Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

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

Laila BAHAA-EL-DIN* *Panthera, 8 West 40th Street, 18th Fl, New York, NY 10018, USA; Wildlife Conservation Research Unit (WildCRU), Department of Zoology, The Recanati-Kaplan Centre, Oxford University, Tubney House, Abingdon Road, Tubney, OX13 5QL, UK, and School of Life Sciences, University of Kwazulu-Natal – Westville Campus, Private Bag X54001, Durban, 4000, South Africa. E-mail: lailab.sp@gmail.com*
Philipp HENSCHEL *Panthera, 8 West 40th Street, 18th Fl, New York, NY 10018, USA. E-mail: phenschel@panthera.org*
Thomas M. BUTYNSKI *Sustainability Centre Eastern Africa, Eastern Africa Primate Diversity and Conservation Program & Lolldaiga Hills Research Programme, PO Box 149, Nanyuki 10400, Kenya. E-mail: TButynski@aol.com*
David W. MACDONALD *Wildlife Conservation Research Unit (WildCRU), Department of Zoology, The Recanati-Kaplan Centre, Oxford University, Tubney House, Abingdon Road, Tubney, OX13 5QL, UK. E-mail: david.macdonald@zoo.ox.ac.uk*
David MILLS *Panthera, 8 West 40th Street, 18th Fl, New York, NY 10018, USA and School of Life Sciences, University of Kwazulu-Natal – Westville Campus, Private Bag X54001, Durban, 4000, South Africa. E-mail: africanleopard@gmail.com*
Rob SLOTOW *School of Life Sciences, University of Kwazulu-Natal – Westville Campus, Private Bag X54001, Durban, 4000, South Africa; Department of Genetics, Evolution and Environment, University College, London, United Kingdom. E-mail: Slotow@ukzn.ac.za*
Luke HUNTER *Panthera, 8 West 40th Street, 18th Fl, New York, NY 10018, USA and School of Life Sciences, University of Kwazulu-Natal – Westville Campus, Private Bag X54001, Durban, 4000, South Africa. E-mail: lhunter@panthera.org*

Keywords
bushmeat, camera trap, conservation, deforestation, *Profelis*

*Correspondence author.

Submitted: 24 February 2014
Returned for revision: 23 April 2014
Revision accepted: 7 October 2014
Editor: KH

doi:10.1111/mam.12033

ABSTRACT

1. 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.

2. 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).

3. 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.

4. 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*.

5. The golden cat is predominantly terrestrial and cathemeral. Its diet consists mainly of rodents and small ungulates.

6. 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.

7. Species-focused camera trap surveys are effective for collecting distribution, abundance, population structure, ecological and behavioural data on golden cats.

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.

METHODS

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. The following search terms were used: African golden cat, *Profelis aurata*, *Caracal aurata*, *Felis aurata*. Papers and reports were supplemented with unpublished information obtained from colleagues who have extensive field experience within the geographic range of the golden cat.

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 ongoing 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 km^2; Ivindo, 3000 km^2); most of the remainder of the region is under logging concessions (Anonymous 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 ongoing golden cat study in northern and central Kibale National Park (ca. 766 km^2), 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 savannas 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 20–42 km^2. 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.

Fig. 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.

REVIEW

Description

The golden cat is a medium-sized, strongly built felid. Adult males weigh 8.0–14.0 kg, whereas 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. 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 1). Melanistic golden cats are present in the Virunga-Bwindi region [where the borders of Uganda, Rwanda and Democratic

Table 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; $n = 50$).

		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

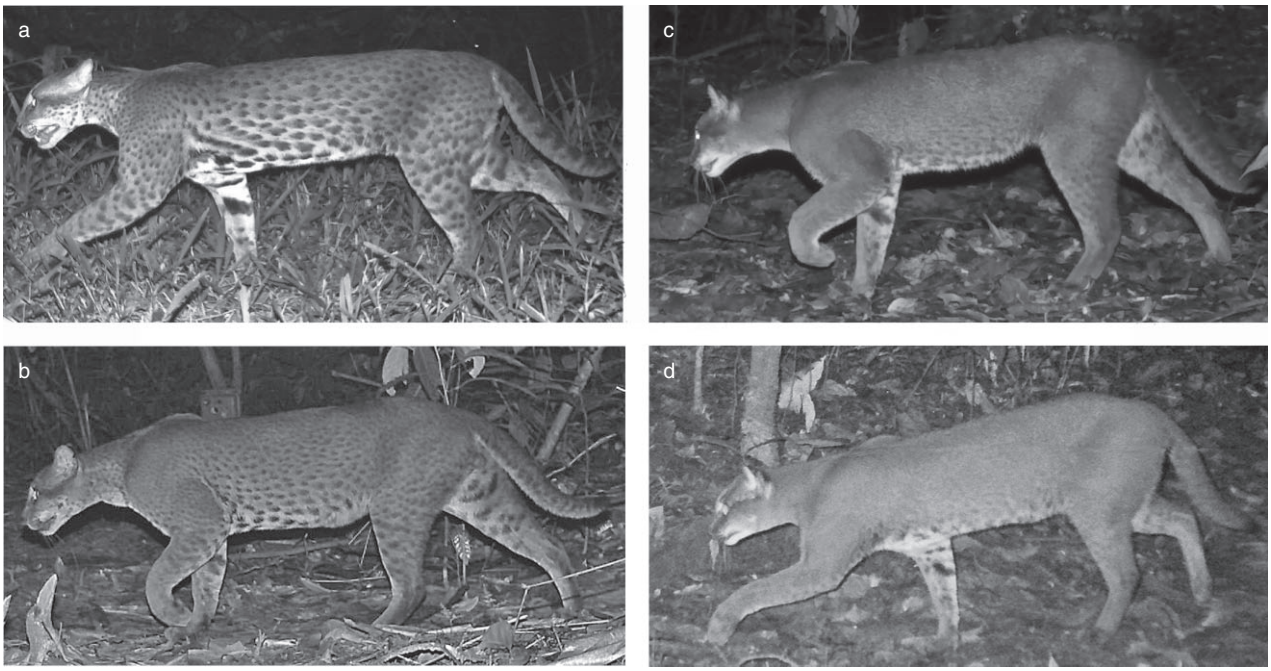

Fig. 2. Camera trap photographs of African golden cats from central Gabon (a–c), showing the range of types and extent of spotting that occur in individuals from the west of the species' geographic range. Spots are, typically, restricted to the belly and inner legs of golden cats from Kibale, SW Uganda, (d) and from other sites east of the Congo River.

Republic of Congo (DRC) meet] (Monfort 1992, Boy 2003; Fig. 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).

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), 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 sub-species 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).

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/savanna 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.

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 (Ma; Janczewski et al. 1995, Pecon-Slattery & O'Brien 1998). The serval then diverged *c.* 5.6 Ma, and the golden cat and caracal diverged *c.* 1.9 Ma (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*.

Habitat

The golden cat is endemic to tropical Africa in two disjunct populations; in both, it is typically associated with moist forests (Fig. 3). This species is found in lowland, mid-altitude (transition), montane, bamboo and subalpine forests, as well as in alpine moorland, wooded savanna, savanna/forest mosaics, gallery forest and riverine forest

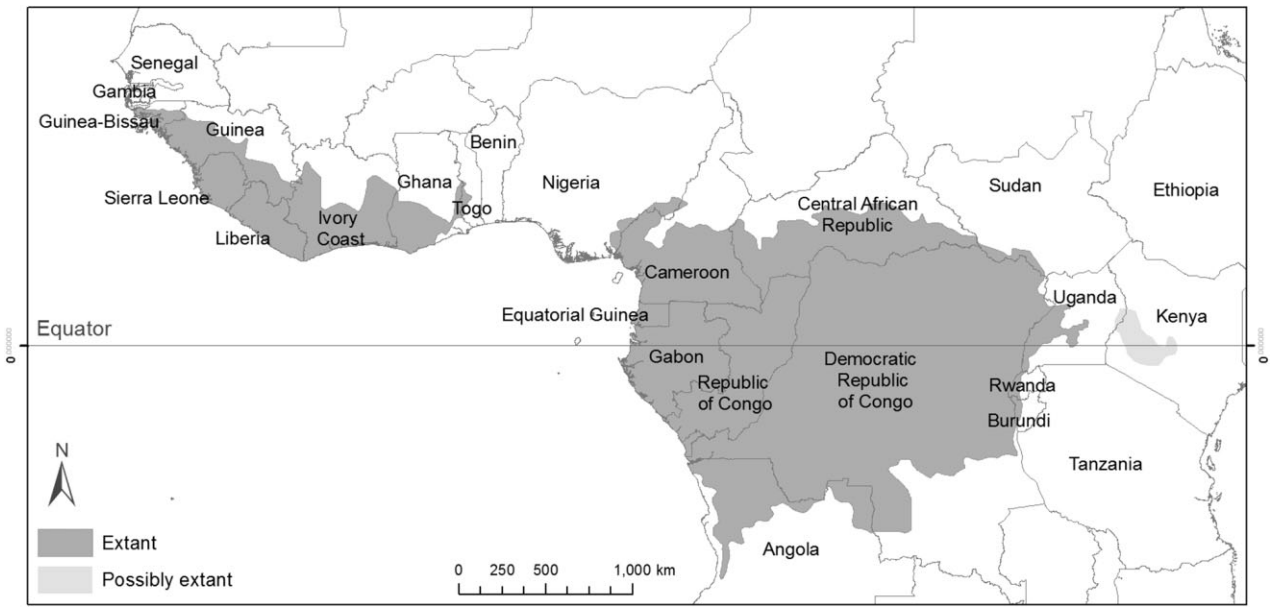

Fig. 3. Geographic range of the African golden cat, mapped according to verified occurrence records and suitable forest habitat (Bahaa-el-din et al. in prep).

(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 3600 m (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/savanna mosaics. In Batéké Plateau National Park, Gabon, golden cats were seen crossing 500 m wide savanna patches, and in gallery forest that is <1 km wide and 20 km from continuous forest (P. Aczel, pers. comm.).

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. 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 3 depicts the golden cat's 'Extent of Occurrence' (the geographic area encompassing all known or inferred sites of occurrence; Anonymous 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; Anonymous 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.

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. 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 percent occurrence for each species or species group by the total occurrence and

Table 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 Source	Ituri, DRC (n = 60) Hart et al. 1996	Ndoki, Republic of Congo (n = 36) Ososky 1998	Dzanga, CAR (n = 17) Ray & Sunquist 2001	Bwindi, Uganda (n = 42) Andama 2000
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 <100 g	16	16	11	
Rodents 100–300 g	15	3		
Rodents 300–500 g	5			
Unknown small rodents		6		
Total rodents	**50**	**69**	**40**	**14 (rodents/shrews)**
Total shrews/insectivora	7	9	6	
Other mammals				
Manis tricuspis		3		
Unknown very small <100 g	1			
Unknown small 100–300 g	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.

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 percent occurrences to group the species, but this was unavoidable without the original data.

In all four dietary studies summarized in Table 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.

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). 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).

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 km^2 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 km^2 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.

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.

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 nighttime hours (Fig. 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).

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

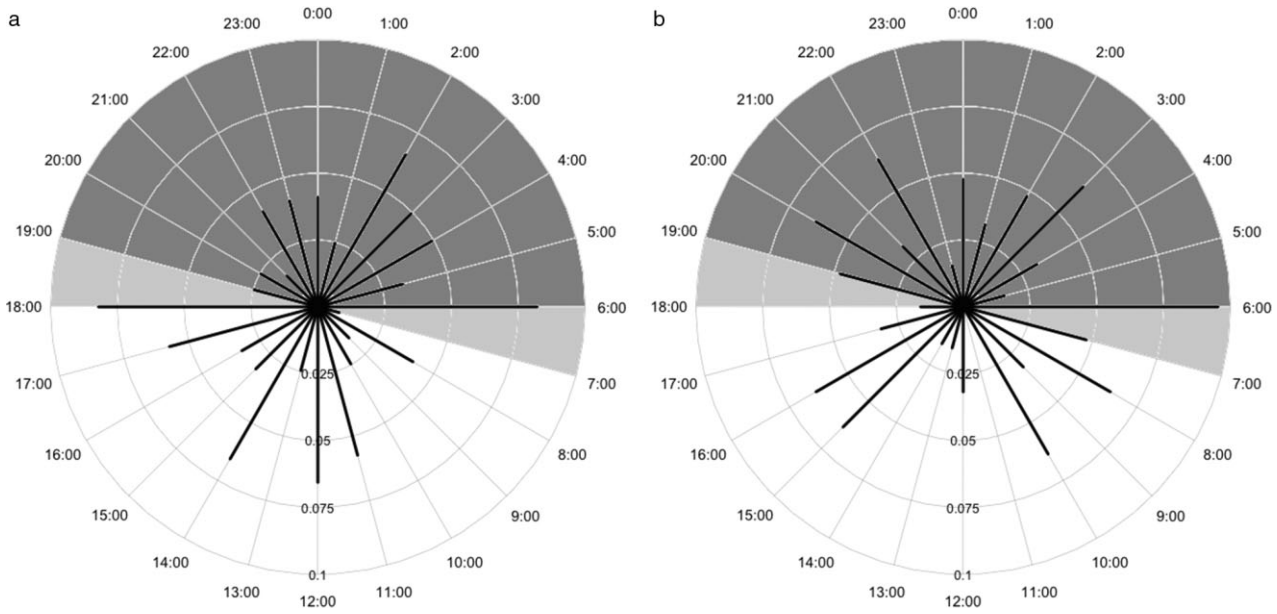

Fig. 4. Activity patterns of the African golden cat based on camera trap surveys at three sites in central Gabon (a) and at three sites in Kibale, SW Uganda (b), presented as proportions of the total number of photo-captures (Gabon, $n = 122$; Kibale, $n = 63$). Circular grid lines (y-axis) represent 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 nighttime and light grey represents twilight.

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 (0.5 s), rhythmical sound sequence, described as 'gurgling', is also produced (Peters 1984).

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.

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).

An estimated 0.46% (15,350 km^2) of West and Central Africa's forest was lost annually between 2000 and 2010 (Anonymous 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 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. 5). Photo-captures indicate that one individual that lost part of his leg to a snare survived for at least 2 months.

In Yaoundé (Cameroon), Kampala (Uganda) and Pointe-Noire (Republic of Congo), golden cat skins are sold alongside medicinal herbs and fetishes (Wilson 2001, T.

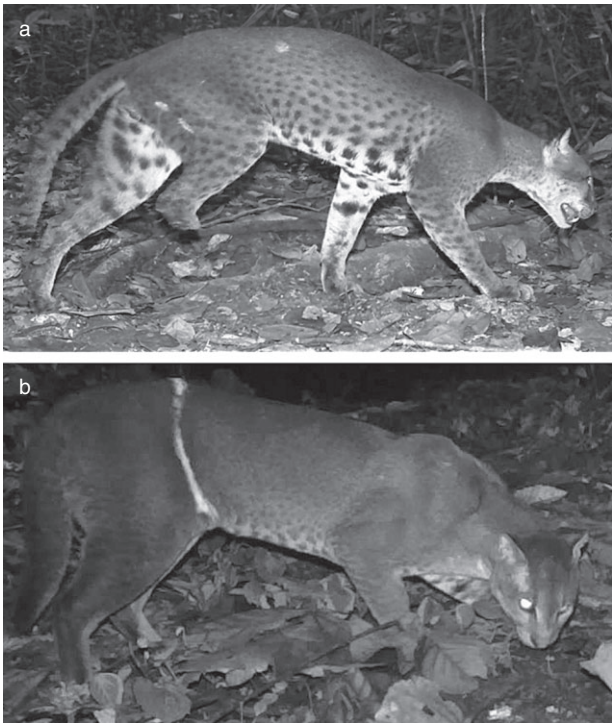

Fig. 5. Camera trap photographs of snare-wounded African golden cats. (a) Back right leg is severed (central Gabon). (b) Cat is scarred on the waist from a snare wound (Kibale, SW Uganda).

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 (Anonymous 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 (Anonymous 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 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/km^2) 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).

CONCLUSION

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.

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 (Anonymous 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.

ACKNOWLEDGEMENTS

We are grateful to our Gabonese partners: Institut de Recherche en Ecologie Tropicale (IRET) and its presiding organization the Centre National de la Recherche Scientifique et technologique (CENAREST), Agence Nationale des Parcs Nationaux (ANPN) and Wildlife Conservation Society (WCS)–Gabon. We thank the Uganda Wildlife Authority, Makerere University Biological Field Station, and WCS-Uganda. We thank A. Kitchener, P. Aczel, S. Angedakin, Y. Tashiro, T. Struhsaker, T. Davenport, G. Ngandjui, E. Sarmiento, C. Chapman, L. Chapman, M. Ghiglieri, J. Kalina, L. Leland, J. Mitani and P. Waser for sharing their observations and data. Thanks to J. Fattebert for commenting on a draft of this manuscript. The photograph of the melanistic golden cat was kindly provided courtesy of TEAM Network, Institute of Tropical Forest Conservation and B. Mugerwa. The Gabon and Uganda surveys were funded by Panthera and Kaplan Graduate Awards Quartermain Small Cat Fund grants to LB and DRM, as well as by Oxford University's Wildlife Conservation Research Unit (WildCRU), WCS-Uganda, International Society for Endangered Cats (ISEC-Canada) and the El Tigre Fund.

REFERENCES

Allen JA (1924) Carnivora collected by the American Museum Congo Expedition. *Bulletin of the American Museaum of Natural History* 47: 73–281.

Andama E (2000) *The Status and Distribution of Carnivores in Bwindi Impenetrable Forest National Park, South-Western Uganda*. MSc thesis, Makerere University, Kampala, Uganda.

Anonymous (2001) *IUCN Red List Categories and Criteria: Version* 3.1. IUCN Species Survival Commission, Gland, Switzerland.

Anonymous (2009) *Interactive Forest Atlas for Gabon*. World Resources Institute, Washington, DC, USA.

Anonymous (2010) *Global Forest Resources Assessment*. Main report. Food and Agriculture Organization of the United Nations, Rome, Italy.

Aronsen GP (2010) New photographic evidence of the African golden cat (*Profelis aurata Temminck*) at Mainaro, Kibale National Park, Uganda. *African Journal of Ecology* 48: 541–545.

Bahaa-el-din L (2012) Observations on a captive African golden cat. *Cat News* 57: 15.

Bahaa-el-din L, Henschel P, MacDonald DW, Hunter L (2011) Systematic survey efforts of the African golden cat – part 1. Results from Gabon. *Cat News* 55: 26–28.

Bahaa-el-din L, Henschel P, Bout N, Coad L, Head J, Inoue E et al. (2013) Notes on the distribution and status of small carnivores in Gabon. *Small Carnivore Conservation* 48: 19–29.

Bahaa-el-din L, Mills DR, Hunter L, Henschel P (in prep) *Caracal aurata*. IUCN Red List of Threatened Species. http://www.iucnredlist.org.

Bertram BCB (1979) Serengeti predators and their social systems. In: Sinclair ARE, Norton-Griffiths M (eds) *Serengeti: Dynamics of an Ecosystem*, 221–285. University of Chicago Press, Chicago, Illinois, USA.

Blake S, Strindberg S, Boudjan P, Makombo C, Inogwabini B-I, Ilambu O et al. (2007) Forest elephant crisis in the Congo Basin. *PLoS Biology* 5: 945–953.

Blonk HI (1965) Einiges über die afrikanische Goldkatze, *Profelis aurata aurata* (Temminck 1827). *Säugetierkundliche Mitteilungen* 13: 132–133.

Borchers DL, Efford MG (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* 64: 377–385.

Boy G (2003) Phantom feline. *SWARA* 25–43. April–June.

Breitenmoser U, Breitenmoser-Wursten C, Kitchener AC (2011) A revised felid classification. *Cat News* 55: 3.

Brodie JF (2009) Is research effort allocated efficiently for conservation? Felidae as a global case study. *Biodiversity and Conservation* 18: 2927–2939.

Brugière D (2001) Range expansion of the African golden cat in Guinea, West Africa. *Cat News* 35: 14–15.

Butynski TM (1984) *Ecological Survey of the Impenetrable (Bwindi) Forest, Uganda, and Recommendations for Its Conservation and Management*. Unpublished report to the Uganda Government and Wildlife Conservation International, New York. http://www.wildsolutions.nl/Publications/Ecological%20Survey%20of%20the%20Impenetrable%20(Bwindi)%20Forest%20-%20Butynski%20-%201984.pdf

Butynski TM (2001) Africa's great apes. In: Beck B, Stoinski TS, Hutchins M, Maple TL, Norton B, Rowan A, Stevens EF, Arluke A (eds) *Great Apes and Humans: the Ethics of Coexistence*, 3–56. Smithsonian Institution Press, Washington, DC, USA.

Butynski TM, Douglas-Dufresne H, de Jong YA (2012) Identification, distribution and conservation status of the African golden cat *Caracal aurata* in Kenya. *Journal of East African Natural History* 101: 3–16.

Carbone C, Gittleman JL (2002) A common rule for the scaling of carnivore density. *Science* 295: 2273–2276.

Carpaneto GM, Germi FP (1989) The mammals in the zoological culture of the Mbuti pygmies in north-eastern Zaire. *Hystrix* 1: 1–83.

Chapman CA, Lambert JE (2000) Habitat alteration and conservation of African primates: case study of Kibale National Park, Uganda. *American Journal of Primatology* 50: 169–185.

Clark CJ, Poulsen JR, Malonga R, Elkan PW (2009) Logging concessions can extend the conservation estate for central African tropical forests. *Conservation Biology* 23: 1281–1293.

Davenport TRB (1996) African golden cat in south-west Uganda. *Cat News* 25: 17.

Davis M (2009) *Densities, Habitat-Use, and Mesopredator Release of the Ocelot in Belize*. MSc thesis, Virginia Polytechnic Institute, Blacksburg, Virginia, USA.

Dekeyser PL (1945) A propos des chats de l'Afrique noire Francaise. *Mammalia* 9: 51–60.

Dillon A, Kelly MJ (2007) Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx* 41: 469–477.

Elliot DG (1883) *A Monograph of the Felidae, or Family of the Cats*. Taylor & Francis, London, UK.

Fa JE, Brown D (2009) Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. *Mammal Review* 39: 231–264.

Fa JE, Seymour S, Dupain J, Amin R, Albrechtsen L, Macdonald DW (2006) Getting to grips with the magnitude of exploitation: bushmeat in the Cross – Sanaga Rivers Region, Nigeria and Cameroon. *Biological Conservation* 129: 497–510.

Farrell LE, Roman J, Sunquist ME (2000) Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology* 9: 1583–1590.

Gaillard F (1969) Sur la présence du chat doré (*Felis aurata Temm.*) et du caracal (*Felis caracal Schreb.*) dans le sud du Sénégal. *Mammalia* 33: 350–351.

Gautier-Hion A (2013) *Miopithecus ogouensis* Northern Talapoin Monkey. In: Butynski TM, Kingdon J, Kalina J (eds) *Mammals of Africa:* Primates, Vol. II, 253–256. Bloomsbury, London, UK.

Grubb P, Jones TS, Davies AG, Edberg E, Starin ED, Hill JE (1998) *Mammals of Ghana, Sierra Leon and The Gambia*. The Trendrine Press, Cornwall, UK.

Guggisberg CAW (1975) *Wild Cats of the World*. Taplinger Publishing Co., New York City, New York, USA.

Haltenorth T, Diller H (1980) *A Field Guide to the Mammals of Africa Including Madagascar*. William Collins Sons & Co Ltd, London, UK.

Happold DCD (1987) *The Mammals of Nigeria*. Clarendon Press, Oxford, UK.

Hart JA, Katembo M, Punga K (1996) Diet, prey selection and ecological relations of leopard and golden cat in the Ituri Forest, Zaire. *African Journal of Ecology* 34: 364–379.

Hayward MW, Slotow R (2009) Temporal partitioning of activity in large African carnivores: tests of multiple

hypotheses. *South African Journal of Wildlife Research* 39: 109–125.
Henschel P, Ray JC (2003) *Leopards in African Rainforests: Survey and Monitoring Techniques*. Wildlife Conservation Society, Global Carnivore Program, New York City, New York, USA.
Henschel P, Abernethy KA, White LJT (2005) Leopard food habits in the Lope National Park, Gabon, Central Africa. *African Journal of Ecology* 43: 21–28.
Henschel P, Breitenmoser-Wursten C, Sogbohossou E (2008) *Caracal aurata*. IUCN 2014. IUCN Red List of Threatened Species. http://www.iucnredlist.org
Henschel P, Hunter LTB, Coad L, Abernethy KA, Muhlenberg M (2011) Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. *Journal of Zoology* 285: 11–20.
Henschel P, Malanda G-A, Hunter L (2014) The status of savanna carnivores in the Odzala-Kokoua National Park, northern Republic of Congo. *Journal of Mammalogy* 95: 882–892.
Hickisch R, Aebischer T (2013) Records of African golden cat and caracal in the Chinko/Mbari Drainage Basin, Central African Republic. *Cat News* 58: 22–23.
Hunter L, Barrett P (2011) *Carnivores of the World*. Princeton University Press, Princeton, New Jersey, USA.
Inskip C, Zimmermann A (2009) Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43: 18–34.
Janczewski DN, Modi WS, Stephens JC, O'Brien SJ (1995) Molecular evolution of mitochondrial-12S RNA and cytochrome-B sequences in the pantherine lineage of Felidae. *Molecular Biology and Evolution* 12: 690–707.
Johnson WE, Eizirik E, Pecon-Slattery J, Murphy WJ, Antunes A, Teeling E et al. (2006) The late Miocene radiation of modern Felidae: a genetic assessment. *Science* 311: 73–77.
Kingdon J (1977) *East African Mammals. An Atlas of Evolution in Africa*, Vol. III, *Part A (Carnivores)*. Academic Press, London, UK.
Kingdon J, Happold D, Butynski T, Hoffmann M, Happold M, Kalina J (eds; 2013) *Mammals of Africa*, Vol. 6. Bloomsbury Publishing, London, UK.
Malbrant R, Maclatchy A (1949) *Faune de l'Equateur Africain Français, Tome II, Mammifères*. Paul Lechevalier, Paris, France.
Meijaard E, Sheil D (2008) The persistence and conservation of Borneo's mammals in lowland rain forests managed for timber: observations, overviews and opportunities. *Ecological Resources* 23: 21–23.
Mills D, Isoke S, Plumptre A, Slotow R, Hunter L (2012) Systematic survey efforts of the African golden cat – Part 2. Results from Uganda. *Cat News* 57: 16–19.
Monfort A (1992) Première liste commentée des mammifères du Rwanda. *Journal of African Zoology* 106: 141–151.
Muchaal PK, Ngandjui G (1999) Impact of village hunting on wildlife populations in the western Dja Reserve, Cameroon. *Conservation Biology* 13: 385–396.
Mugerwa B, Sheil D, Ssekiranda P, Heist M, Ezuma P (2013) A camera trap assessment of terrestrial vertebrates in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology* 51: 21–31.
Nasi R, Billand A, van Vliet N (2012) Managing for timber and biodiversity in the Congo Basin. *Forest Ecology and Management* 268: 103–111.
Noss AJ (1998) The impacts of cable snare hunting on wildlife populations in the forests of the Central African Republic. *Conservation Biology* 12: 390–398.
Nowell K, Jackson P (1996) *Wild Cats – Status Survey and Conservation Action Plan*. IUCN/SSC Cat Specialist Group, Gland, Switzerland.
Ososky JJ (1998) *Diet of Leopards and Golden Cats in Ndoki Park, Republic of Congo*. MSc thesis, University of Chicago, Chicago, Illinois, USA.
Pecon-Slattery J, O'Brien SJ (1998) Patterns of Y and X chromosome DNA sequence divergence during the Felidae radiation. *Genetics* 148: 1245–1255.
Peters G (1984) On the structure of friendly close range vocalizations in terrestrial carnivores (Mammalia: Carnivora: Fissipedia). *Zeitschrift für Säugetierkunde* 49: 157–182.
Pocock RI (1907) Notes upon some African species of the genus *Felis*, based upon specimens recently exhibited in the Society Gardens. *Proceedings of the Zoological Society of London* 77: 656–677.
Pocock RI (1917) The classification of the existing felidae. *Annals and Magazine of Natural History* 8: 329–350.
Purvis A, Gittleman JL, Cowlishaw G, Mace GM (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267: 1947–1952.
Putz FE, Zuidema PA, Synnott T, Peña-Claros M, Pinard MA, Sheil D et al. (2012) Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters* 5: 296–303.
Rabinowitz A, Nottingham BG (1986) Ecology and behaviour of the jaguar in Belize, Central America. *Journal of Zoology* 210: 129–159.
Rahm U, Christiaensen AR (1963) *Les mammifères de la région occidentale du Lac Kivu.* Annales Musée Royale de l'Afrique Centrale Série No. 8. *Sciences Zoologiques* 118: 1–83.
Ray JC (2001) Carnivore biogeography and conservation in the African forest: a community perspective. In: Weber W, White L, Vedder A, Naughton-Treves L (eds) *African Rainforest Ecology and Conservation – An Interdisciplinary Perspective*, 214–232. Yale University Press, New Haven, Connecticut, USA.
Ray JC, Butynski TM (2013) *Profelis aurata* African Golden Cat. In: Kingdon J, Hoffmann M (eds) Mammals of Africa*: Carnivores, Pangolins, Equids, Rhinoceroses*, Vol. V, 168–173. Bloomsbury, London, UK.
Ray JC, Sunquist ME (2001) Trophic relations in a community of African rainforest carnivores. *Oecologia* 127: 395–408.

Ray JC, Hunter L, Zigouris J (2005) *Setting Conservation and Research Priorities for Larger African Carnivores*. WCS Working Paper 24. Wildlife Conservation Society, New York City, New York, USA.

Robinson J, Bennett E (2000) *Hunting for Sustainability in Tropical Forests*. Columbia University Press, New York City, New York, USA.

Romero-Munoz A, Maffei L, Cuéllar E, Noss AJ (2010) Temporal separation between jaguar and puma in the dry forests of southern Bolivia. *Journal of Tropical Ecology* 26: 303–311.

Rosevear DR (1974) *The Carnivores of West Africa*. British Museum of Natural History, London, UK.

Sayer J (1992) A future for Africa's tropical forests. In: Sayer JA, Harcourt CS, Collins NM (eds) *Africa: The Conservation Atlas of Tropical Forest*, 81–93. Macmillan, London, UK.

Schouteden H (1948) Faune du Congo Belge et du Ruanda-Urundi, I. Mammifères. *Annales du Musée du Congo Belge, Zoologie, Tervuren* 8: 1–331.

Seidensticker JC, Hornocker MG, Wiles WV, Messick JP (1973) Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monographs* 35: 1–60.

Sheil D (2011) An encounter with an African golden cat *Caracal aurata*: one of the world's least known felids. *African Journal of Ecology* 49: 367.

Sheil D, Mugerwa B (2013) First pictures of a hunting African golden cat. *Cat News* 58: 20–21.

Sicuro FL, Oliveira LFB (2011) Skull morphology and functionality of extant Felidae (Mammalia: Carnivora): a phylogenetic and evolutionary perspective. *Zoological Journal of the Linnean Society* 161: 414–462.

Sollmann R, Furtado MM, Gardner B, Hofer H, Jácomo ATA, Tôrres NM et al. (2011) Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation* 144: 1017–1024.

Struhsaker TT (1981) Polyspecific associations among tropical rain-forest primates. *Zeitschrift für Tierpsycologie* 57: 268–304.

Struhsaker TT (1997) *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. University Press of Florida, Gainesville, Florida, USA.

Struhsaker TT (2010) *The Red Colobus Monkeys: Variation in Demography, Behavior, and Ecology of Endangered Species*. Oxford University Press, Oxford, UK.

Sunquist ME (1981) The social organization of tigers in Royal Chitwan National Park. *Smithsonian Contributions to Zoology* 336: 35796.

Temminck C-J (1827) *Monographies de mammalogie ou description de quelques genres de mammifère dont les espèces ont été observées dans les différents musées de l'Europe, I*. Dufour et d'Ocagne, Paris, France.

Tonkin B, Kohler E (1978) Breeding the African golden cat. *International Zoo Yearbook* 18: 147–150.

Toschi A (1946) Some interesting mammals from the Mau. *Journal of the East Africa Natural History Society* 19: 132–133.

van Mensch PJA, van Bree PJH (1969) On the African golden cat, *Profelis aurata* (Temminck, 1827). *Biologia Gabonica* 5: 235–269.

Vande Weghe JP (2006) *Ivindo et Mwagna. Eaux noires, forêts vierges et baïs*. Wildlife Conservation Society, Libreville, Gabon, Africa.

Vande Weghe JP (2011) *Lopé, Waka et Monts Birougou*. Wildlife Conservation Society, Libreville, Gabon, Africa.

Vedder A, Naughton-Treves L, Plumptre A, Mubalama L, Rutagarama E, Weber W (2001) Conflict and conservation in the African rain forest. In: Webber W, White LJT, Vedder A, Naughton-Treves N (eds) *African Rain Forest Ecology and Conservation*, 557–562. Yale University Press, New Haven, Connecticut, USA.

Virani M (1993) Golden cat in Arabuko-Sokoke. *East African Natural History Society Bulletin* 23: 51–52.

Wilkie DS, Shaw E, Rotberg F, Morelli G, Auzel P (2000) Roads, development, and conservation in the Congo Basin. *Conservation Biology* 14: 1614–1622.

Wilkie DS, Bennett EL, Peres CA, Cunningham AA (2011) The empty forest revisited. *Annals of the New York Academy of Sciences* 1223: 120–128.

Wilson VJ (2001) *Duikers of Africa*. Chipangali Wildlife Trust, Bulawayo, Zimbabwe.

Wilting A, Mohamed A, Ambu LN, Lagan P, Mannan S, Hofer H et al. (2012) Density of the Vulnerable Sunda clouded leopard *Neofelis diardi* in two commercial forest reserves in Sabah, Malaysian Borneo. *Oryx* 46: 423–426.