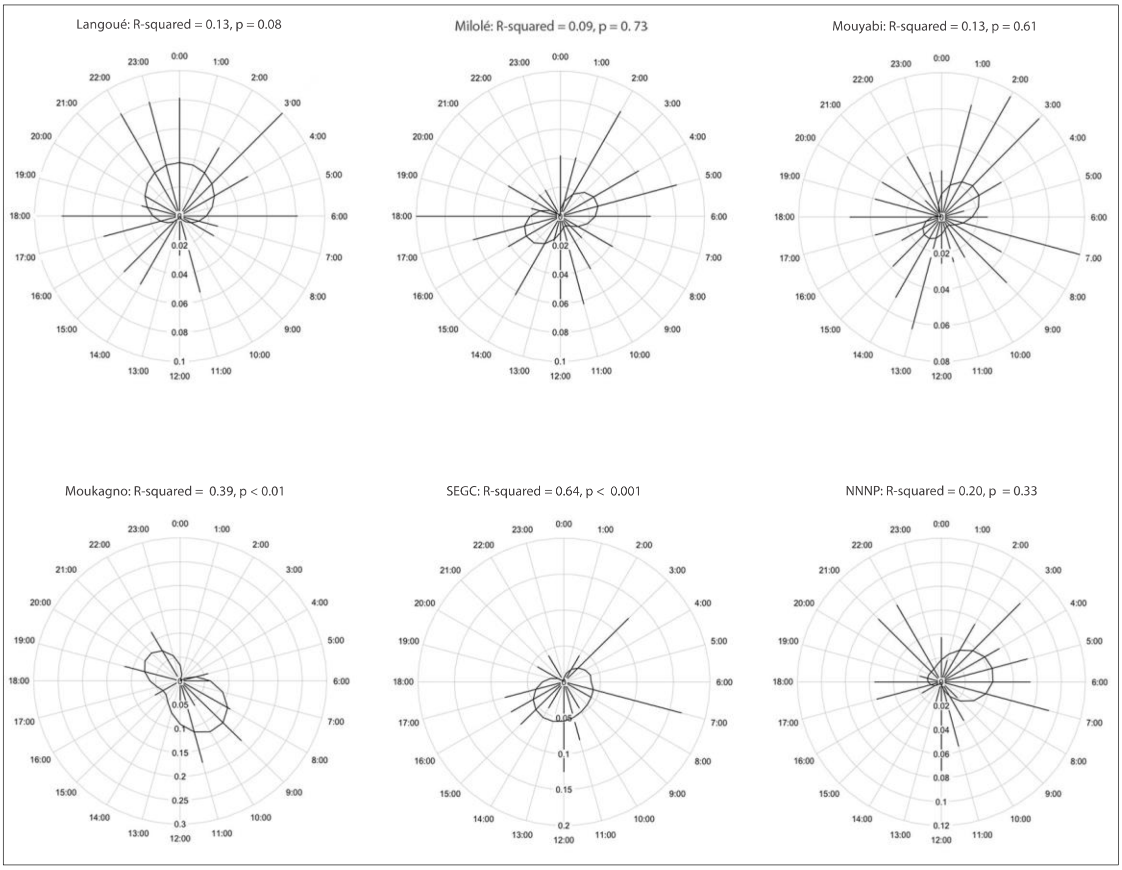

Figure 4.SM.1. Temporal activity pattern of golden cats at six sites in Gabon and the Republic of Congo where leopards are present. Radial lines depict raw activity data. Curved polygons are modelled activity patterns generated from regression models (with model results above each graph). Activity patterns are plotted hourly, where the proportion of detection events per hour is shown on axis at 12.00 h.

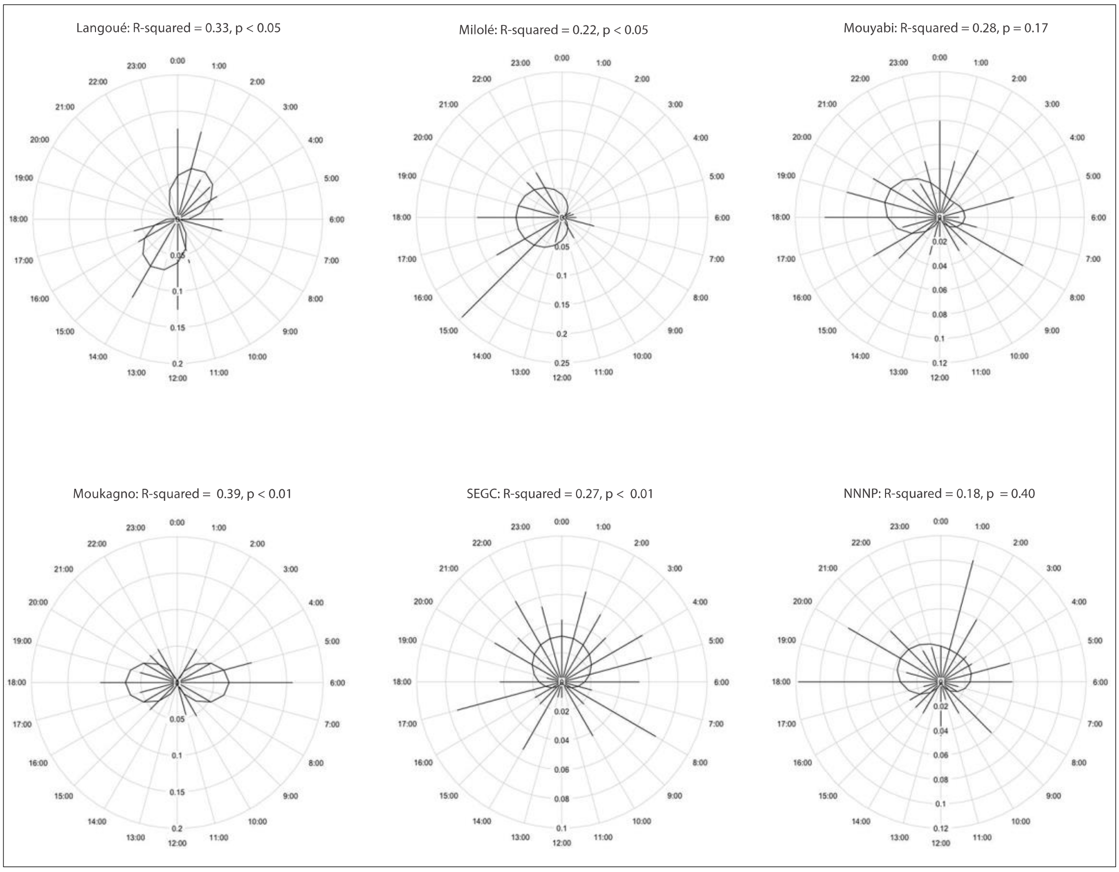

Figure 4.SM.2. Temporal activity pattern of leopards at six sites in Gabon and Republic of Congo. Radial lines depict raw activity data. Curved polygons are the modelled activity patterns generated from regression models (with model results above each graph). Activity patterns are plotted hourly, where the proportion of detection events per hour is shown on axis at 12.00 h.

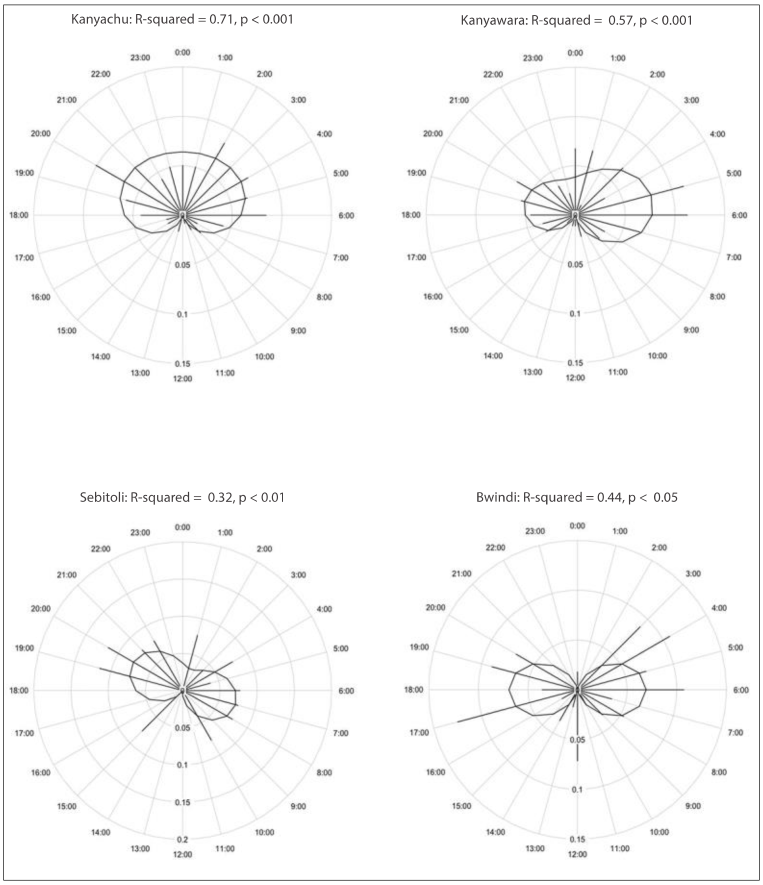

Figure 4.SM.3. Temporal activity pattern of golden cats at four sites in Uganda where leopards are absent. Radial lines depict raw activity data. Curved polygons are the modelled activity patterns generated from regression models (with model results above each graph). Activity patterns are plotted hourly, where the proportion of detection events per hour is shown on axis at 12.00 h.

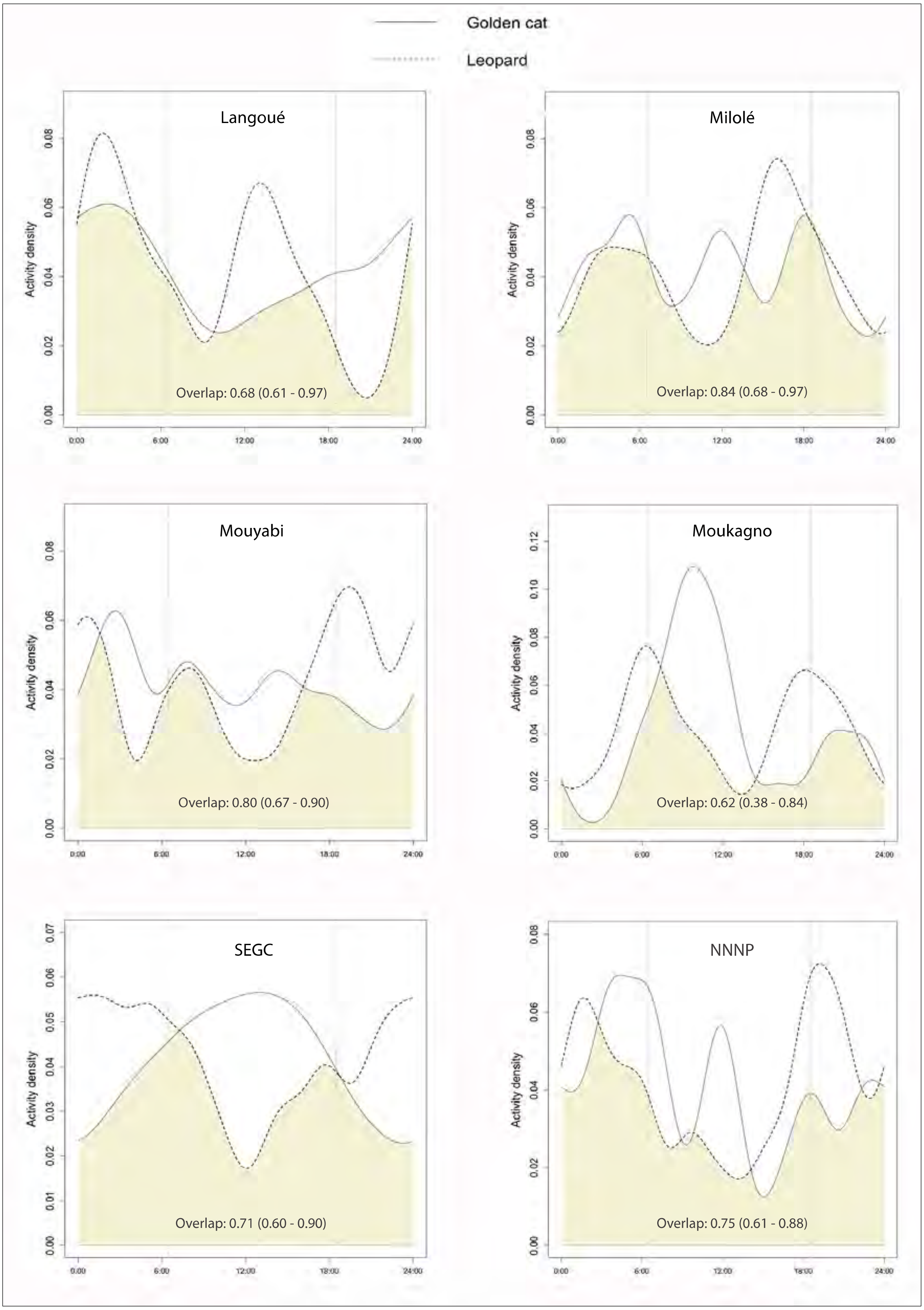

Figure 4.SM.4. Estimated temporal activity overlap between golden cats and leopards at six sites in Gabon and Republic of Congo where the two species co-occur. The coefficient of overlap (corresponding to the shaded area) is included in the figure with 95% confidence intervals in brackets and is the area under the minimum of the two density estimates.

5. Co-existence of the two African rainforest felids under increasing disturbance from land-use

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Cover image: The African golden cat competes with and is preyed on by the larger leopard (two images combined into one using Adobe Photoshop). © Laila Bahaa-el-din

5.1. Abstract

Large carnivores play a pivotal role in structuring ecosystems through top-down processes. The nature of such pressures varies by species, with larger carnivores generally also exerting pressure on smaller ones. We explore mechanisms of co-existence between the medium-sized African golden cat Caracal aurata and the larger leopard Panthera pardus, using camera trap data and dietary data derived from scats. We carried out negative binomial regressions at two spatial scales to assess the effect of various camera station and study site variables on photo-capturing golden cats and leopards. We carried out temporal analyses at camera stations to assess fine-scale spatio-temporal avoidance of leopards by golden cats. Spatial overlap at camera sites was generally high (mean: 52%), and the number of leopard photo-captures was positively correlated with golden cat captures; in fact, it was the highest preforming predictor of where golden cats were captured. Trail width was the best predictor of leopard capture. At the larger spatial scale, land-use was also a top predictor, with hunting negatively affecting both species. Avoidance appeared to occur at a spatio-temporal level, with a decrease in golden cat activity at camera stations within ca. 20 hours of a leopard passing. Golden cat diet was dominated by rodents in both rate of occurrence and species' diversity. Ungulates were most important leopard prey. Food niche overlap was lower than estimated in previous studies at 0.18 when it was calculated by prey species, and 0.49 when calculated by prey body mass category. Golden cat mean prey body mass differed significantly between sites, perhaps mediating competition with leopards that switch to smaller prey under anthropogenic stress. We conclude that co-existence between golden cats and leopards is facilitated by fine-scale reactive temporal avoidance as well as food niche segregation. Our findings shed light on mechanisms of co-existence within simple large carnivore communities, and may also be of use in exploring interactions within larger communities.

5.2. Introduction

Community interactions influence the viability of carnivore species, and understanding these interactions is important for conservation planning (Linnell & Strand 2000). This is particularly true for carnivores that are subject to interference competition which can result in mortality (intra-guild predation; Polis et al. 1989), with large carnivores often exerting a controlling pressure on mid-ranking (meso) carnivores. But competition between carnivores does not only have direct effects on species abundance. Food niche, space/habitat use and temporal activity of mesocarnivores may be adapted as mechanisms for co-existence with larger carnivores (Chesson & Kuang 2008, Vanak et al. 2013), and these changes can affect their growth, reproduction and survival (Ritchie & Johnson 2009).

The central African rainforest is host to a small community of felids, with just two species adapted to living within continuous rainforest habitat (Chapter 4). These are the medium-sized, forest-obligate African golden cat Caracal aurata and the larger, habitat-generalist leopard Panthera pardus. Leopards have been studied predominantly within African savannahs where they are subordinate to lions Panthera leo and spotted hyenas Crocuta crocuta (Vanak et al. 2013, Hayward & Slotow 2009), and forests in Asia where they are subordinate to tigers Panthera tigris (Odden et al. 2010, Harihar et al. 2011). In the African rainforest, however, leopards are the largest carnivore, and therefore act as the dominant, apex species. The golden cat is a mesocarnivore within the system, which is itself dominant to the small carnivores of the rainforest. Two carnivore species overlap in size with golden cats: the African civet Civettictis civetta and the honey badger Mellivora capensis. The former has very low dietary overlap with golden cats (Ray & Sunquist 2001), while the latter's rainforest distribution is patchy, and the species seems to occur at low abundance (Bahaa-el-din et al. 2013). It is, therefore, reasonable to assume that the leopard is the most important natural competitor for golden cats within dense forest habitat, which comprises the majority of golden cat range (Bahaa-el-din et al. 2015a).

Little is known about golden cats, but our camera trap study has shown that they are not as naturally rare as once thought (Chapter 3). We found that golden cat density ranged from 3.8 to 16.2 individuals per/ 100 km2, similar to small-to-medium-sized felids from other regions (e.g. Dillon and Kelly 2008, Mohamed et al. 2013), and that density correlated negatively with the amount of human disturbance. We also found that golden cat density was low at the site with the highest leopard photo-capture rate and number of leopard individuals, suggesting that a high leopard density may negatively impact golden cat populations. Indeed, Henschel et al. (2005) found golden cat remains in 2.5 % of leopard scats in northern Lopé National Park in central Gabon, one of our study sites, providing direct evidence of interference competition. We would therefore expect golden cats to operate within a "landscape of fear" (Laundré et al. 2001) where they minimise spatial and temporal overlap with leopards. Paradoxically, these species overlap in space use (Chapter 3) and golden cats do not appear to restrict their activity to low-risk areas as has been found for other mesopredators (e.g. wild dogs Lycaon pictus avoiding lions; Swanson et al. 2014). We also found that overall temporal overlap in our study sites was quite high (overlap coefficient ranging from 0.6 to 0.87, with 0 representing no overlap and 1 complete overlap), with both species displaying cathemeral activity, though leopards were generally more nocturnal. Golden cats may display temporal avoidance of leopards at a fine spatio-temporal scale, allowing the species to make use of the same areas as leopards, but at different times (sensu Broekhuis et al. 2013).

Finally, the food niches of golden cats and leopards are reported to exhibit high overlap (Hart et al. 1996, Ososky 1998, Ray & Sunquist 2001), with golden cats generally consuming prey species on the smaller end of the leopard prey spectrum. However, previous studies relied on scat width and size of bone fragments contained in the scats as criteria to differentiate between golden cat and leopard scats. The substantial weight overlap between juvenile leopards and adult golden cats may have led to the misidentification of leopard scats as golden cat, which might in turn have resulted in overestimates of food niche overlap (Bahaa-el-din et al. 2015a). This is a common problem where sympatric felids occur, and it is recommended that molecular identification of scats be used (Farrell et al. 2000, Haag et al. 2009, Roques et al. 2011).

Carnivore interactions are expected to vary with anthropogenic disturbance (Ritchie & Johnson 2009). African rainforests face extensive disturbance through widespread and increasing deforestation (FAO 2011, Edwards et al. 2014, Wich et al. 2014). They are also threatened by the unselective hunting of wild animals for meat (bushmeat) which is pervasive throughout the African rainforest (Wilkie et al. 2011) and is increasing as a result of a booming human population in West and Central Africa (FAO 2011) and increased access to remote areas through an expanding road network (Blake et al. 2007, Laporte et al. 2007). Henschel et al. (2011) found that leopards shift to smaller prey in the vicinity of settlements as a result of competition with human hunters. Such shifts may drive corresponding shifts in golden cat diet, with potential effects throughout the food-web (through, for example, under- or overexploitation of prey species).

We studied the ecological interactions between golden cats and leopards at different spatial scales to explore possible mechanisms for their coexistence across multiple land-uses. We hypothesise that spatial overlap is dictated by features at the camera site level. For example, we expect both species to make higher use of large trails. We also hypothesise that temporal avoidance is revealed as we scale down within study sites to camera trap sites. We further hypothesise that dietary overlap between golden cats and leopards is lower than previously estimated due to the likely misidentification of golden cat scats as those of leopards, thereby overestimating the golden cat’s consumption of larger prey. We hypothesise that the effects of different human land-uses on interactions are minimised by food niche adaptation.

5.3. Methods

5.3.1. Study area

We carried out surveys at six sites that differed in land-use in the central African country of Gabon (Fig. 5.1, Table 5.1). The area consists mostly of mature lowland semi-evergreen rainforest and elevations range between 100 – 1000 m (Henschel et al. 2011). The main land-uses in the area include national parks (Lopé and Ivindo) and logging concessions. The human population density in this area is low (1.5-2.0 inhabitants/km2). All sites consisted of continuous forest habitat, with the exception of the Station D'Etudes des Gorilles et Chimpanzes (SEGC), which is a forest-savannah mosaic (Table 5.1).

5.3.2. Camera trapping

We used camera traps at five sites (sites 1 – 5; Fig. 5.1). We began with a thorough exploration of each site prior to camera trap placement, recording roads, trails and signs of golden cats and leopards during reconnaissance walks using a handheld GPS (Garmin eTrex Legend HCx). We then used these records to design an array of 38 – 41 camera trap stations selected to maximise captures of golden cats.

Each station consisted of two camera traps placed on opposite sides of the trail, facing each other with a slight offset to avoid flash interference. We placed cameras on trees, about 25 cm off the ground, facing the trail at a perpendicular angle. We spaced cameras 600 – 800 m apart and our camera grids covered areas of ca. 20 km2. We defined camera spacing and grid extent based on a pilot study to optimize camera trapping designs for golden cat density estimation via Spatially Explicit Capture Recapture (SECR) analysis (Bahaa-el-din et al. 2011). At each camera station, we recorded the GPS point, trail type and width, and ground vegetation density. We assessed the latter by counting stems within four 1 m2 plots, and then averaging the four numbers to get one density per camera station. We selected plots by walking 5 m in four directions (cardinal when possible) from the camera station. We left camera traps out for at least 50 days; and up to 102 days where golden cat captures were infrequent.

5.3.3. Camera trap data preparation

We ensured temporal independence of photo-captures by keeping only the first capture within a one-hour time period at a camera station for species that could not be individually identified (i.e. prey), and keeping only captures of different individuals within a one-hour time period for individually identifiable species (i.e. predators). This was to avoid overestimation of species captures for gregarious species, or where individuals delayed moving from camera stations (Tobler et al. 2008). For the predator species whose response we were interested in, we calculated the number of photo-capture events per camera station. For species used as explanatory variables (see below), we then calculated a photo-capture rate by dividing the number of independent captures at each camera station by the number of trapping days (the number of days the cameras were active) at that station, and multiplying by 100 to account for trapping effort (O'Brien et al. 2003).

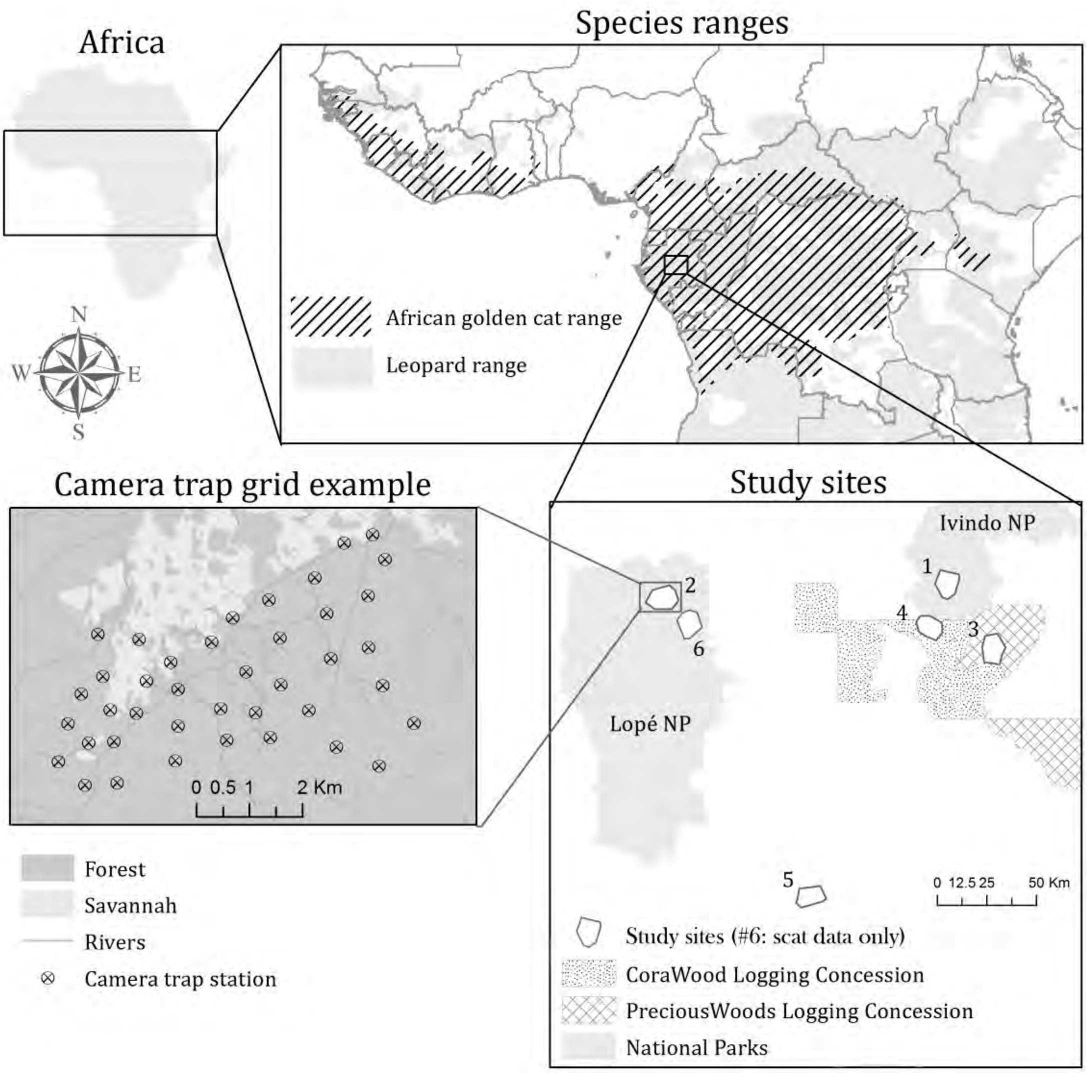

Figure 5.1. Maps showing the global distribution of golden cats (Bahaa-el-din et al. 2015b), and the central, west and east African leopard distribution (Peter Grengross/Biogeomaps); the location of our study sites; and an example trapping grid from SEGC (Site 2; layers from CIRMF)

Table 5.1. Location, habitat and survey details at six study sites in central Gabon. Camera trap data from sites 1 – 5, and scat data from sites 1 – 6, were used in our analyses.

Site # (Fig. 5.1)	**Site name**	**Manage-ment**	**Trapping Location**	**Forest description**	**Disturbance history**	**Period**	**Survey duration (days)**
1	**Langoué**, Ivindo NP	National Park	0°8'-0°12'S, 12°31'-12°34'E	Mature semi-evergreen rainforest	Pristine forest, with no evident past disturbance	Sep - Nov 2011	55
2	Station D'Etudes des Gorilles et Chimpanzes (**SEGC**), Lopé NP	National Park	0°11'-0°14'S, 11°34'-11°38'E	Forest-savannah mosaic, with post-logging and colonising secondary forest	Logged in 1970s	Sep - Dec 2013	102
3	PreciousWoods, **Milolé**	Logging concession (FSC-certified)	0°20'-0°24'S, 12°40'-12°42'E	Mature semi-evergreen rainforest, with post-logging secondary forest	Logged 2 years prior	June - Aug 2011	54
4	CoraWood, **Mouyabi**	Logging concession (not-certified)	0°17'-0°20'S, 12°27'-12°30'E	Mature semi-evergreen rainforest, with post-logging secondary forest	Logged 2 years prior	Aug - Oct 2012	79
5	**Moukagno**	Village hunting area (ca. 21 households)	1°10'-1°12'S, 12°3'-12°7' E	Mature semi-evergreen rainforest, with post-logging secondary forest	Hunting, logged in 1990s	May - Aug 2013	89
6	**Mikongo**, Lopé NP	National Park	0°27'-0°33'S 11°67E-11°72'E	Mature semi-evergreen rainforest, with post-logging secondary forest	Logged in 1970s	June - Sept 2010	118

5.3.4. Analysis of space use

We carried out all analyses in the programme R (version 3.1.2; R Core Team 2015). To test which variables most affected golden cat and leopard photo-capture, we carried out negative binomial regressions on the number of photo-captures (as counts) of golden cats or leopards at each camera station (in the R package “MASS”; Venables & Ripley 2002). We chose a negative binomial regression to account for the over-dispersion (particularly the high number of zeros; Hilbe 2011) in our photo-capture data. We included explanatory variables that we expected would influence the number of photo-captures of golden cats and leopards, including trail width, ground vegetation density, prey photo-capture rate, elevation, and distance to savannah edge (Table 5.2).

To account for potential spatial autocorrelation in target species photo-captures, we calculated autocovariates (Augustin et al. 1996) as the number of records of the target species at camera-traps within a radius of 1000 m (Acov1) and 2000 m (Acov2), and included these as covariates in the models.

We analysed the data individually for each site (i.e. at a local scale) as not all variables were relevant to all sites. For example, “distance to savannah” was only relevant at SEGC. We also pooled the data from all sites to assess the effect of land-use (national park, logging concession or village hunting area) on felid photo-captures. We included camera station variables in these pooled-site models, to see whether variable effects were consistent at the different spatial scales. We did not use forest cover as a variable, as there was too little inter- and intra-site variation. We used trapping effort (the number of days the cameras were active at each station) as an offset to account for differences in sampling intensity. Leopard capture rate was used as a variable in golden cat models, as the former may influence where the latter was captured. Golden cat capture rate was not included in leopard models, as there was no reason to believe that golden cats influence where dominant leopards are captured.

To obtain a measure of prey availability at the camera-trap site level, we computed the combined capture rates for a set of prey species. We selected three main golden cat prey species based on the literature (Hart et al. 1996, Ososky 1998, Ray & Sunquist 2001) and our findings in this paper: blue duiker Philantomba monticola, brush-tailed porcupine Atherurus africanus and giant pouched rat Cricetomys emini. This was a compromise between species that featured most in golden cat diet and were also caught on camera traps (the small rodents were infrequently photo-captured and therefore not included). The main leopard prey species were selected based on Henschel et al. (2011) and our findings in this paper, and included red duiker species (Cephalophus callipygus, C. ogilbyi, C. dorsalis, C. leucogaster and C. nigrifrons) and red river hogs Potamochoerus porcus.

Table 5.2. Camera station and study site variable details, including mean and standard error, for each site, and expected effect of the variable on golden cat (GC) and leopard photo-captures.

		Langoué	**SEGC**	**Milolé**	**Mouyabi**	**Moukagno**	**Expected effect** on GC (top) &**
Camera station variable	**Abbreviation**	**Mean ±SE**	**Mean ±SE**	**Mean ±SE**	**Mean ±SE**	**Mean ±SE**	**leopard (Bottom)**
Trail width (mm)	Trail	501.3 ±21	844 ±314	921.9 ±178	1778 ±222	1371 ±174	+ +
Vegetation (# of stems)	Veg	24.5± 1.7	46.2 ±3.2	23.3 ±1.5	46.4 ±2.7	42.7 ±4.4	+ =
Leopard (photo-capture rate)	Leopard	0.9± 0.3	2.7 ±2.6	1.0 ±0.3	2.4 ±0.6	0.6 ±0.2	+ N/A
Golden cat prey (photo-capture rate)	Prey	20.9± 2.9	17.8 ±3.2	26.3 ±3.5	16.4 ±2.7	10.5 ±2.6	+ N/A
Leopard prey (photo-capture rate)	Prey	36.1± 3.4	89.0 ±10.6	32.5 ±3.4	16.6 ±2.9	9.5 ±2.8	N/A +
Distance from savannah (m)	Sav	N/A	973.2 ±142	N/A	N/A	N/A	+ =
Elevation (m)*	Elev	483.2 ±9.6	329.2 ±10.9	274.8 ±2.8	403.8 ±5.2	519.6 ±7.1	= =
Study site variable	**Category Levels**						
Land-use	National Park	✓	✓				+ +
	Logging Concession			✓	✓		= =
	Hunting area					✓	- -

photo-capture rate = the number of independent photo-captures per 100 trapping days
* Calculated as the mean elevation within a 100 m circular buffer
** positive effect (+), no effect (=), and negative effect (-)

We first ran negative binomial regressions with each variable individually. We then compared these models using the Akaike Information Criterion (AIC; Burnham & Anderson 2002) and built models up by combining variables that featured in the top three models. We did not combine any variables that had a higher correlation coefficient than 0.7 in the same model. We used the R package visreg (Breheny & Burchett 2012) to plot the relationships between felid photo-captures and covariates in the most supported model (by AIC) at each site.

5.3.5. Temporal avoidance analysis

Cusack et al. (in prep) developed a method for assessing fine-scale temporal avoidance from camera trap data. This involves plotting the distribution of photo-captures of a subordinate species around the captures of a dominant species at each camera station. We plotted golden cat activity density, based on camera trap photo-captures, in relation to leopard photo-captures, in order to establish whether golden cats avoid leopard at a fine (camera station level) scale.

5.3.6. Scat collection and preparation for further analyses

We collected scat samples opportunistically at six sites during the site prospection period, and while setting up, checking, and taking down camera traps. We had one additional site to our camera trap survey sites (Table 5.1) because we collected scat samples at a pilot study site (Bahaa-el-din et al. 2011) for which we could not include the camera trap data due to differences in camera trapping protocols.

When we found a felid scat, we took a photograph and recorded the GPS location and scat width. We then proceeded to remove the outer layer of the scat (a source of DNA from epithelial cells that are shed from the lining of the intestines; Höss et al. 1992), which we then placed in a falcon tube with uncontaminated silica gel beads to dessicate the sample for genetic analysis. Because of the risk of disrupting territorial marking, we left a small section of the scat behind when scat size was sufficient. We transported the remainder of the scat to our base where it was washed over 1 mm wire-mesh to remove organic material. This left us with a sample of hair, bone, tooth, nail, scale, shell and insect exoskeleton remains, which we dried in the sun and stored for later analysis.

5.3.7. DNA extraction and identification of scat origin

We extracted genomic DNA and identified species from scat as described in Caragiulo et al. (2014). We identified all scat samples to species by amplifying regions of four mitochondrial genes (Table 5.3). We sequenced PCR amplicons as described in Caragiulo et al. (2014) using the thermocycler of Platt et al. (2007). We purified sequencing amplifications via ethanol precipitation and sequenced them in an ABI 3730xl DNA Analyser (Applied Biosystems, Carlsbad, California, USA). We manually edited sequences using Geneious (Drummond et al. 2012), and compared them to both an in-house database of carnivore mtDNA sequences and the NCBI nucleotide BLAST database (Benson et al. 2000) to confirm species identification.

5.3.8. Analysis of prey remains

We used a hair reference collection of species that occur in Gabon, collected at SEGC (Henschel et al. 2005) and in bushmeat markets in Libreville (own data), and compared these with hairs from scats using a stereoscopic binocular microscope. We used macroscopic features such as colour, shape and size of hair to identify it to species level where possible. Hair from the closely-related Cephalophus species, including C. callipygus, C. dorsalis, C. nigrifrons, and C. ogilbyi, cannot be distinguished to species level using macroscopic or microscopic features (Henschel et al. 2005) and we grouped them as "red duikers" (i.e. Cephalophus sp.). We also included C. leucogaster within the "red duikers", a species not present in the Henschel et al. (2005) study.

Table 5.3. Mitochondrial DNA primer sets. The table shows the four mitochondrial genes being amplified.

Mitochondrial target gene	**Primer set**	**Primer name**	**Amplicon size**	**Annealing temp.**	**Reference**
Cytochrome b	Carnivorous	H15149 Farrel-R	110 bp	50 °C	(Kocher et al. 1989) (Farrell et al. 2000)
	Canideos	H15149 Canid-L1	380 bp	52 °C	(Kocher et al. 1989) (Paxinos et al. 1997)
12S rRNA		L1085 H1259	170 bp	57 °C	(Kitano et al. 2007) (Kitano et al. 2007)
16S rRNA	16Scp	16Scp-F 16Scp-R	294 bp	52.5 – 51.5 °C (touchdown cycle)	(Pomilla et al. 2009) (Pomilla et al. 2009)
	16Suni	L2513 H2714	200 bp	57 °C	(Kitano et al. 2007) (Kitano et al. 2007)
NADH-5	Heminested set a	ND5-1F ND5-2NR	119 bp	48 °C	(Johnson et al. 1998) (Johnson et al. 1998)
	Heminested set b	ND5-1NF ND5-2R	196 bp	48 °C	(Johnson et al. 1998) (Johnson et al. 1998)

We identified bone and hair fragments of small mammals with the aid of comparative collections in the Zoologisches Forschungsmuseum Alexander Koenig in Bonn. We mainly based identifications on teeth, skull fragments, and long bones examined under a stereomicroscope. We immersed molars in a water and alcohol solution and cleaned them with ultrasound. We mounted molars and sputtered them with gold to avoid specimen charging by the electron beam and to improve resolution, and examined them under a Hitachi Stereo Electron Microscope (Echlin et al. 2013). The number of teeth within each scat gives an indication of the number of individuals of small mammal species consumed, and we therefore counted the minimum number of individuals (MNI) of each species per scat using the number of teeth. There is no way of determining the number of individuals from hair, feathers or scales and we applied an automatic MNI of 1 to samples that consisted purely of these.

We extracted body mass data for the larger species from White (1994) and the Encyclopaedia of Life (eol.org; accessed October 2015) and for the small mammals from species accounts in Happold (2013) (Table 5.8). In cases where body mass data were given separately for males and females, we used the values for females for consistency. We followed the small mammal taxonomy of Carleton & Musser (2005) and Happold (2013), with recent changes summarized by Monadjem et al. (2015).

5.3.9. Scat and dietary analysis

We used the t-test to investigate differences in scat width and bone fragment length between the scats of golden cats and leopards. We calculated frequency of occurrence as the proportion of scats in which a food item occurred and percent occurrence as the proportion of the prey item MNI out of the total MNI. We note that frequency of occurrence methods can overestimate the importance of small prey (Ackerman et al. 1984) and underestimate the importance of large prey (Weaver 1993), but our data were not appropriate for using a correction factor to counteract this issue. We used Levins' Standardised Measure of Niche Breadth (Levins, 1968) for both leopards and golden cats. Finally, we used Pianka's Index (Pianka, 1973) to assess food niche overlap between the two species in two ways: (1) with each prey item independently, and (2) with prey divided into five body mass categories (< 2 kg, 2 – 5 kg, 5 – 10 kg, 10 – 20 kg, and > 20 kg). We only included items identified to genus level in these calculations.

We performed an analysis of variance (ANOVA) to assess whether the prey samples were significantly different among sites, and then used Tukey's test for multiple comparisons between sites. We only did this for golden cats, as the number of leopard samples per site was too small. We also used ANOVA and Tukey's test to explore differences in golden cat and leopard prey photo-capture rates in order to assess whether differences in diet across sites could be accounted for by difference in relative abundance of prey.

5.4. Results

Golden cats and leopards were photo-captured at a total of 88 and 77 camera stations, respectively (Table 5.4). Overlap in space use, measured as the proportion of camera stations where, for each species the proportion of traps at which it was captured at which the other species was also captured, ranged from 27.3% to 92.3% (mean = 52%; Table 5.4) across the five study sites.

Table 5.4. Summary of golden cat (GC) and leopard photo-captures and spatial overlap.

	# GC captures	# Leopard captures	# Stations GC captured	# Stations leopard captured	# Stations both captured	% GC stations where leopards also captured	% Leopard stations where GC also captured
Langoué	37	16	22	9	7	31.8%	77.8%
SEGC	24	94	13	29	12	92.3%	41.4%
Milolé	48	21	19	10	6	31.6%	60.0%
Mouyabi	78	63	25	18	13	52.0%	72.2%
Moukagno	17	19	9	11	3	33.3%	27.3%

5.4.1. Golden cat space use

At the local scale, leopard photo-capture rate was a variable in the best (lowest AIC-scoring) model for golden cat photo-captures at four out of five sites (Table 5.5, Fig. 5.2). There was evidence of spatial autocorrelation at some sites, and we therefore included autocovariates in models where relevant. Golden cat prey photo-capture rate and ground vegetation density also featured in the best models. Golden cat photo-captures were negatively correlated with prey at four out of five sites and positively correlated with vegetation at three sites. Golden cat photo-captures were positively correlated with trail width at four sites, but trail width did not feature in the best models. Elevation consistently ranked poorly (Table 5.S.1). At the larger scale with data from all sites pooled, our best ranking model still included leopard photo-capture rate as a positive association, with the addition of land-use as a site-level variable (Table 5.5, Fig. 5.3). Photo-captures were highest in logging concessions, followed by national parks and then village hunting area.

5.4.2. Leopard space use

At the local scale, trail width was the variable that featured most in the top models, and was positively correlated with leopard photo-captures (Table 5.5, Fig. 5.3). There was spatial autocorrelation at some sites, and we again included autocovariates in relevant models. Leopard prey varied in importance, but where it ranked highly, leopard capture rate was negatively correlated with prey. As with the golden cat, elevation was generally unimportant, as was vegetation density, with the exception of one site (Table 5.S.2). With sites pooled, trail width remained in the best ranking model as a positive association, with the addition of land-use as a site-level variable (Table 5.5, Fig. 5.4). Photo-captures of leopard were highest in national parks, followed by logging concessions and lowest in the village hunting area.

Table 5.5. Effects of camera site variables on the number of golden cat and leopard photo-captures, analysed using negative binomial regression. These are results from the best performing model for each site, and all sites combined (selected using the Akaike Information Criterion); results for all candidate models can be found in Supplementary Materials.

Golden cat					**Leopard**				
	Estimate	Std. Error	z-value	p-value		Estimate	Std. Error	z-value	p-value
Langoué					Langoué				
(Intercept)	-0.930	0.332	-2.802	0.005	(Intercept)	-2.091	0.365	-5.722	< 0.0001
Acov1	-0.126	0.150	-0.842	0.400	Trail width	0.709	0.274	2.587	0.010
Leopard	0.147	0.083	1.761	0.078					
SEGC					SEGC				
(Intercept)	-2.227	0.472	-4.718	< 0.0001	(Intercept)	0.796	0.212	3.759	< 0.0001
Prey	-1.648	0.766	-2.151	0.032	Acov1	-0.452	0.092	-4.911	0.000
Veg	0.549	0.293	1.873	0.061	Trail width	0.258	0.113	2.273	0.023
Milolé					Milolé				
(Intercept)	-1.380	0.390	-3.538	0.000	(Intercept)	-1.913	0.376	-5.088	< 0.0001
Acov1	0.206	0.134	1.538	0.124	Prey	-0.756	0.415	-1.823	0.068
Mouyabi					Mouyabi				
(Intercept)	-0.955	0.231	-4.128	< 0.0001	(Intercept)	-0.917	0.234	-3.924	< 0.0001
Leopard	0.083	0.049	1.719	0.086	Trail width	0.862	0.225	3.831	< 0.0001
Prey	-0.655	0.298	-2.198	0.028					
Moukagno					Moukagno				
(Intercept)	-0.679	0.810	-0.839	0.402	(Intercept)	-0.550	0.564	-0.975	0.329
Acov2	-4.039	1.978	-2.042	0.041	Acov1	-2.705	1.146	-2.360	0.018
Leopard	0.427	0.246	1.736	0.083					
All Sites					All Sites				
(Intercept)	-1.128	0.261	-4.321	0.000	(Intercept)	-0.506	0.410	-1.236	0.216
Land-use: NP	-0.513	0.255	-2.012	0.162	Land-use: NP	0.219	0.321	0.681	0.496
Land-use: Village	-1.002	0.375	-2.670	0.044	Land-use: Village	-1.378	0.436	-3.159	0.002
Acov1	0.109	0.078	1.399	0.008	Acov2	-0.380	0.163	-2.340	0.019
Leopard	0.111	0.038	2.920	0.004	Trail width	0.506	0.109	4.660	0.000

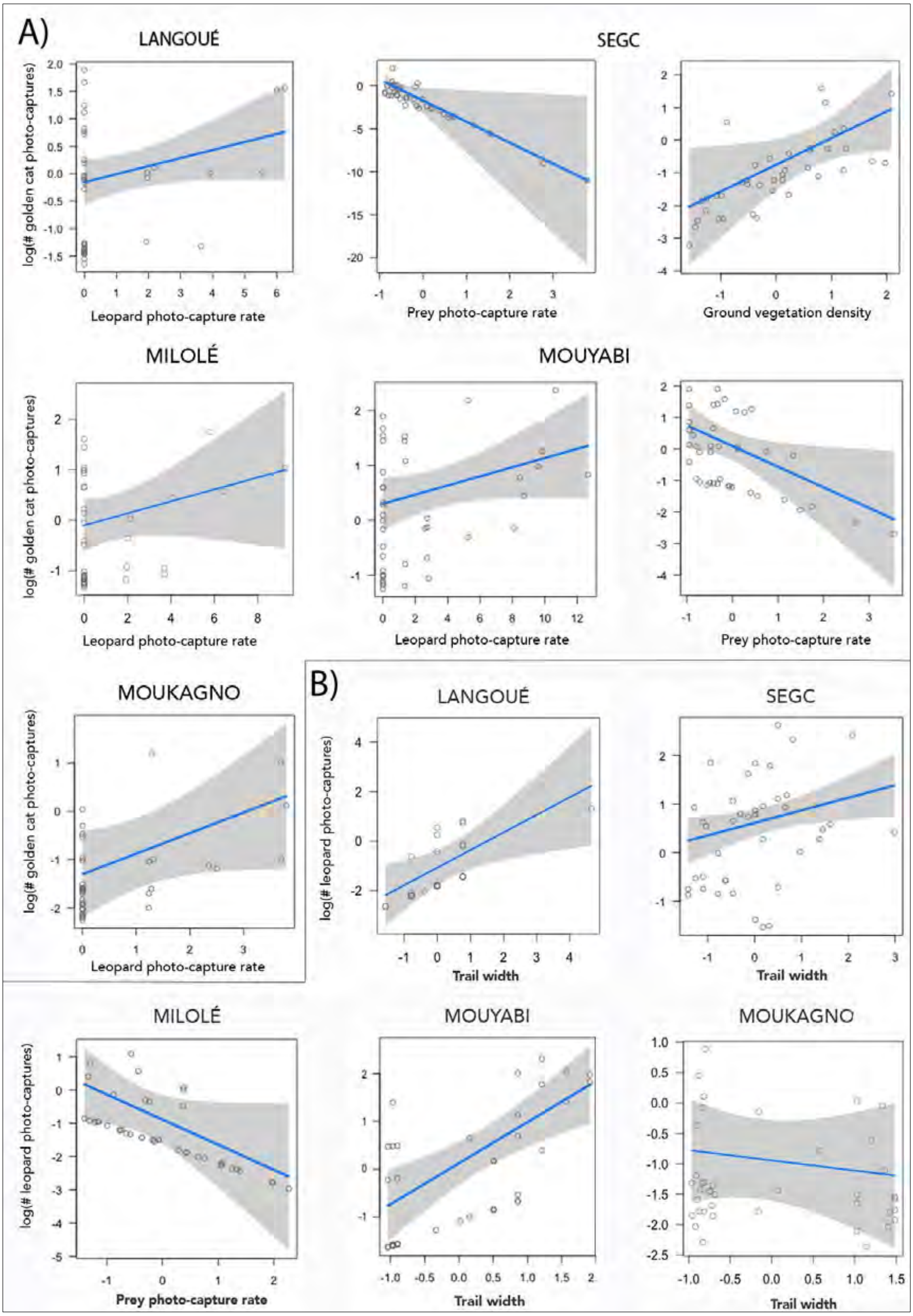

Figure 5.2. Plotted negative binomial regressions for best scoring model candidates (ranked by AIC) for each site, showing the variables that predict number of A) golden cat and B) leopard photo-captures. (The explanatory variable values, with the exception of leopard photo-capture rate, have been standardised.) Regression line is in blue, with confidence band in grey and partial residuals as dots.

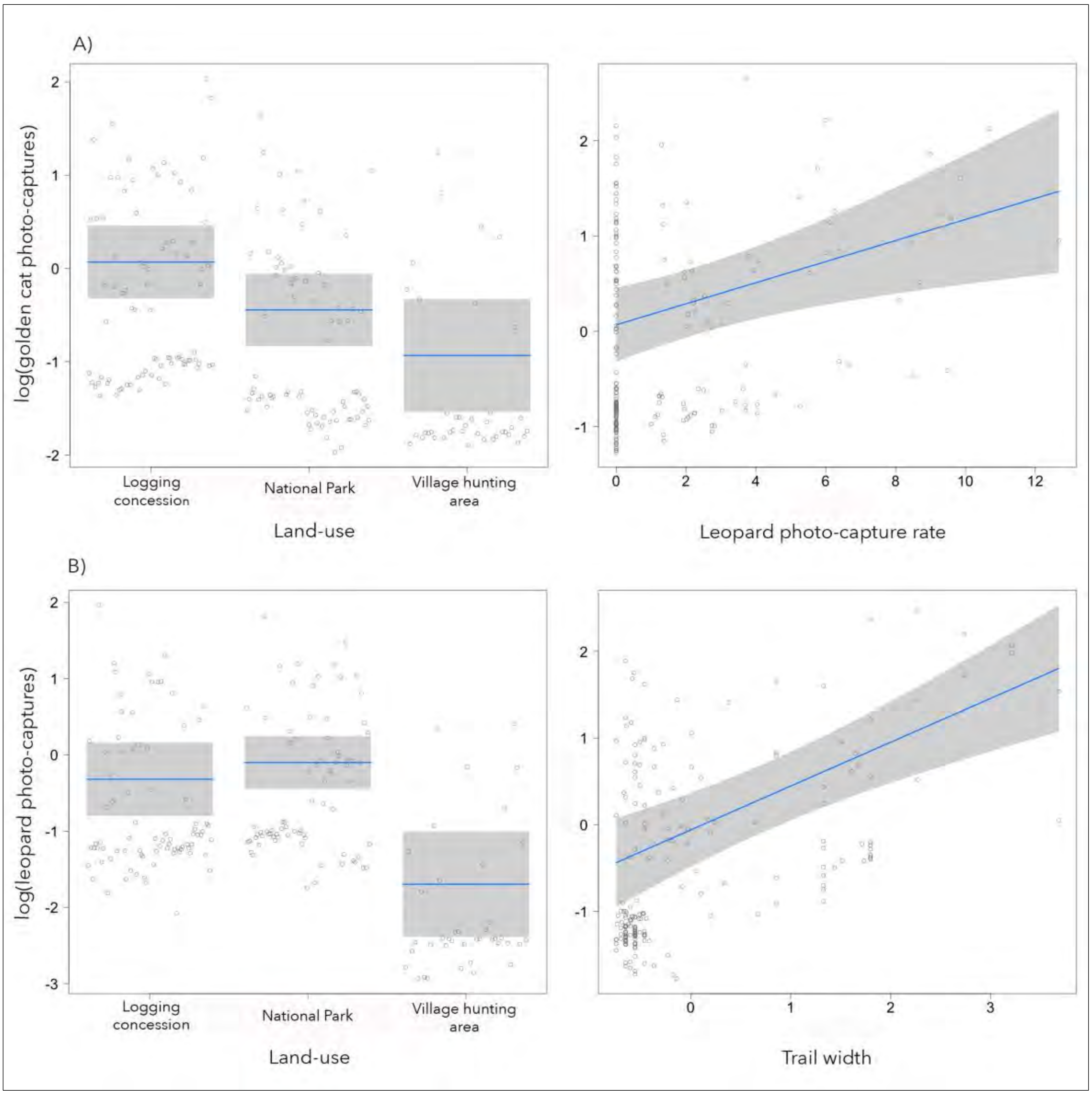

Figure 5.3. Plotted negative binomial regressions for best scoring model candidates (ranked by AIC) with all sites pooled, showing the variables that best predict number of A) golden cat and B) leopard photo-captures. (Trail width values have been standardised.) Regression line is in blue, with confidence band in grey and partial residuals as dots.

5.4.3. Temporal avoidance

There was evidence of temporal avoidance at camera stations, with a visible dip in golden cat activity starting ca. 30 hours prior to leopard capture (Fig. 5.4). Golden cat activity then peaked at 20 – 60 hours after leopard capture. We do not expect the lack of golden cat activity at the time of leopard photo-capture to be a result of differing daily activity patterns (see Chapter 4 for overall golden cat and leopard temporal activity patterns).

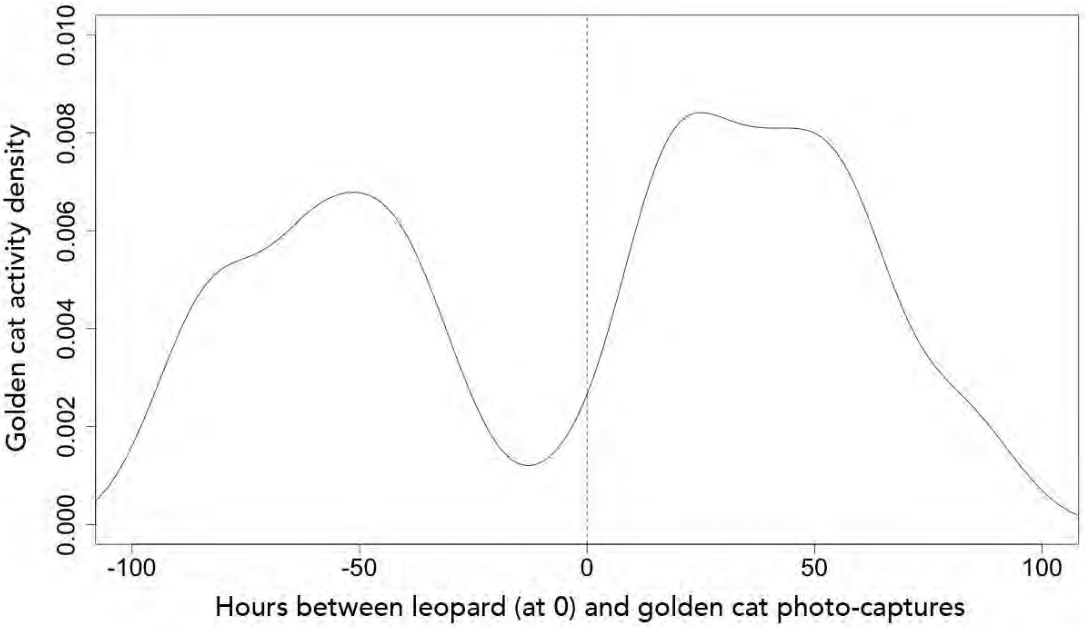

Figure 5.4. Temporal avoidance graph, showing the number of hours between leopard photo-capture (at 0 hours) and golden cat photo-captures at camera stations (n = 101).

5.4.4. Scat and diet

We collected a total of 186 scat samples, 122 of which were confirmed to originate from golden cat and 30 from leopard. There was a significant difference in width (t = 3.96, df = 20.34, p-value < 0.001) and bone fragment length (t = 5.44, df = 28.07, p-value < 0.001) between leopard and golden cat scats. However, the ranges of both measures overlapped (Table 5.7).

Table 5.7. Summary of scat measurements for leopards and golden cats (sample sizes differ as width and bone fragment length measurements could not be taken for all scats due to scat consistency and content.)

	Scat width (mm)			Bone fragment length (mm)		
	Mean	Std. Error	Range	Mean	Std. Error	Range
Golden cat	16.78 (n = 126)	0.12	10 - 25	13.49 (n = 127)	0.40	2 - 23
Leopard	22.00 (n = 20)	1.30	15 - 39	24.74 (n = 27)	2.03	10 - 59

Eight percent of golden cat and 7% of leopard scats contained insect remains. Twenty percent of golden cat and 17% of leopard scats contained grass. Thirty-nine percent of golden cat and 3% of leopard scats contained ticks.

Rodents were the most important golden cat prey in both occurrence and diversity (16 species). These consisted of 8 murids, 5 sciurids, likely 2 anomalurids, and one species of porcupine. Shrews were consumed in low numbers (Table 5.8). Leopards preyed predominantly on ungulates and primates, with red duikers showing the highest relative occurrence (Table 5.8).

Levins' standardised measure of niche breadth (which ranges between 0 for narrowest niche and 1 for widest) was 0.31 for golden cats and 0.23 for leopards. Pianka's index of food niche overlap (which varies from 0 for exclusive food niches, to 1 for complete overlap; Pianka 1973) between golden cats and leopards was 0.18 when it was calculated by prey species, and 0.49 when it was calculated by prey body mass category.

There was a significant difference in golden cat prey body mass among sites ($F(4,180) = 6.97$, $p < 0.0001$; Fig. 5.5), with mean prey body mass significantly lower at the logging sites (Milolé and Mouyabi) than at the sites in Lopé NP (SEGC and Mikongo) (Tukey's Test: $p < 0.05$). Sample sizes for leopard prey at each site were too small to compare.

There were significant differences in photo-capture rates between sites for the following golden cat and leopard prey species: giant pouched rat ($F(4,195) = 5.37$, $P < 0.001$), blue duiker ($F(4,195) = 3.36$, $P < 0.05$), red duiker species ($F(4,195) = 30.92$, $P < 0.001$), and red river hog ($F(4,195) = 17.23$, $P < 0.001$). Only brush-tailed porcupine photo-capture rate did not differ significantly between sites ($F(4,195) = 1.58$, $P = 0.18$). The giant pouched rat was more frequently photo-captured in Langoué, Milolé and Mouyabi (Fig. 5.S.2A). The main leopard prey species were more frequently photo-captured in the protected areas, with the exception of red duikers in the Milolé certified logging concession that had a higher photo-capture rate than in the Langoué pristine area (Fig. 5.S.2B).

Table 5.8. Prey results from genetically-identified scats of golden cats and leopards (all sites combined). Frequency of occurrence was calculated as the proportion of scats in which a certain prey item occurs out of the total number of scats. Percentage occurrence was calculated as the minimum number of individuals (MNI) of a prey item out of the total MNI for all species.

		Golden cat (n = 131)				Leopard (n = 28)			
Prey species	Average prey weight (kg)	# scats per prey item	MNI	Frequency of occurrence	% occurrence	# scats per prey item	MNI	Frequency of occurrence	% occurrence
Ungulates									
Potamochoerus porcus	61.9					8	8	28.6	16.3
Red duiker (*Cephalophus*) sp.	15.5	4	4	3.1	1.4	14	14	50.0	28.6
Philantomba monticola	4.5	33	33	25.2	11.8	4	4	14.3	8.2
Duiker (*Cephalophinae*) sp.						1	1	3.6	2.0
Tragelaphus scriptus	43.25					1	1	3.6	2.0
Total ungulates		**37**	**37**		**13.2**	**28**	**28**		**57.1**
Primates									
Colobus satanas	8.4	1	1	0.8	0.4	1	1	3.6	2.0
Lophocebus albigena	4.1					1	1	3.6	2.0
Cercopithecus nictitans	3.2	3	3	2.3	1.1	7	7	25.0	14.3
Total primates		**4**	**4**		**1.4**	**9**	**9**		**18.4**
Carnivores									
Herpestes naso	2.8					1	1	3.6	2.0
Pangolins									
Phataginus tricuspis	1.9					3	3	10.7	6.1
Rodents									
Atherurus africanus	2.950	27	27	20.6	9.6	1	1	3.6	2.0
Anomalure sp.	0.543	2	2	1.5	0.7				
Cricetomys emini	0.903	16	17	12.2	6.1				
Dendromurid	0.010	2	2	1.5	0.7	1	1	3.6	2.0
Deomys ferrugineus	0.056	6	6	4.6	2.1				
Hybomys univittatus	0.049	57	80	43.5	28.6	1	1	3.6	2.0
Lophuromys sp.	0.040	4	4	3.1	1.4				
Praomys misonnei	0.035	2	2	1.5	0.7				
Stochomys longicaudatus	0.071	2	5	1.5	1.8				
Hylomyscus sp.	0.018					1	1	3.6	2.0
Muridae sp.		18	18	13.7	6.4				
Protoxerus stangeri	0.691	2	2	1.5	0.7				
Heliosciurus rufobrachium	0.351	2	2	1.5	0.7				
Funisciurus pyrropus	0.283	3	3	2.3	1.1				
Funisciurus isabella	0.104	7	7	5.3	2.5				
Funisciurus sp.	0.194	2	2	1.5	0.7				
Paraxerus poensis	0.105	1	1	0.8	0.4	1	1	3.6	2.0
Sciuridae sp.		2	2	1.5	0.7				
Rodentia sp.		13	13	9.9	4.6	1	1	3.6	2.0
Total rodents		**168**	**195**		**69.6**	**6**	**6**		**12.2**
Shrews									
Paracrocidura schoutedeni	0.013	7	8	5.3	2.9				
Reptiles									
Varanus ornatus	15					1	1	3.6	2.0
Lizard (*Lacertilia) sp.*		11	11	8.4	3.9				
Snake (*Serpentes*) sp.		1	1	0.8	0.4				
Gecko (*Gekkota)* sp.		1	1	0.8	0.4				
Reptilia sp.		3	3	2.3	1.1	1	1	3.6	2.0
Total reptiles		**16**	**16**		**5.7**	**2**	**2**		**4.1**
Other									
Mammalia sp.		10	10	7.6	3.6				
Amphibian sp.		1	1	0.8	0.4				
Aves sp.		7	7	5.3	2.5				
Egg shell		2	2	1.5	0.7				
*Insecta sp.**		11		8.4		2		7.1	

* Not included in MNI and % occurrence calculations

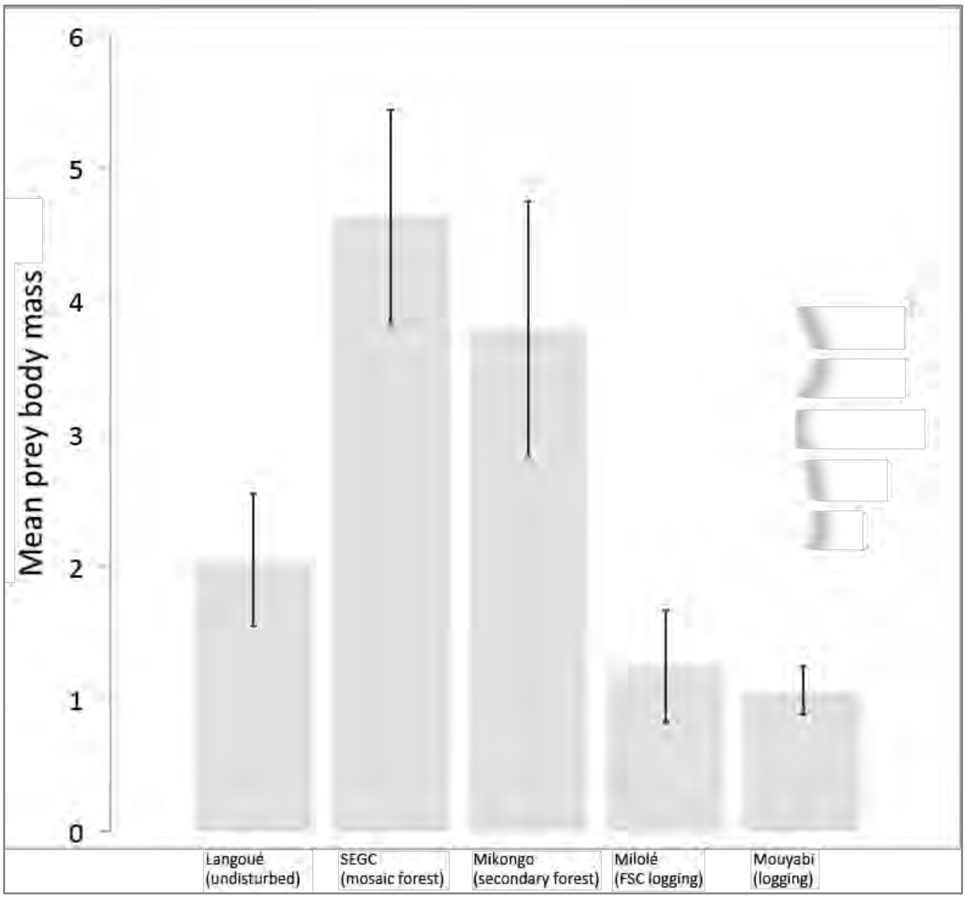

Figure 5.5. Golden cat mean prey body mass with standard error bars, shown by site (Moukagno is excluded due to a lack of samples).

5.5. Discussion

5.5.1. Space

Golden cats and leopards appear to use the landscape similarly, with both species being captured at many of the same camera sites. Leopard photo-capture rate at camera sites was the best predictor of golden cat site usage at both spatial scales, providing additional evidence (to Chapter 3) that the species share space on a fine scale. This is due to the shared use of larger trails, which facilitate movement through the forest understory. However, golden cats had a weaker association with larger trails than leopards. These results are similar to those of Swanson (2014) who showed that hyenas and cheetahs are positively associated with dominant lions, with the exception of areas of very high lion use, due to the shared use of shade trees. The only site for which leopard photo-capture rate was not in the best ranking model for golden cat photo-captures was SEGC where there was the highest number of leopard individuals (Chapter 3). This may indicate that the positive association between these species is dependent on the density of the dominant species.

At the larger spatial scale, land-use was an important factor for photo-captures of both felids. Both species had the lowest numbers of photo-captures in the village hunting area, but while leopards had slightly more photo-captures in national parks than logging concessions, golden cats had notably more photo-captures in the logging concessions. Bahaa-el-din et al. (Chapter 3) discuss that detection of golden cats may be high in logging concessions due the extensive large road/trail network created during the course of wood extraction. The higher detections did not, however, translate to higher population density (Chapter 3). Henschel et al. (2011) found that leopard population density was highest in national parks versus a logging concession and village hunting area. It is possible that, at high density, leopards displace golden cats from large trails (as was found for cheetahs and hyenas being displaced from shade trees at high lion density; Swanson 2014), making them harder to detect.

The negative correlation between predator and prey camera sites may be an artefact of the study targeting trails and camera traps having narrow detection zones. At a larger spatial scale, there is likely a positive correlation.

5.5.2. Time

Bahaa-el-din et al. (Chapter 4) found that leopards and golden cats overlap in their temporal activity, but that golden cats were less active during peaks in leopard activity. In our finer spatial scale analyses at individual camera stations, we found that golden cat activity dropped more than a day before a leopard was photo-captured and peaked again 1 – 2.5 days after the leopard passed. The drop prior to leopard photo-capture indicates that golden cats are spatially aware of leopards, and supports our hypothesis that golden cats use fine-scale temporal avoidance of leopards.

Our findings correspond with recent studies using GPS collars (Broekhuis et al. 2013, Vanak et al. 2013) and remote camera trapping (Swanson 2014) on the African savannah large carnivore guild. For example, Broekhuis et al. (2013) found that cheetahs prioritised resource acquisition while using fine-scale avoidance to minimise encounters with lions and hyenas. This type of avoidance has been dubbed “reactive” (Broekhuis et al. 2013) as it is based on individuals’ reactions to the immediate presence of a dominant species. It has also been described for ungulates avoiding predation by large carnivores (Creel et al. 2005, Valeix et al. 2009). Vanak et al. (2013) also found that cheetahs and leopards used fine-scale avoidance of lions, suggesting that mesocarnivores are spatially aware of competitors, and base movement decisions on the presence of dominant species. Swanson (2014) found that while African wild dog populations were suppressed and suffered landscape-level displacement from lions (and perhaps hyenas), cheetahs persisted alongside lions by using fine-scale reactive avoidance. Within a different, Neotropical environment, Harmsen et al. (2009) found that temporal avoidance between jaguars Panthera onca and pumas Puma concolor in Belize only became apparent at a camera station rather than study site scale.

5.5.3. Food niche

Ours is the first estimate of food niche overlap between golden cats and leopards based on genetically confirmed scat origin, thus avoiding subjective judgements which may have biased earlier estimates. We found overlap to be much lower than estimated in previous studies including Ray & Sunquist (2001) who estimated an overlap of 0.92 and Ososky (1998) with an estimate of 0.67. This appears to be a result of the greater importance of rodents for golden cats, and reduced importance of blue duikers for leopards in our study. These could be due to differences in prey availability, but may also partly result from misidentification of golden cat scats as leopard scats in previous studies. Indeed, our findings showed that the previously used width cut-off point of 21 cm, with scats larger than this automatically assumed to be from a leopard, is erroneous. Genetically identified golden cat scats reached 25 cm in width. We therefore recommend that future dietary studies of similar-size felids use genetic identification of scat origin, even in very simple carnivore communities such as the one we studied (and see Farrell et al. 2000).

Food niche overlap was higher, however, when species were categorised by body mass. Ultimately, leopards generally preyed on larger prey than golden cats, with the latter mostly consuming prey weighing 4.5 kg or less. Golden cats consumed smaller prey, on average, in the logging concessions and at the pristine site. Correspondingly, the photo-capture rate of the smallest prey species that we analysed, the giant pouched rat, was highest in the logging concessions and pristine site. The difference in golden cat diet may therefore be a result of greater availability of smaller (rodent) prey, as has been reported for logging concessions (Mongo et al. 2012). Alternatively, golden cats may switch to smaller prey to avoid competition with leopards. Henschel et al. (2011) carried out leopard surveys across a similar disturbance gradient, including two of the same sites. They found that leopards consumed smaller prey with increased disturbance as a result of exploitative competition with human hunters for the same prey. Ecological plasticity may therefore benefit golden cats, allowing them to co-exist alongside leopard, even in disturbed areas where leopards switch to smaller prey.

5.5.4. Conclusion

Prior studies have estimated high temporal (Chapter 4) and food niche (Ososky 1998, Ray & Sunquist 2001) overlap between leopards and golden cats, and findings from Bahaa-el-din et al. (Chapter 3) also indicated shared space use. Our results help to clarify aspects of the competitive relationship within this small felid community. Space use does indeed seem to be similar, but with leopards using larger trails to a greater extent than golden cats. Overlap in temporal activity patterns may be high, but golden cats appear to reactively avoid leopards at a small spatio-temporal scale, which is not surprising given that golden cats are also leopard prey (Henschel et al. 2005). Finally, our findings on food niche overlap indicate that the species have clearly separate niches, and that prey is probably not a significant driver of competition between leopards and golden cats. Even at sites exposed to human disturbance, golden cats exploit smaller prey, thereby reducing the risk of competing with leopards that are also having to switch to smaller prey.

This simple two-felid community has allowed us to explore mechanisms of co-existence between sympatric large carnivores, which included fine-scale spatio-temporal avoidance and food niche segregation. These findings will help when considering conservation interventions. For example, the reintroduction of leopards in rainforest areas where they have been extirpated should not negatively impact golden cats, provided the leopards' ecological needs are met. These findings may apply to simple carnivore communities more widely and may also help in building up models for more complex communities.

5.6. References

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5.7. Supplementary materials

Table 5.S.1. Golden cat space use models: output from negative binomial regressions assessing the effects of camera station variables on the number of golden cat photo-captures for all candidate models, ranked using the Akaike Information Criterion (AIC). Variables with a significant effect are ranked using the * system (see table footnote).

	Langoué	SEGC	Milolé	Mouyabi	Moukagno
Model AIC # parameters.	104.89 4	80.74 4	124.10 4	139.46 4	66.14 4
Variable coefficients	Acov1 = -0.13, Leopard° = 0.15	Prey* = -1.65; Veg° = 0.55	Acov1° = 0.23; Leopard = 0.12	Leopard° = 0.08; Prey* = -0.65	Acov2* = -4.04; Leopard° = 0.43
Model AIC # parameters.	105.14 3	81.92 5	124.42 2	139.73 5	69.12 3
Variable coefficients	Leopard° = 0.14	Acov2 = 0.86; Prey* = -1.68; Veg° = 0.56	Null Model	Acov2 = -0.41; Leopard° = 0.08; Prey° = -0.57	Leopard = 0.42
Model AIC # parameters.	105.68 2	81.99 3	124.77 4	140.14 3	69.73 2
Variable coefficients	Null model	Prey* = -1.58	Acov1 = 0.19; Trail = 0.24	Prey** = -0.95	Null Model
Model AIC # parameters.	106.95 5	82.05 4	125.03 3	140.81 4	71.01 3
Variable coefficients	Acov1 = -0.44; Leopard° = 0.16; Veg = -0.01	Leopard = 0.14; Prey* = -1.39	Trail = 0.30	Prey* = -0.72; Trail = 0.25	Veg = 0.31
Model AIC # parameters.	107.25 4	83.38 5	125.36 3	142.76 3	71.39 3
Variable coefficients	Acov 1 = -0.12; Veg = -0.13	Veg° = 0.5681	Leopard = 0.10	Leopard** = 0.14	Elev = 0.29
Model AIC # parameters.	107.58 3	86.39 3	126.16 3	143.90 3	71.67 3
Variable coefficients	Veg = -0.07	Leopard = 0.18	Veg = -0.16	Trail** = 0.52	Trail = 0.10
Model AIC # parameters.	107.60 3	87.34 2	126.23 3	148.99 2	71.71 3
Variable coefficients	Prey = -0.05	Null model	Prey = 0.10	Null Model	Prey = -0.06
Model AIC # parameters.	107.67 3	88.28 3	126.42 3	149.18 3	
Variable coefficients	Trail = 0.02	Sav = 0.39	Elev = 0.02	Veg = 0.26	
Model AIC # parameters.	107.68 3	89.25 3		150.71 3	
Variable coefficients	Elev = 0.01	Trail = -0.11		Elev = 0.12	
Model AIC # parameters.		89.27 3			
Variable coefficients		Elev = 0.10			

*** = p< 0.001; ** = p< 0.01; * = p < 0.05; ° = p < 0.1

Table 5.S.2. Leopard space use models: output from negative binomial regressions assessing the effects of camera station variables on the number of leopard photo-captures for all candidate models, ranked using the Akaike Information Criterion (AIC). Variables with a significant effect are ranked using the * system (see table footnote).

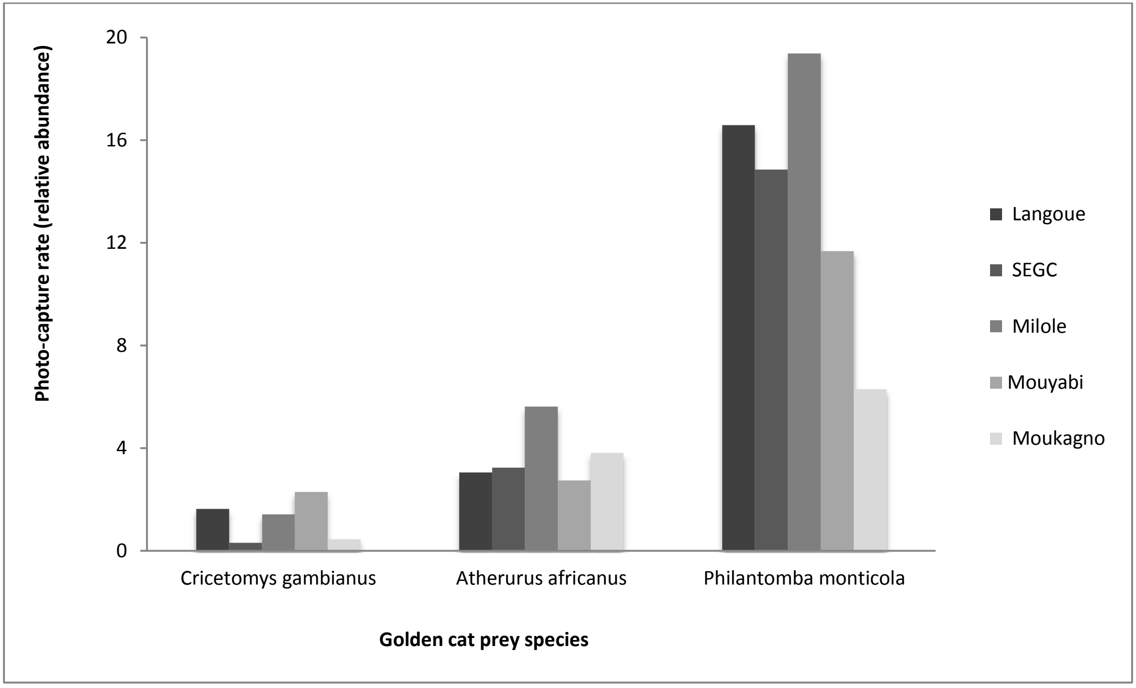
	Langoué	SEGC	Milolé	Mouyabi	Moukagno
Model AIC # parameters.	66.24 3	141.60 4	77.24 3	129.87 3	72.58 4
Variable coefficients	Trail** = 0.71	Acov1*** = -0.45; Trail* = 0.26	Prey° = -0.76	Trail*** = 0.86	Acov2* = 2.74; Trail = -0.17
Model AIC # parameters.	66.99 4	141.93 4	77.86 3	131.60 4	72.85 4
Variable coefficients	Trail* = 0.59; Veg = -0.54	Acov1*** = -0.45; Veg* = 0.26	Trail = 0.48	Acov1 = 0.061; Trail*** = 0.83	Acov2* = -2.66; Prey = -0.04
Model AIC # parameters.	67.71 4	161.15 3	77.87 4	140.94 2	73.98 2
Variable coefficients	Acov1 = -0.02; Trail* = 0.69	Trail° = 0.27	Prey = -0.62; Veg = -0.44	Null Model	Null Model
Model AIC # parameters.	68.50 2	162.40 2	77.89 3	142.79 3	75.21 3
Variable coefficients	Null Model	Null Model	Veg = -0.58	Elev = 0.10	Prey = -0.39
Model AIC # parameters.	68.70 3	163.19 3	78.23 2	142.90 3	75.84 3
Variable coefficients	Veg = -0.63	Veg = 0.17	Null Model	Veg = 0.06	Trail = -0.12
Model AIC # parameters.	69.96 3	163.78 3	78.24 4	142.90 3	75.96 3
Variable coefficients	Elev = 0.28	Prey = 0.11	Prey = -0.56; Trail = 0.33	Prey = 0.05	Elev = 0.05
Model AIC # parameters.	70.49 3	164.32 3	79.76 3		75.98 3
Variable coefficients	Prey = 0.04	Sav = 0.05	Elev = 0.20		Veg = -0.02
Model AIC # parameters.		164.39 3			
Variable coefficients		Elev = -0.02			

*** = p< 0.001; ** = p< 0.01; * = p < 0.05; ° = p < 0.1

Table 5.S.3. Pooled site space use models: All candidate models for negative binomial regression, assessing the effects of camera station and study site variables on the number of golden cat and leopard photo-captures at the larger (pooled site) spatial scale, ranked using the Akaike Information Criterion (AIC).

Golden cat				**Leopard**			
Model #	Variables	# parameters.	AIC	Model #	Variables	# parameters	AIC
1	Acov1+Land-use+Leopard rate	6	530.74	1	Acov2+Land-use+Trail width	6	511.10
2	Acov1+Leopard rate	4	535.16	2	Land-use+Trail width	5	514.62
3	Acov1+Land-use	5	538.04	3	Acov2+Trail width	4	519.55
4	Land-use	4	538.81	4	Trail width	3	526.85
5	Acov1+Trail width	4	541.78	5	Acov2 + land-use	5	530.02
6	Leopard rate	3	542.45	6	Land-use	4	535.79
7	Trail width	3	546.97	7	Vegetation	3	540.31
8	Prey	3	551.26	8	Null Model	2	540.70
9	Null Model	2	552.22	9	Elevation	3	542.09
10	Elevation	3	553.10	10	Prey	3	542.70
11	Vegetation	3	554.13				

A)



B)

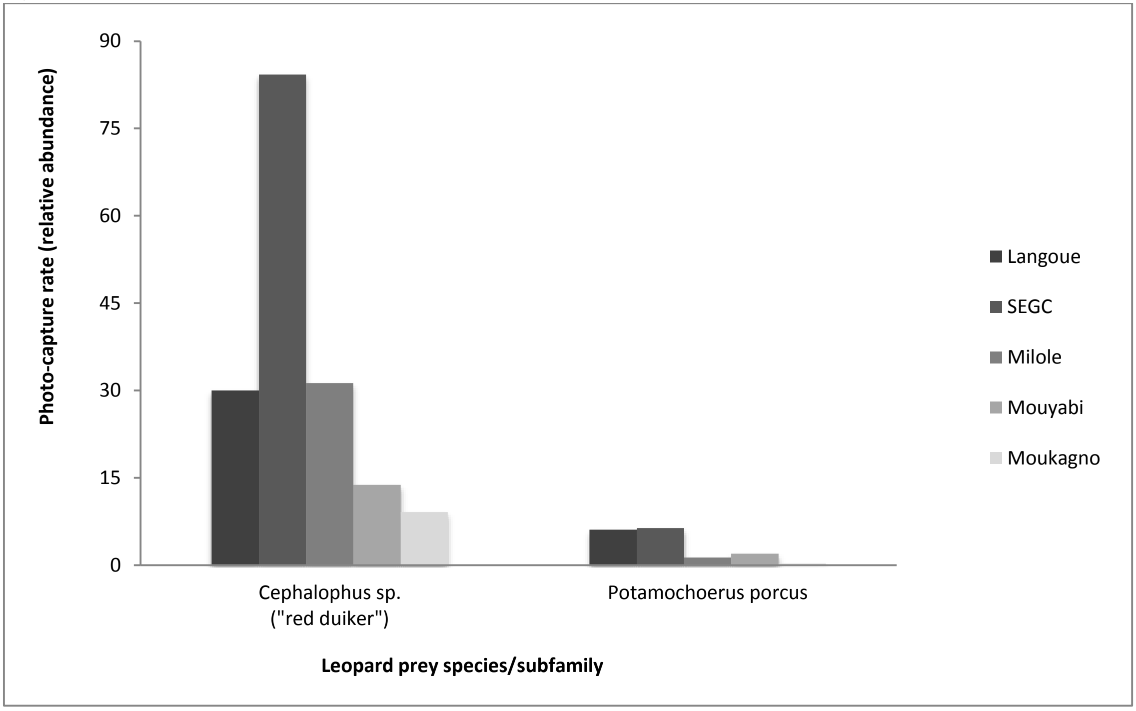
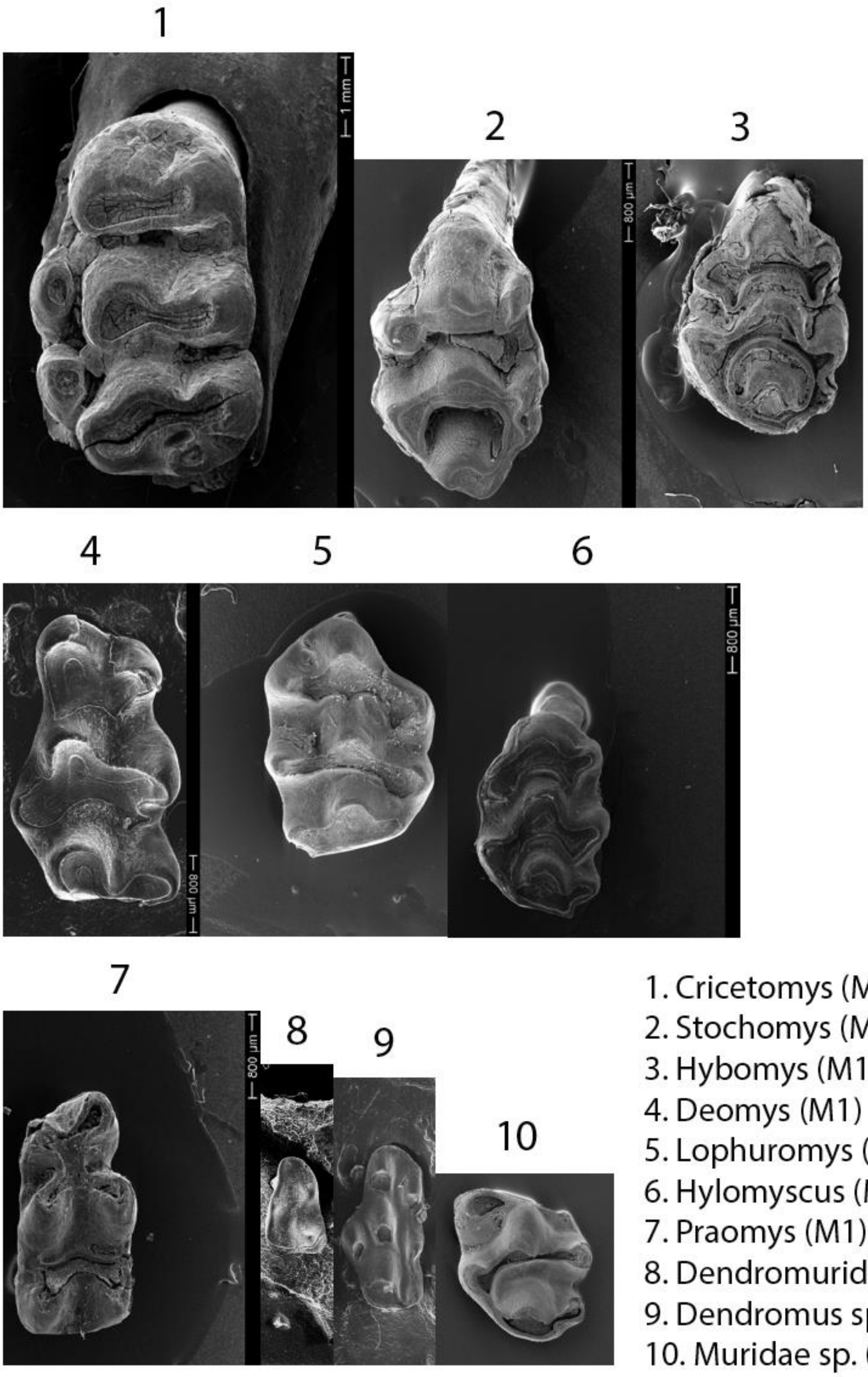


Figure 5.S.2 Photo-capture rates, by site, for A) main golden cat prey species and B) main leopard prey species.

Figure. 5.S.3 Photographic scans from a Hitachi Stereo Electron Microscope of small rodent genera, used for identifying prey remains in leopard and golden cat scats.



1. Cricetomys (M1)
2. Stochomys (M1)
3. Hybomys (M1)
4. Deomys (M1)
5. Lophuromys (M1)
6. Hylomyscus (M1)
7. Praomys (M1)
8. Dendromuridae sp. (?)
9. Dendromus sp. (M1)
10. Muridae sp. (M2)

6. General Conclusions

6.1. Summary results

African golden cats were not as naturally rare as originally suspected, and had the highest population density estimate at the undisturbed, continuous forest site (16.23 individuals per 100 km2; Chapter 3). They were sensitive to human hunting, with density dropping by 77% at a site with low-intensity subsistence hunting. Population density in two logging concessions was relatively high. Golden cat temporal activity patterns differed significantly between sites where leopards are present and sites where leopards have been extirpated (Chapter 4). They were cathemeral in the former with lots of diurnal activity, and nocturno-crepuscular in the latter. This “release” from leopards allowed them to decrease their temporal overlap with humans. Where golden cats and leopards co-occur, golden cats used fine spatio-temporal scale reactive avoidance of leopards, and food niche segregation, as mechanisms of co-existence (Chapter 5).

The significance of this work is two-fold: 1) We have provided baseline information on golden cats, as well as management recommendations that can help to conserve this and sympatric species (Chapter 3); and 2) Our study has shed light on current topics in ecology, including mesopredator release and carnivore co-existence, that have relevance for similar systems worldwide (Chapters 4 & 5).

6.2. Conservation of golden cats and sympatric carnivores

Assessments of African golden cat population status, including for the IUCN Red List of Threatened Species (the Red List), have hitherto been based on anecdotal reports. Our estimates of population density (Chapter 3) not only provide baseline information to which future studies can compare, but also give insight into the effects of human disturbance on golden cat populations. This formed part of the basis for the most recent Red List assessment (Bahaa-el-din et al. 2015a; Appendix 1). A key finding of our research was that golden cats persist in newly logged concessions, providing support for Clark et al.’s (2009) suggestion that including logging concessions within the conservation estate would expand the area in which threatened species are protected. Logging is known to have adverse effects on forest ecosystems and diversity (e.g. Asner et al. 2005, Peh et al. 2005, Wells et al. 2007). However, our results contribute to a growing body of work (Johns 1985, Rayan & Mohamad 2009, Berry et al. 2010, Putz 2012) that acknowledges that, while selectively logged forests may not conserve the entire ecological diversity therein, they can be important strongholds for wildlife.

The conservation community should now fill the “research-implementation gap” (Knight et al. 2008) and use these findings to put pressure on governments and extractive companies (such as loggers) to function under a sound management plan (see de Blas & Perez 2008), ensuring that emphasis is placed on maintaining wildlife populations during and after extraction. Such is often not the case, as extractive industries regularly increase demand for, and provide access to, wildlife products by opening up previously inaccessible areas, and bringing in people (Poulsen et al. 2009). Avoiding the establishment of permanent settlements should be part of the strategy to minimise long-term consequences of extraction, as well as destruction of infrastructure that provides access to remote forests (Poulsen et al. 2009).

It was encouraging to find that golden cats are not as naturally rare as previously supposed, and, in the absence of threats, can thrive (Chapter 3). However, their rapid decline in the presence of even low-intensity hunting is cause for concern, particularly in light of increasing human populations in their range countries (FAO 2011), and increasing access by humans to remote areas (Bahaa-el-din et al. 2015a; Appendix 1). For example, over 64% of forest in the Congo Basin were already within 10 km of a road in 2007 and therefore at high risk of human hunting (Blake et al. 2007), and road networks are rapidly expanding (Laporte et al. 2007). We found that hunters rarely encounter golden cats in person, suggesting that mortality is likely rarely caused by guns. Instead, it is wire snares that frequently capture golden cats and depress their populations (Bahaa-el-din et al. 2015a), and there is evidence from Equatorial Guinea that the golden cat is one of the first species to disappear in the face of human disturbance (Martinez Marti 2011). Legislating against wire snares, with concurrent enforcement, is therefore critical to the persistence of golden cats outside of protected areas. In areas where people depend on bushmeat, methods of hunting that are more species-selective and less wasteful than wire snares should be used as alternatives (Newing 2001).

The behavioural plasticity of golden cats, described in Chapters 4 and 5, may also be promising in light of potential changes in environment, land-use and guild structure. Their cathemeral activity patterns (Chapter 4) and their reactive response to predator presence (Chapter 5) mean that they can adapt their activity in response to direct threats, as well as to maximise prey acquisition in response to the indirect threat of prey depletion. Their relatively wide food niche breadth (Chapter 5), including small rodents, will also benefit them under these circumstances, making them less prone to exploitative competition with human hunters than has been found for leopards (sensu Henschel et al. 2011).

One of the benefits of using camera traps to collect data is the access to data on a whole range of species aside from the target species. I have so far included the species whose interactions were most likely to influence golden cat conservation biology, but golden cats also form part of a more extensive carnivore guild. Using data on small carnivores collected as part of my study, and collating data from other surveys across the country, I led a collaborative paper assessing the status and distribution of all 12 small carnivores in Gabon (Bahaa-el-din et al. 2013; Appendix 2). We extended the known ranges of three species as part of the assessment and examined the use of carnivores for consumption and trade of bushmeat. Carnivores form a small proportion of village hunting off-takes and bushmeat markets, and golden cats form a yet smaller proportion of these. The more common small carnivores, including the marsh mongoose

Atilax paludinosus, servaline genet Genetta servalina, and African palm civet Nandinia binotata, were more frequently caught and sold as bushmeat (Appendix 2).

For a species to persist beyond protected areas in central and west Africa, where the human population is among the fastest growing in the world (FAO 2011), it needs to be tolerated by humans (sensu Dickman 2010). Understanding the perceptions of people living alongside species of conservation concern is therefore key in establishing the potential for positive conservation outcomes in human-inhabited landscapes (Dickman 2010). Golden cats were placed in the low conflict category by Inskip & Zimmerman (2009), and there are only a couple of anecdotal reports of them preying on livestock (Kingdon 1977, Davenport 1996). These were from the area around Bwindi Impenetrable National Park where the forest is a fragment surrounded by high human population density (Kingdon 1977, Davenport 1996). If these isolated incidents do occur in the Bwindi area, it is perhaps an artefact of these factors, which are not replicated in most of golden cat range. However, because of the predicted population increase (FAO 2011), these conditions may soon apply to more areas within golden cat range. I carried out interview surveys to assess local people's perceptions towards golden cats and other carnivores, and to explore which species were considered problematic (methodology in Appendix 3).

Positive perceptions of local people towards species were generally due to: tasty and/or large quantity of meat on the animal, body parts (e.g. skin) important for use in traditional ceremonies and healing, and valuable meat or skin to sell. The main reasons for negative perceptions included: destruction of plantations, danger to people, predation on poultry/livestock, and bad omen. Golden cats were generally considered unproblematic, and their skins useful for ceremonial purposes. This contrasts with a large number of the small carnivores assessed, which were reported to prey on poultry (e.g. marsh mongoose, servaline genet, and African palm civet). Leopards were said to be dangerous to people and to prey on goats, though neither issue had been directly experienced by interviewees. Their skins were of most value, both financially, and for ceremonial purposes. The positive finding that golden cats do not appear to be a cause of conflict is good news for their continued persistence, even as the human population grows (provided, as we have seen, that wire snares are not a factor).

One concern is that most of the reasons for positive perceptions towards wildlife involve the death of the animal. Conservation strategies aiming to facilitate the co-existence of people and wildlife may therefore aim to promote non-consumptive benefits of living alongside wildlife. As many of Africa's rainforest areas do not lend themselves to tourism (and income from tourism itself is unlikely to be sufficient to conserve most species; Alexander 2000), such benefits may include ecosystem services that provide health and well-being benefits to local people (Ma 2005). However, most rural communities in Central Africa have few options other than consumptive utilisation of wildlife, and ultimately, only improvement of local people's lives within Africa's forests will allow for the long-term conservation of wildlife (sensu Hackel 1998).

6.3. Mesopredator release and species co-existence

Golden cats are subordinate to leopards in the majority of their range. Their temporal behaviour changes when they become the dominant species in the ecosystem, supporting the hypothesis that the effects of mesopredator release go beyond changes in abundance (sensu Prugh et al. 2009). Reducing overlap with human activity and increasing the potential for prey acquisition may be at the root of this shift, and such behavioural release of golden cats likely results, ultimately, in increases in abundance. I therefore propose that one of they key mechanisms by which mesopredator release works is through "temporal release" whereby the removal of one threat facilitates access to resources and avoidance of remaining threats.

Because golden cats and leopards co-exist across large tracts of the African rainforest, we can assume that despite the competitive and predator relationship that exists, there are mechanisms to enable golden cats to live alongside their larger competitor. And indeed, our findings show that these mechanisms include fine-scale spatio-temoral avoidance and food niche segregation. What is less clear is whether such mechanisms hold up under anthropogenic change. Research that has broached this subject is predominated by effects of climate change on species interactions (e.g. Gilman et al. 2010, Kordas et al. 2011), which is arguably slower acting than land-use change. I suggest that there be an increase in focus on the effects of rapid anthropogenic change on species interactions, which will increasingly occur alongside development in Central and West Africa. Humans may drive increases in spatial, temporal, and food niche overlap (Luiselli 2006), leading, perhaps, to negative population-level effects such as decrease in abundance of one or both interacting species. Our results suggest that the mechanisms do hold up under a certain level of anthropogenic change, with shifts in golden cat diet occurring alongside shifts in leopard diet in response to competition between the latter and humans.

6.4. Future research

In order to assess the effects of human land-uses, we monitored several sites, and due to time and material constraints, could only monitor each site for a limited amount of time. To gain insight into population dynamics over time, long-term studies are valuable (Lindenmayer & Likens 2009), both in "natural" (uninfluenced by human disturbance) systems, and in areas set to undergo anthropogenic change. Upcoming booms in mining (Edwards et al. 2014) and forest clearing for oil palm plantations (Wich et al. 2014) are predicted to have severe consequences for African forest-dependent species, including golden cats (Bahaa-el-din et al. 2015a). Long-term studies could be established prior to the commencement of exploitation in order to monitor its effects over time. Lindenmayer & Likens (2009) emphasise the importance of such long-term studies being adaptive, well-designed, and outlining tractable questions from the outset, and we recommend such studies be initiated for golden cat population monitoring. Also, as deforestation continues within Central and West Africa (FAO 2011), forests will become increasingly fragmented, potentially affecting the persistence of forest-dependent species such as golden cats (sensu Offerman et al. 1995). It is therefore important to understand species' responses to fragmentation, and population viability within varying forest fragment sizes.

The bulk of this research has been carried out in one of the strongholds for the golden cats where human population density is low, and pressure on wildlife and ecosystems has been lower than in neighbouring countries. I therefore recommend that future research on African golden cats be carried out in other parts of the species' range, particularly areas that are imminently threatened. I also encourage data-gathering across the species' range, and particularly along the fringes of their range and in areas of high human population density to refine the golden cat's distribution map, which is currently based on few records and forest cover maps (Bahaa-el-din, et al. 2015a). In addition, I would also recommend that attitudinal surveys be carried out in different areas of golden cat range, among different cultures, to assess whether our findings on perceptions apply more widely. Finally, our leopard scat sample size was too small to do a site-by-site analysis of food niche overlap between golden cats and leopards. A valuable contribution to our understanding of the effects of anthropogenic change on species interactions would therefore be to carry out extensive scat surveys across a human land-use gradient.

6.5. Final conclusion

This study has shed light on the ecology and conservation of the previously almost unknown African golden cat. Our findings that golden cats are not as naturally rare as previously thought, and that they display behavioural plasticity allowing them to adapt to change, are encouraging. However, threats remain, and I hope that our recommendations will be integrated into conservation planning, helping to secure a future for golden cats and other forest-dependent species.

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Appendix 1: Species Status Assessment for the IUCN Red List of Threatened Species

Cover image: The IUCN Red List of Threatened Species “Provides taxonomic, conservation status, and distribution information on taxa that are facing a high risk of global extinction” (http://www.iucnredlist.org).

A1.1 Taxonomy

Scientific Name: *Caracal aurata*

Species Authority: (Temminck, 1827)

Common Name(s):	English – African golden cat
	French – Chat doré, Chat doré Africain
	Spanish – Gato dorado

Synonym(s): *Profelis aurata* (Temminck, 1827)

Taxonomic Notes: Taxonomy is currently under review by the IUCN SSC Cat Specialist Group. This species has traditionally either been included in the genus *Felis* (Kral and Zima 1980) or *Profelis* (Pocock 1917, Wozencraft 2005). More recent molecular data unequivocally reveal that the Caracal *Caracal caracal* and the Serval *Leptailurus serval* are closely allied with the African golden cat (Johnson et al. 2006).

A1.2 Assessment Information

Red List Category & Criteria: Vulnerable A2c+3c ver 3.1

Year Published: 2015

Date Assessed: 2014-04-20

Assessors: Bahaa-el-din, L., Mills, D., Hunter, L. & Henschel, P.

Reviewers: Nowell, K., Hoffmann, M., Breitenmoser-Würsten, C., Lanz, T. & Breitenmoser,U.

Contributor(s): Sogbohossou, E.

Justification: The African golden cat is a forest-dependent species restricted to equatorial Africa, where high deforestation and bushmeat hunting levels are causing substantial reductions in their area of occupancy (AOO). Data on the extent of African golden cat AOO loss is unavailable due to a lack of population monitoring. We can infer, however, an approximate AOO loss using data on deforestation and bushmeat hunting, as well as evidence of the effects of these on African golden cats.

We infer that the cumulative loss of AOO from deforestation and bushmeat hunting along expanding road networks amounts to >30% in the past 15 years (three golden cat generations; Pacifici et al. 2013) and qualifies the African golden cat for Vulnerable status under criterion A2c. Additionally, the exacerbation of these threats due to population growth, projected mining activities and forest clearance for oil palm plantations will likely cause further reduction in AOO for the golden cat and we therefore predict that the AOO will be reduced by at least a further 30% in the next 15 years, lending additional support to the species' listing as Vulnerable under criterion A3c.

Previously published Red List assessments:	2008 – Near Threatened (NT)
	2002 – Vulnerable (VU)
	1996 – Least Concern (LC)
	1994 – Insufficiently Known (K)

A1.3 Geographic Range

Range Description: The African golden cat is endemic to the forests of Equatorial Africa. There are no confirmed records from The Gambia and Guinea Bissau, nor from Togo and Benin (Ray and Butynski 2013), which suggests a separation between Western and Central African populations (Nowell and Jackson 1996).

Countries occurrence: Angola; Cameroon; Central African Republic; Congo; Congo, The Democratic Republic of the; Côte d'Ivoire; Equatorial Guinea; Gabon; Ghana; Guinea; Liberia; Nigeria; Sierra Leone; Uganda. [For range map, see fig. 2.3 on page 19.]

Upper elevation limit (metres): 3600

A1.4 Population

The African golden cat is infrequently observed in the wild, and generally considered rare. In areas of heavy human hunting, golden cats were not recorded (e.g. Dibouka village in central

Gabon (Henschel 2008) and Korup National Park (NP) in southwest Cameroon (TEAM)). In an area of putatively suitable habitat in Equatorial Guinea, just 16% of the area was found to be occupied by African golden cats due to human disturbance (Martinez Marti 2011).

Current Population Trend: ↓ Decreasing

Additional data: Population severely fragmented: No

A1.5 Habitat and Ecology

While the Neotropical and Indomalayan regions have several sympatric forest-dependent felid species, this is Africa's only one. The African golden cat occurs mainly in primary moist equatorial forest, although on the periphery of its range it penetrates savannah regions along riverine forest. It also occurs in montane forest and alpine moorland in the east of its range (Nowell and Jackson 1996, Ray and Butynski 2013).

Two studies of scats - from the Ituri forest of the Congo (Hart et al. 1996) and the Dzanga-Sangha forest of the Central African republic (Ray and Sunquist 2001) - found similar results. Rodents and squirrels were the main prey item (70 % and 62% respectively), followed by small and medium-size duikers (antelopes) (25% and 33% respectively). Primates made up 5% of the prey items in both studies, and there have been several observations by primate researchers of African golden cats hunting arboreal primates (Ray and Butynski 2013, Bahaa-el-din et al. 2015). The same general diet items were reported by Kingdon (1977) from Uganda's Bwindi National Park. Birds are also taken, and pangolin remains were frequently found in scats from the Ivory Coast's Tai National Park (D. Jenny pers. comm. in Nowell and Jackson 1996).

African golden cats have turned up in the diet of leopards, the only other felid to occur in African moist forest. African golden cat remains were found in five of 196 Leopard *Panthera pardus* scats from Gabon's Lopé National Park (Henschel et al. 2005); a single carcass killed by a Leopard was found in the Ituri (Hart et al. 1996).

Systems: Terrestrial

Continuing decline in area, extent and/or quality of habitat: Yes

Generation Length (years): 5

Movement patterns: Not a migrant

A1.6 Use and Trade

The African golden cat is often not a target species for bushmeat hunters, but is eaten when caught and the skin used or sold. Skins are sometimes found for sale in markets, for example in Yaoundé and Kampala where they are often sold alongside medicinal herbs and fetishes (T. Davenport pers. comm. in Ray and Butynski 2013). Skins may be used during circumcision rites or to wrap valuable objects, or as good luck charms for hunting success (Nowell and Jackson 1996).

A1.7 Threats

At least 6.5% of forest (projected from FAO 2011) in golden cat range countries has been lost in the past three golden cat generations (15 years, Pacifici et al. 2013). This translates into, at minimum, an equivalent loss of range for the golden cat as a result of habitat loss and fragmentation. Prior to the year 2000, West and East Africa had already suffered an 88-92% reduction in rainforest, while Central Africa's rainforest extent was reduced by 40% (Laurance et al. 2006).

Intensive hunting for bushmeat (>1 million tonnes per year harvested in the Congo Basin, the species' main stronghold; Wilkie and Carpenter 1999), leading to 'empty forest syndrome' (Sayer 1992), likely accounts for greater reduction in area of occupancy (AOO) for the golden cat than deforestation, but is more difficult to quantify. Within 10–15 km of roads and settlements, large and medium bodied mammals experience sharp declines in population (Laurance et al. 2006, Blake et al. 2007, Henschel 2008). In excess of 64% of forest habitat in the Congo Basin lies within 10 km of a road and is also predicted to be affected by higher hunting pressure (Blake et al. 2007). Development of roads increased rapidly in the past 15 years (e.g. 35% increase in the Democratic Republic of Congo and >300% increase in northern Republic of Congo since the year 2000; Laporte et al. 2007). Golden cat populations within these highly impacted areas are likely to be severely reduced or extirpated through direct mortality and loss of prey.

Golden cats are often not a primary target species, but are frequently killed by wire-snares (four individuals in two months in 20 km^2 in Gabon; Bahaa-el-din pers. obs.; and 13 individuals in three months in Lobéké, Cameroon; Ray et al. 2005), probably owing to similarities in body size and trail use to target species such as duikers. In an area of moderate bushmeat hunting, golden cats were recorded at less than a quarter of the population densities that they are found at in pristine areas (Chapter 3). Where more intense hunting occurs, such as in village hunting areas (e.g. Dibouka village in central Gabon; Henschel 2008) and national parks (e.g. Korup NP in southwest Cameroon; TEAM, http://www.teamnetwork.org), camera trap and bushmeat studies did not record the species despite the presence of suitable habitat contiguous with the main forest of the Congo Basin.

Recent landscape-scale golden cat surveys in mainland Equatorial Guinea (Rio Muni) emphasize that prior range estimates based on forest cover may have significantly overestimated remaining golden cat range. An estimated 78% of Rio Muni consists of tropical dense forest and therefore putatively suitable habitat, but golden cats were found to occupy just 16% of the area (Martinez Marti 2011). Its presence in the area was correlated with rugged, inaccessible terrain away from human disturbance (Martinez Marti 2011). Golden cats were reported by locals to be easy to hunt and locally extirpated long before other medium-to-large mammal species (Martinez Marti 2011).

These threats will intensify, as the human population within the species' range shows the fastest growth rates in the world (+2.6-2.8% per annum for West, Central and East Africa; FAO 2011). The population in main golden cat range countries, estimated at nearly a quarter of a billion for 2013, is projected to almost quadruple by 2100 (UN 2012, http://esa.un.org/wpp/).

The current "stampede of foreign investment" in mining activities and associated infrastructure development in Africa is of immediate concern (Edwards et al. 2014). In Central Africa, 42% of ecologically important areas would be directly impacted if there were complete development of mineral resources in the region (assuming that ecological impacts extend within 10 km of mines; Edwards et al. 2014). China's mineral investment alone has quadrupled in 10 years (Zhang 2011). In addition, it is predicted that the conversion of forests to oil palm plantations, which has caused extensive loss of forest habitat and biodiversity in Southeast Asia, will have similar impacts in Africa (particularly in West and Central Africa) as it expands over the coming years (Wich et al. 2014). The realisation of these investments includes habitat destruction and degradation, relocation of human populations into previously remote areas and massive-scale infrastructural development including road and rail which in turn lead to the aforementioned surge in bushmeat hunting in these areas (Edwards et al. 2014).

A1.8 Conservation Actions

Included on CITES Appendix II. Hunting of this species is prohibited in Angola, Benin, Burkina Faso, Congo, Ghana, Côte d'Ivoire, Kenya, Liberia, Nigeria, Rwanda, Sierra Leone and Democratic Republic of Congo, with hunting regulations in place in Gabon, Liberia and Togo (Nowell and Jackson 1996).

Key protected areas for the species include: Gola F.R. (Sierra Leone), Mount Nimba Strict N.R. (Liberia, Côte d'Ivoire, Guinea), Sapo N.P. (Liberia), Taï and Comoé National Parks (Côte d'Ivoire), Gashaka Gumti N.P. (Nigeria), Dja Faunal Reserve (Cameroon), Lopé N.P. and Ivindo N.P. (Gabon), Odzala and Nouabale-Ndoki National Parks (Congo Republic) and Dzangha-Ndoki National Parks (CAR), Virunga N.P. (DR Congo), Queen Elizabeth and Bwindi Impenetrable National Parks (Uganda) (Butynski and Ray 2013).

There is a need for further survey work to acquire reliable population density estimates in various forest types, including disturbed habitats, in order to help better determine the population status across the range of the species.

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Appendix 2: Notes on the distribution and status of small carnivores in Gabon

Cover image: Camera trap images of small carnivores in Gabon (clockwise from top: Servaline Genet, African Palm Civet, Black-legged Mongoose, African Civet).

A2.1 Abstract

The distribution and status of small carnivore species in Gabon have never been comprehensively assessed. We collated data from general wildlife surveys, camera-trap and transect studies and analyses of bushmeat consumption and trade, to map their country-wide occurrence and assess current exploitation levels. Records of Common Slender Mongoose *Herpestes sanguineus* and Cameroon Cusimanse *Crossarchus platycephalus* represent the first confirmation of their occurrence in Gabon. Cameroon Cusimanse was believed to extend into north-east Gabon, but the Slender Mongoose records extend its known range well outside that previously suspected. We furthermore extended the known range for Egyptian Mongoose *Herpestes ichneumon*. Crested Genet *Genetta cristata* has also been proposed to occur in Gabon but our records were not suited to evaluating this possibility given the difficulties of separation from Servaline Genet *G. servalina*. Most species appear to be distributed widely across the country. While several are commonly recorded in hunter catch and bushmeat markets, they form only a small proportion (3.4% and 3.1%, respectively) of all bushmeat records. However, in proximity to settlements, small carnivore exploitation, for bushmeat and use of body parts in traditional ceremonies, appears to have adverse effects on species richness and abundance.

A2.2 Introduction

The African rainforest harbours a diverse guild of small carnivores, of which several species are endemic to Equatorial such forests (Ray 2001). Gabon is on the west coast of Central Africa (Fig. A2.1), with a low human population density and large tracts of rainforest that cover 85% of the country (Ernst *et al*. 2012). The importance of Gabon for the conservation of threatened taxa has been highlighted for a number of larger species (e.g. Walsh et al. 2003, Blake et al. 2007, Henschel et al. 2011), and it might be equally important for the conservation of small carnivores. While several studies investigated the feeding habits of individual small carnivore species (e.g. Charles-Dominique 1978, Emmons et al. 1983), there have been no comprehensive efforts to date to assess the status and distribution of all small carnivore species occurring in Gabon.

Most wildlife surveys in Gabon have concentrated on general biodiversity monitoring, with several focusing on primates, elephants *Loxodonta* and cats (Felidae). Fortunately, data on small carnivores have been collected opportunistically over the course of several such surveys. In addition, a recent boom in the use of remotely-triggered camera-traps for wildlife surveys in Gabon has meant that many carnivore data have been gathered incidentally. Here we collate opportunistic observations of small carnivores obtained during general wildlife and species-specific surveys and data from 16 different camera trap study sites across Gabon, to assess the current distribution of small carnivores in this country. To explore how these species may be affected by the bushmeat crisis sweeping West and Central Africa (see Fa & Brown 2009), we investigated available bushmeat offtake data from 65 villages across Gabon and bushmeat trade data from 11 towns throughout the country.

A2.3 Methods

A2.3.1 Study area

Gabon is a central African country that straddles the equator and borders the Atlantic Ocean (Fig. A2.1). The habitat in Gabon consists predominantly of moist tropical forest, with savannah, swamps and mangroves making up about 15% of the land area (Fig. A2.1) (Lahm 2001, Ernst et al. 2012). The human population is small (1.6 million) and largely urban (86% of population) (CIA 2012). This, coupled with a relatively strong economy supported by natural resource extraction, has meant that Gabon has not suffered from landscape degradation similar to that experienced in some other countries in the region (CIA 2012). In 2002, 13 national parks were created, encompassing 30,000 km^2, or 11% of the country's land surface (Fig. A2.1).

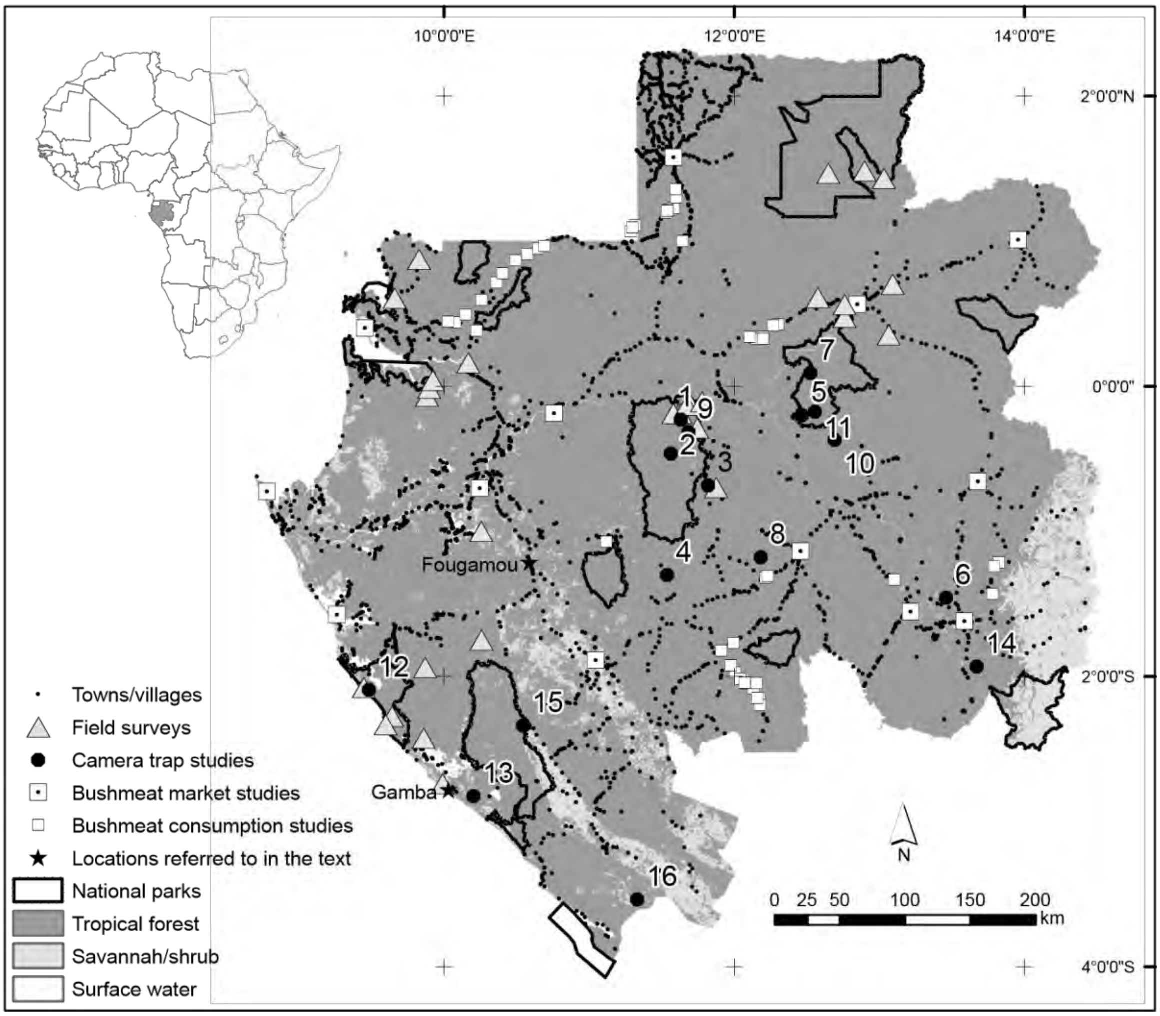


Figure. A2.1. Vegetation map of Gabon, showing population centres, protected areas and locations of the various surveys included in this study.

A2.3.2 Study species

Of the species under the remit of the IUCN SSC Small Carnivore Specialist Group, nine had been recorded in a faunal inventory of Gabon prior to its independence (Malbrant & Maclatchy 1949). Malbrant & Maclatchy (1949) furthermore speculated about the occurrence of Long-nosed Mongoose *Herpestes naso*, Cameroon Cusimanse *Crossarchus platycephalus* and Common Slender Mongoose *Herpestes sanguineus* in Gabon. All 12 species (Table A2.1) are currently listed as Least Concern on *The IUCN Red List of Threatened Species* (IUCN 2012).

Table A2.1. Distribution and habitat use for the small carnivores of Gabon.

Species	Africa distribution (see Fig. A2.3)	Habitat
Marsh Mongoose *Atilax paludinosus*	Most of sub-Saharan Africa	Dense habitat near water (including watercourses, marshes, mangroves and estuaries)
Long-nosed Mongoose *Herpestes naso*	Endemic to Equatorial rainforest	Rainforest, usually near watercourses and in areas with dense understorey
Black-footed Mongoose *Bdeogale nigripes*	Endemic to the Equatorial rainforest	Rainforest, with preference for dense understorey
Cameroon Cusimanse *Crossarchus platycephalus*	Southern Nigeria to northern Gabon	Rainforest and forest–savannah mosaic
Slender Mongoose *Herpestes sanguineus*	Most of sub-Saharan Africa	Most habitats, except true desert
Egyptian Mongoose *Herpestes ichneumon*	Most of sub-Saharan Africa, except the north-east, the horn, and parts of Southern and Central Africa	Most open habitats except true desert, including cultivated land
African Civet *Civettictis civetta*	Most of sub-Saharan Africa except the extreme south	Most habitats with cover, except very arid areas, including cultivated land
Servaline Genet *Genetta servalina*	Endemic to the Equatorial rainforest	Rainforest and dense woodland
Rusty-spotted Genet *Genetta maculata*	Most of sub-Saharan Africa, except the extreme south	Forest (including rainforest), woodland and moist savannah
Central African Oyan *Poiana richardsonii*	Endemic to the Equatorial rainforest	Rainforest
African Palm Civet *Nandinia binotata*	Endemic to Equatorial Africa	Rainforest, forest–savannah mosaics and dense woodland
Honey Badger *Mellivora capensis*	Most of sub-Saharan Africa	All habitats; requires cover

Sources: Hunter & Barrett (2011), IUCN (2012).

[1] See Fig. A2.3.

[2] Crested Genet *G. cristata* has also been reported from Gabon, but subsequent authors have called for corroboration (see text).

As well as these 12, two otter species occur in Gabon, the Congo Clawless Otter *Aonyx congicus* and Spotted-necked Otter *Lutra maculicollis*, but these are not discussed here except for within the bushmeat data used to make an overall assessment of the hunting pressure on carnivores. Finally, Gaubert et al. (2006) recorded Crested Genet *Genetta cristata* for Gabon (and Congo), more than 500 km south of the Sanaga River. These records were considered "equivocal" by Hunter & Barrett (2011: 90) and were mapped only as "?" by Van Rompaey & Colyn (2013d: 223). Crested Genet and Servaline Genet *G. servalina* are morphologically similar and perhaps hybridise (Gaubert et al. 2006). Thus, their identification requires care and often they cannot be distinguished on camera-trap images such as form the bulk of our records. Hence, it is possible that the records presented here as 'Servaline Genet' include some that are in fact of Crested Genet, or of hybrids between these two.

A2.3.3 Mapping of species distribution

We collated data from 33 wildlife field surveys and 16 camera-trap studies (Table A2.2, Fig. A2.1), and plotted confirmed small carnivore records to assess the distribution of each species. In addition, we used bushmeat hunting records for which the species and the site of catch could be confirmed, as well as faecal DNA records from a study in Moukalaba-Doudou National Park (NP). Faeces were identified to species level using a part of the mitochondrial cytochrome b which was amplified according to the method of Veron & Heard (2000).

Field survey sites were distributed across large parts of Gabon (Fig. A2.1). Some surveys used line transects conducted by day and at night, with observers walking at about 1 km/h (see Lahm 1993). Camera trap studies used various camera trap models and trapping protocols, depending on their aims (Table A2.2). These differences affect the likelihood of capturing each species and we therefore could not use non-detection (sites where the species were not photo-captured) as strong evidence of absence. We do discuss, however, trends that appear from consistent non-detection in certain areas or habitat types.

Where the species identity was in question, data were discarded. Marsh Mongoose *Atilax paludinosus* and Long-nosed Mongoose posed the greatest difficulty, being closely related and difficult to tell apart in the field (Ray 1997). The best diagnostic feature is the lack of webbing between the toes in Marsh Mongoose (Baker & Ray 2013, Van Rompaey & Colyn 2013c). More visible on images, Marsh Mongoose has a blunt, triangular face, whilst Long-nosed Mongoose has a long muzzle and prominent nose (Hunter & Barrett 2011). The latter also has a longer and brushier tail (Baker & Ray 2013) that can be seen on certain images (Fig. A2.2).

Figure. A2.2. Camera-trap images showing distinction between Marsh Mongoose *Atilax paludinosus* (above) and Long-nosed Mongoose *Herpestes naso* (below). See main text for a description of distinctive criteria.

Table A2.2. Camera-trapping protocols at each site in Gabon supplying small carnivore records.

# in Fig. 1	Study site[1]	Study species[2] and aim	Year of study	Habitat type	Human activity	Principal investigator	Camera-trap type/ model	Trap height (cm)	Target areas
1	SEGC	Leopard ecology	2002	Predominantly Marantacae forest	Research	P. Henschel	35 mm Camtrakker	40–45	Game trails
2	former SO-FORGA logging concession	Leopard ecology	2002	Formerly logged, secondary forest	None	P. Henschel	35 mm Camtrakker	40–45	Old logging roads
3	NSG concession	Leopard ecology	2002	Recently logged, secondary forest	Logging	P. Henschel	35 mm Camtrakker	40–45	Old logging roads
4	Massima	Leopard ecology	2002	Pristine, primary forest	Village hunting	P. Henschel	35 mm Camtrakker	40–45	Game trails
5	Dilo	Leopard ecology	2003	Formerly logged, secondary forest	Research & Tourism	P. Henschel	35 mm Camtrakker	40–45	Old logging roads
6	Lekabi Ranch	Lion survey	2003	Forest/savannah mosaic	Cattle ranching	P. Henschel	35 mm Camtrakker	40–45	Roads
7	Massouna 2000	Leopard ecology	2004	Recently logged, secondary forest	None	P. Henschel	35 mm Camtrakker	40–45	Old logging roads
8	Lolo	Leopard ecology	2005	Recently logged, secondary forest	Village hunting	P. Henschel	35 mm Camtrakker	40–45	Old logging roads
9	Mikongo	African Golden Cat ecology	2010	Predominantly Marantacae forest	Research & Tourism	L. Bahaa-el-din	35 mm DeerCam & digital DLC Covert II	25–30	Game trails & old logging roads
10	Milolé	African Golden Cat ecology	2011	Recently logged, secondary forest	Logging	L. Bahaa-el-din	Digital Panthera & Scoutguard	25–30	Game trails & old logging roads
11	Langoué	African Golden Cat ecology	2011	Pristine, primary forest	Research	L. Bahaa-el-din	Digital Panthera & Scoutguard	25–30	Game trails
12	Loango	Ape / elephant population assessment, Chimpanzee tool use	2009/ 2010	Formerly logged, primary forest, coastal forest, mangroves	Research	J. Head	Scoutguard & Bushnell	80–100	Elephant trails, natural bridges, clearings, swamp edges
13	Gamba area	Impact of roads and other human disturbances on mammals	2010/ 2011	Littoral savannah/ gallery forests/ swamp mosaic	Roads, settlements, oil extraction, agriculture, hunting	H. Vanthomme	Reconyx RC55 rapid-fire	40–50	Game trails & transects
14	SE Gabon	Spotted Hyaena survey	2011	Forest/savannah mosaic	Hunting, roads, settlements	T. Bohm	Reconyx HC500, Cuddeback Capture & Bushnell 2009, 2010	30–40	Game trails & roads
15	Moukalaba-Doudou	Assessment of species diversity	2010	Logged secondary forest (1960s–1980s), savannah	None	Y. Nakashima	Bushnell Trophy Cam 2010	25–30	Random places
16	Mayumba	Faunal inventory	2012	Formerly logged, primary forest	None	R. Aba'a	DLC Covert & Reconyx	30	Game trails near random grid locations

[1] Locations of camera-trap study sites are shown on Fig. 1. SEGC = Station d'Études des Gorilles et Chimpanzés.

[2] Species: Leopard *Panthera pardus*; Lion *Panthera leo*; African Golden Cat *Profelis aurata*; African Elephant *Loxodonta africana*; Chimpanzee *Pan troglodytes*; Spotted Hyaena *Crocuta crocuta*.

A2.3.4 Analysis of small carnivore offtakes through bushmeat hunting

Data on village hunting offtakes in Gabon were collated from a number of existing studies, as part of an on-going study of hunting offtakes across West and Central Africa (Taylor 2012), including data from published and grey literature, as well as unpublished data. We included only studies that provided complete village hunting offtake data (not those covering only a particular family or genus), and that identified animals to species level. Village offtake data were collected using two methods: 1) ‘bag counts’: hunter offtake was directly recorded on their return to the village from hunting; 2) ‘3-day recall’: households were asked, using a questionnaire, what they had caught in the last three days. Offtakes provided as biomass were converted into number of animals using empirical weights for Gabon in Abernethy et al. (2006) and Coad (2007) or, where empirical weights were not available, published weights from Kingdon (1997) or the Pantheria database (Jones et al. 2009). For a few bird and rodent species, expert opinion from Gabon was solicited to provide an estimate.

We identified three studies from Gabon (Wilkie et al. 2006, Carpaneto et al. 2007, Coad 2007), comprising offtake data for 65 villages (Fig. A2.1). Data from the ‘Parks and People’ study (see Wilkie et al. 2006) accounted for most of these villages (n = 56), and come from the surrounds of the then newly-created national parks of Birougou, Monts de Cristal and Ivindo. Sample sizes per village were small (mean of 10 days’ survey effort), so we grouped data for these villages by location (protected area). This resulted in a total of 11 village samples for this study, with a median of 96 animals per sample (range: 42–1,756). Although larger sample sizes are more likely to uncover rare species, we are confident that these sample sizes provide a representative depiction of the catch in each village/protected area (Taylor 2012). Village hunting studies in Gabon (e.g. Starkey 2004, Coad 2007) suggest that hunters have good species identification skills, and specific local names for the carnivore species considered in this paper. However, for Marsh and Long-nosed Mongooses, we cannot be certain that identification was always reliable, especially in the case of 3-day recall surveys and market surveys where animals may have been smoked to preserve the meat. We have therefore grouped records of these two mongooses together, for all hunting and market survey results.

A2.3.5 Analysis of small carnivore trade for bushmeat consumption

To investigate the representation of small carnivores in the commercial trade in Gabon, we used market data collected as part of the ‘Projet Gibier’, conducted by the Government of Gabon and the University of Stirling (Abernethy et al. 2006), which collected data on bushmeat market sales in 11 town and village markets across Gabon during 2000 − 2006 (Fig. A2.1). Animals were sold both whole and butchered, and sales were recorded by species and part of the animal. Because small carnivores are very rarely traded as cuts in Gabon, we converted butchered cut sale records into an approximate number of whole animals using the same species weights as for the village offtake dataset. The dataset included a median of 4,387 animals per market (range: 36–35,215), with 105,903 animals recorded in the entire markets dataset (Abernethy et al. 2006). As with village hunting offtakes, records of Marsh Mongoose and Long-nosed Mongoose are grouped together.

A2.3.6 Statistical analyses

We calculated the proportion of the village offtake represented by each order, for each of the 11 village samples. From this we then calculated the mean proportion (and associated standard errors) of the catch represented by each order (n = 11 villages). We then repeated this at the species level within Carnivora, to examine the proportion of the village offtake represented by individual carnivore species. We repeated this for the market samples (n = 11 markets).

A2.4 Results

A2.4.1 Species occurrence and distribution

We recorded 12 small carnivore species in Gabon and used a total of 1,028 records to map species occurrences across the country (Fig. A2.3). We obtained the first records of Common Slender Mongoose in Gabon, >350 km outside its range on *The IUCN Red List of Threatened Species* (IUCN 2012) (Fig. A2.3). We furthermore produced the first definitive records of Cameroon Cusimanse in Gabon, and recorded Egyptian Mongoose *Herpestes ichneumon* about 105 km north of its current *IUCN Red List* range (Fig. A2.3). Most species are distributed across the country, although Cameroon Cusimanse was recorded only in the north-east and Egyptian Mongoose only in the south (Fig. A2.3).

A2.4.2 Small carnivore offtakes and trade

Carnivores comprised 3.4% of village offtakes and 3.1% of all sales in bushmeat markets (Fig. A2.4). Village offtakes and market sales were both dominated by ungulates, rodents and primates, with all other taxa making up <5% of all hunter catch and sales, respectively (Fig. A2.4). Among the carnivores recorded, Marsh/Long-nosed Mongoose were the most numerous (group of) species caught in villages (Fig. A2.5). African Palm Civets *Nandinia binotata* were the second most numerous species in village offtakes and the most numerous species in bushmeat markets, where they were three times more common than any other carnivore species (Fig. A2.5).

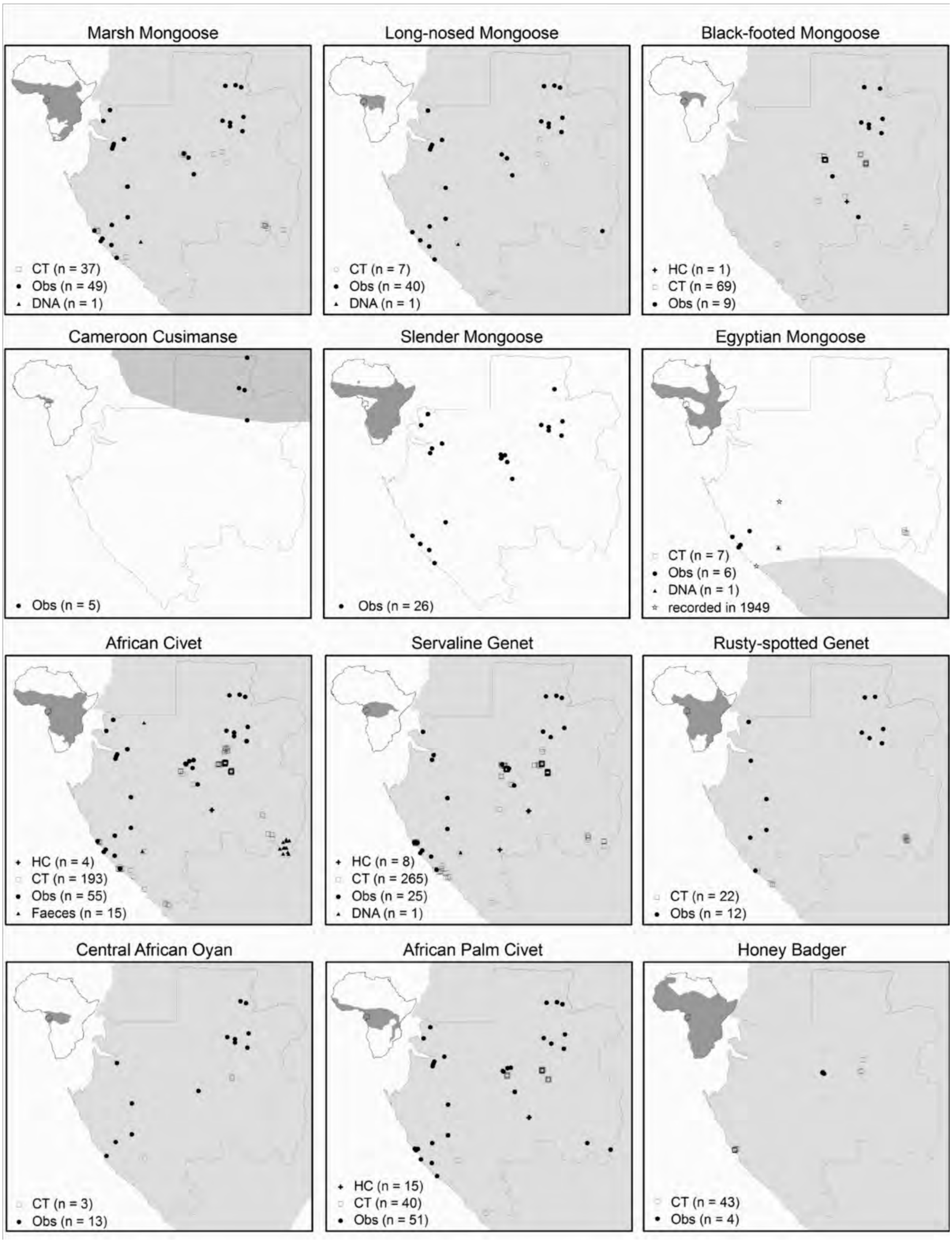
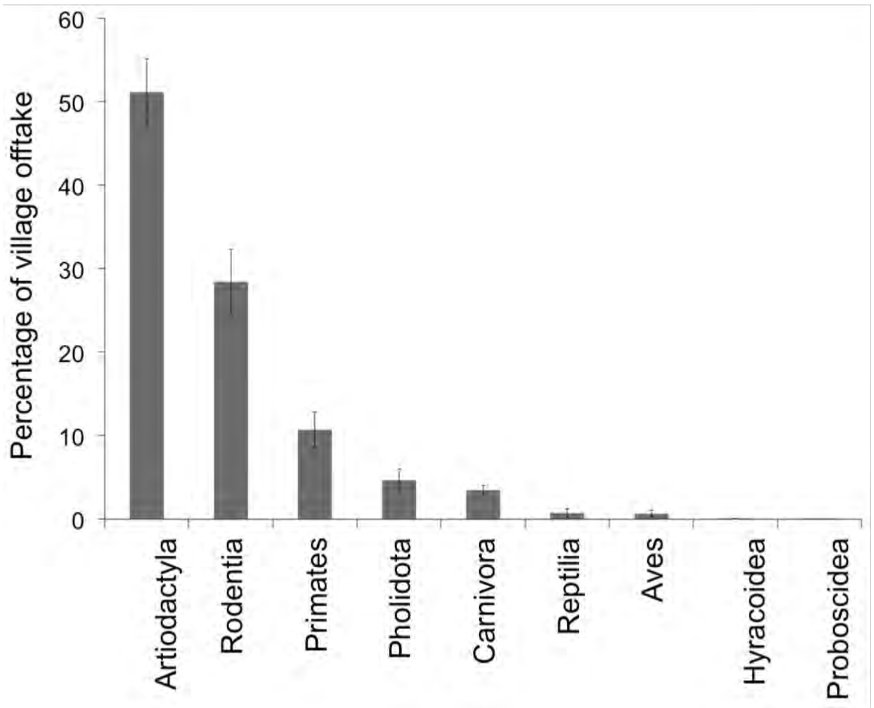


Figure. A2.3. Distribution maps for the small carnivores of Gabon, showing detection points. Grey shading represents generalised range according to *The IUCN Red List of Threatened Species*, both in the Gabon and the inset Africa maps (Data type: HC = hunter catch; CT = camera-trap record; Obs = direct observation; DNA = faecal DNA).



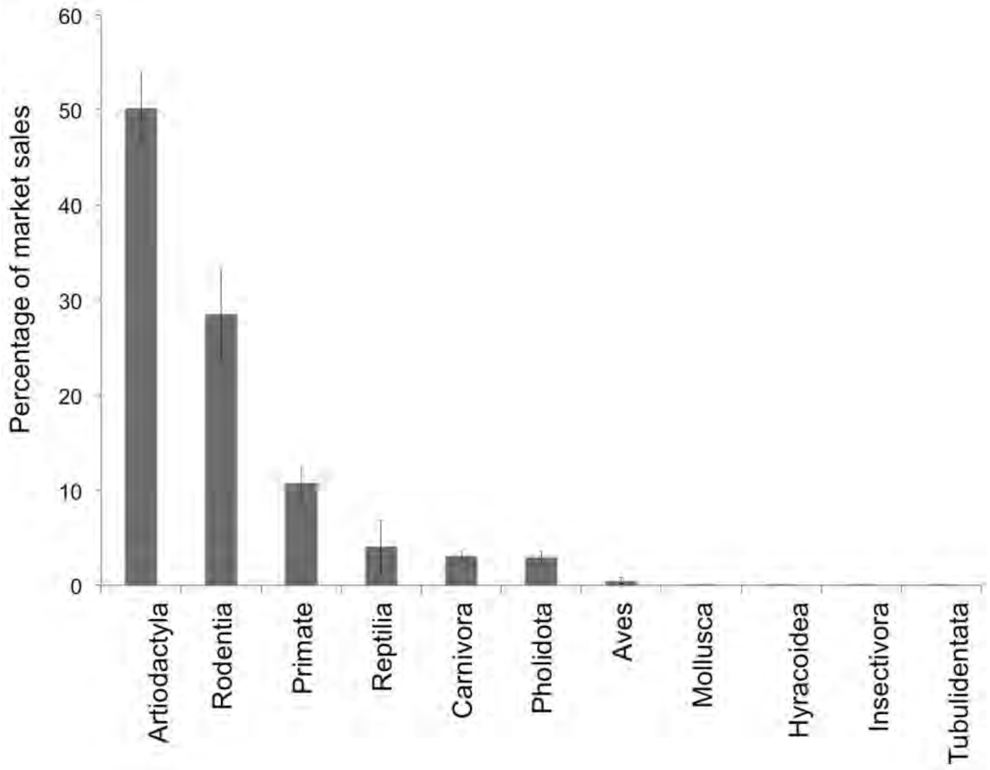


Figure. A2.4. Proportion of carnivores out of all animals (above) harvested in villages and (below) sampled at bushmeat markets during several surveys in Gabon (error bars represent the SE).

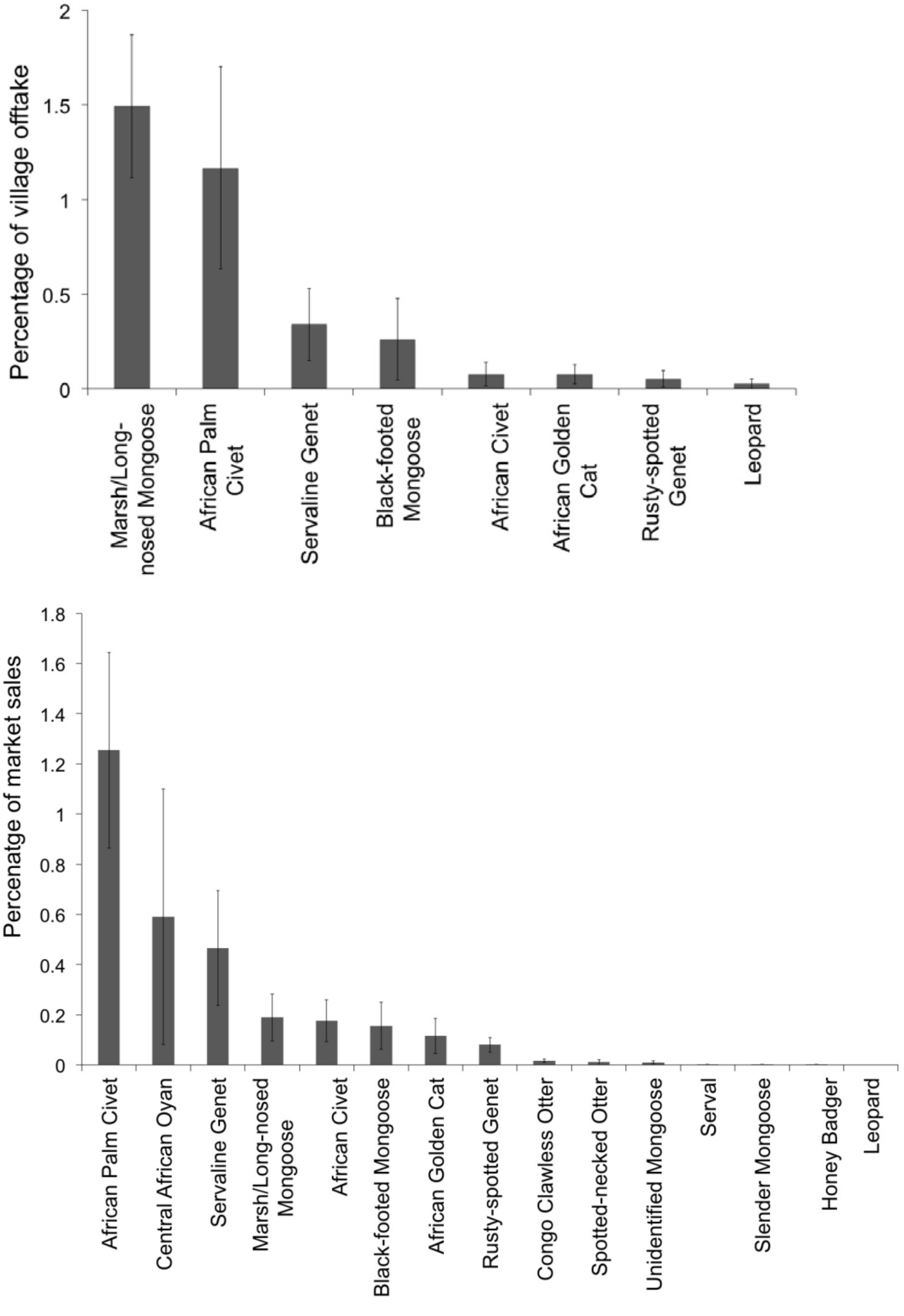


Figure. A2.5. Proportion of carnivores out of (above) total catch (number of animals) in villages and (below) total sample (number of animals) at bushmeat markets (error bars represent the SE). Scientific names are given in A2. 1, save: African Golden Cat *Profelis aurata*; Leopard *Panthera pardus*; Congo Clawless Otter *Aonyx congicus*; Spotted-necked Otter *Lutra maculicollis*; Serval *Leptailurus serval.*

A2.5 Discussion

A2.5.1 Species extensions of known range

Malbrant & Maclatchy (1949) speculated that Slender Mongoose might occur in Gabon and neighbouring Congo. However, to date, there had been no confirmed records of the species from the northern bank of the lower Congo River, its presumed western range limit in Central Africa (IUCN 2012). We recorded this species through direct observations at 26 locations, spread across almost the entire country (Fig. A2.3). While no hard evidence (e.g. photographs or specimens) for the species in Gabon was obtained, observations were made independently by five experienced field biologists (KA, NB, PH, SL and FM). Most records came from a forest–savannah mosaic in northern Lopé NP, where KA, PH and FM made close to 100 independent observations of the species. Observations here were restricted to daytime hours and open savannah habitats, and included multiple observations at close range (<5 m), lasting up to 1 minute. We are therefore confident that our records represent *H. sanguineus*.

The presence of Cameroon Cusimanse in north-east Gabon had been suspected (Hunter & Barrett 2011, IUCN 2012), but not confirmed anywhere in the country (Goldman 2013). As with Slender Mongoose, we were not able to collect hard evidence for this species's occurrence, but cusimanses were observed directly at five locations by experienced field biologists (PH and SL). Observations included one observation in broad daylight and at close range (<5 m) by PH in September 1998 in what is now Minkébé NP, of a group of four individuals in an open-understorey riparian forest, over about two minutes. Cusimanses are difficult to identify to species in the field, but the location of the observations and suspected range limits of Cameroon Cusimanse (Hunter & Barrett 2011, IUCN 2012), indicate that our observations represent that species.

In Gabon only the south-western tip is currently recognised as within the range of Egyptian Mongoose by IUCN (2012). Our camera-trap records place the species 105 km north of its *IUCN Red List* range, and Malbrant & Maclatchy (1949) listed one record about 100 km further north, near the town of Fougamou (Figs. A2.1, A2.3). All our records were in or near the extensive savannahs in south-east and south-west Gabon (Fig. A2.1). The record from Fougamou, near the northern tip of the south-western savannahs, aligns well with this pattern. Egyptian Mongoose might thus occur in all extensive savannah areas in southern Gabon.

2.5.2 Species distribution and habitat preferences

Marsh Mongoose, Black-footed Mongoose *Bdeogale nigripes*, Long-nosed Mongoose, African Civet *Civettictis civetta*, Servaline Genet and African Palm Civet were recorded throughout Gabon, and across most habitat types. While Rusty-spotted Genet *Genetta maculata* appears to have a country-wide distribution, it was generally recorded in or near savannah areas. Extensive camera-trapping in more pristine, dense forest in the Lopé-Ivindo region yielded no record of the species. Although Rusty-spotted Genet occurs in rainforest, it generally prefers open corridors and secondary growth (Angelici & Gaubert 2013). This habitat preference may explain the lack of records (and potential absence) from more contiguous primary forests in central Gabon. Conversely, Central African Oyan *Poiana richardsonii* (Fig. A2.6) was not recorded in the savannah areas. As a canopy species (Van Rompaey & Colyn 2013b), it may have more of an affinity to contiguous forest habitat.

Figure. A2.6. Central African Oyan *Poiana richardsonii* is endemic to Africa's Equatorial rainforest. Owing to its arboreal nature, ground-level camera traps rarely photograph this species (Photo: L. Bahaa-el-din/Panthera).

The paucity of Honey Badger *Mellivora capensis* records constrains conclusions on its distribution and habitat preferences in Gabon. It was recorded by camera-traps in just two areas, Ivindo NP in central Gabon and Loango NP near the coast. It was most frequently photo-captured in Loango, where a subset of cameras was placed at subterranean honey nests. There are few direct sightings and bushmeat records of the species in Gabon, and most field surveys and camera-trap studies have failed to record it. While it is known locally by hunters across Gabon, it is generally considered rare (e.g. Mazzocchetti 2005). All evidence suggests it occurs patchily and/ or at very low densities in Gabon. Both entirely black- and white-mantled morphs of Honey Badger occurred at both sites where they were camera-trapped (Fig. A2.7). All photographs of pale-mantled individuals portrayed conspicuous white mantles, not the grizzled, greyish ones often seen on this species.

Figure. A2.7. Both entirely black (above) and white-mantled morphs (below) of Honey Badger *Mellivora capensis* occurred at each of the two sites where they were camera-trapped (Photos: L. Bahaa-el-din/Panthera).

Despite Black-footed Mongoose generally being considered rare (Hunter & Barrett 2011), it was frequently camera-trapped at several sites. In Moukalaba-Doudou, it was photographed more times than any other carnivore species. Direct observations were much less frequent, which may indicate that it is more secretive than other carnivore species. It is thought to be generally absent from disturbed sites (Van Rompaey & Colyn 2013a), but was photo-captured at several actively logged and previously logged sites.

While these observations are based on data collated from many studies, there are gaps in the area coverage and survey intensity is uneven; for example, central Gabon, and areas in and around Lopé and Ivindo National Parks in particular, have been extensively surveyed (see Fig. A2.1). Our observations on distribution and habitat associations are conservative as a result. Dedicated research effort is required to fill these gaps. Surveys in north-east Gabon could help refine range limits of Cameroon Cusimanse. Likewise, further surveys in the southern forest–savannah landscapes could improve knowledge of Egyptian Mongoose range and Rusty-spotted Genet habitat associations.

A2.5.3 Hunting pressure on small carnivores in Gabon

African Palm Civet makes up an important proportion of carnivores found in village offtakes and market sales (Fig. A2.5). This may result from its relative abundance (estimated to occur at a minimum of about five individuals per km² in Gabon; Van Rompaey & Ray 2013), and ease of location through its loud, distinctive call. Coad (2007) found that most small carnivores, excepting Palm Civet, were much more frequently caught than sold to towns. This was certainly the case for Marsh/Long-nosed Mongoose, which was ten times more numerous, proportionally, in hunter catches than in market sales (Fig. A2.5). Central African Oyan made up a large proportion of market sales (Fig. A2.5), but this figure was inflated by one particular site; the species was found infrequently in all other markets.

Overall, carnivores do not represent a large proportion of bushmeat sales or village offtakes in Gabon. They may be underrepresented in market surveys, because certain ethnic groups have social restrictions against their consumption. The Bakota of northeast Gabon, for example, have restrictions against eating carnivore meat (Mazzocchetti 2005). While traditional restrictions appear to be fading, the consumption of carnivores remains taboo for many ethnic groups, and in particular for women (Lahm 1993, Starkey 2004, Mazzocchetti 2005). While small carnivores may not be targeted for their meat, they may, however, be caught for their skins and body parts, which are used in traditional ceremonies (Lahm 1993). Small carnivores may furthermore be targeted to prevent, or in retribution for, predation on small livestock, mainly poultry (Mazzocchetti 2005).

While no in-depth study has focused on the effects of hunting on small carnivore populations in Gabon, Lahm (1993) found in north-east Gabon that a significantly higher richness of small carnivore species occurred in remote areas than near villages where hunting took place. Carnivores were also observed ten times more frequently in remote areas (Lahm 1993). Contrary patterns were observed near the town of Gamba (Fig. A2.1), where the abundance of small ground-dwelling carnivores (mainly African Civet and unidentified mongooses) was not negatively affected by proximity to settlements, and where higher abundances for those species were associated with proximity to plantations (Vanthomme et al. 2013). Similarly, studies of trap offtakes in the villages of Dibouka and Kouagna, central Gabon (Coad 2007), show higher catch-per-unit-effort (CPUE) of African Civet and mongooses in plantation areas than in adjacent hunted forests. However, hunters interviewed in these villages (Coad et al. 2013) reported that Marsh Mongoose and unidentified genet species had become rare within their hunting territories over their lifetimes, and recounted general declines in hunted species. These three studies highlight that while, overall, small carnivore species richness and the abundance of certain species may be negatively affected by village hunting, some species may adapt more readily to (and even benefit from) land conversion to agriculture. However, differences in relative abundance of carnivores within different habitat types may mask longer-term declines over all habitats due to over-hunting, and care must be taken in the interpretation of these data.

A2.5.4 Future considerations

Given Gabon's low human population density, its largely intact forest and savannah biomes, and its extensive protected area network, its small carnivore populations are unlikely to be imperilled at this time. However, Gabon is entering a new phase of industrial development, with changes in land use and human disturbance anticipated. In the face of such potential change, national parks are Gabon's first line of defence against biodiversity loss. All 12 small carnivore species known unequivocally from the country inhabit at least one, and up to five, national parks. Species confirmed in only one or two parks may merit recognition in park management plans: Cameroon Cusimanse in Minkébé NP, and Egyptian Mongoose in Loango NP. In addition, changes in habitat may influence the distribution of species across Gabon. Under new development, parks could become increasingly important refuges for species that might depend on contiguous forest or other little-degraded habitat conditions, such as Black-footed Mongoose, Servaline Genet and Central African Oyan. On the other hand, new developments might expand suitable habitat for species favouring anthropogenic conditions, such as African Civet or Rusty-spotted Genet, if hunting is controlled.

Our study represents the first synthesis of collective knowledge about observations of small carnivores in Gabon. Much is still unknown about these species: continued assimilation of new information, in research studies as well as environmental impact studies, will help manage for viable wildlife populations under future development scenarios.

A2.6 References

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Appendix 3: Methodology for assessing perceptions of local communities towards golden cats and other African rainforest species

Cover image: Field assistant Arthur Dibambou carries out an interview in the village of Divindé, Gabon

We carried out perception surveys with people in four adjacent villages in the Ogooué-Lolo Province of Gabon. These villages were predominantly of Pouvi ethnicity and included Dibouka, Moukagno, Divindé and Ndanda. Two major studies (Starkey 2004, Coad 2007) had already taken place in the area, and people's trust in researchers had already been built. For thorough descriptions of the study area, see Starkey (2004) and Coad (2007). Research ethics approval for these surveys was awarded to Dr Lauren Coad by Oxford University on 25 April 2013 (reference number: SSD/CUREC1A/13-069).

Within each village, we used two methodologies:

1) Interviews with individuals, which we kept oral, anonymous and informal as we were surveying a predominantly illiterate population that is suspicious of formality (Coad 2007). One person was interviewed at a time (66 interviews in total), and we focused on people's knowledge of and perceptions towards carnivores. We were particularly interested in conflict, cultural values and bushmeat consumption. We used photographs of species of interest, including felids, viverrids, herpestids and mustelids. Due to respondents' tendency of wanting to give affirmative answers, we kept questions open-ended and non-guiding. For example, we never mentioned conflict or predation, but used other means of addressing these topics, such as asking if the species in question is seen close to or far from the village. In

most cases, this question led people to respond that either a) yes, the animal comes close the village and kills our chickens/goats or b) no, this animal does not approach the village.

2) Focus group discussions. These included two focus groups, one for men and one for women, in each village. As a group, they had to categorise each species (carnivores and many other forest species) twice by placing pictures into categories:
    a) By attitude, including “very bad”, “bad”, “indifferent”, “good”, “very good”
    b) By perceived rarity, including “rare”, “standard”, “common”

    All members of the group had to agree before they could place the animal picture into the category, thereby ensuring discussion and a chance to hear the thought process.

We introduced ourselves to each village on arrival by arranging a village meeting. We explained our research in detail and took questions. A similar meeting was held at the end of surveying in each village to thank the villages for their accommodation and cooperation. Villagers' enthusiasm to participate in the survey could be related to their interest in wildlife or, conversely, because they were keen to complain about wildlife. We therefore made sure to not only interview people that directly made themselves available to us, but also to seek people out. People were given the choice to refuse the interview, which only 2 people did. We interviewed people of both genders and of all adult ages.

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