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Non-Human Predator Interactions with Wild Great Apes in Africa and the Use of Camera Traps to Study Their Dynamics

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Key Words

Predation · Gorilla · Chimpanzee · Leopard · Antipredator behaviour · Camera traps · Species co-occurrence

Abstract

The slow life histories of great apes (hereafter 'apes') combined with a growing inventory of predation incidents suggest that apes may be strongly affected by direct predation, as well as by predation risk. Predation risk may shape and increase behavioural flexibility by forcing individuals to adapt their behaviour to predator patterns. Forest leopards are an apex predator of primates in African rain forests and may represent a significant risk to ape populations. More field data are needed to further elucidate the behavioural modifications of apes in response to predation. We present research methods that combine the use of remote camera traps, capture-mark-recapture statistics and occupancy modelling to study predator-African ape relationships and potential antipredator behaviour through spatial variation in species co-occurrence patterns.

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Introduction

Though theory recognizes predation pressure as a crucial determinant of sociality for many mammals [e.g. van Schaik et al., 1983], the importance of predation to primate evolution has been subject to debate [e.g. Anderson, 1986]. Its role in shaping the behaviour and morphology of primate species was thought to be immensely significant by early field primatologists [e.g. Chance, 1955; De Vore and Hall, 1965;

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Crook and Gartlan, 1966; Alexander, 1974; reviewed in Cheney and Wrangham, 1987; Van Schaik and Höstermann, 1994; reviewed in Janson, 1998]. Unlike the chronic consequences of poor food or mate choice, an individual's future lifetime fitness can be devastated by only one failure to avoid a predator [Lima and Dill, 1990].

Direct measurements of the impact of predation on primate evolution have proven difficult to obtain [Stanford, 2002]. Predation is rarely seen due to (a) the cryptic nature of predators and some prey, and (b) the influence of researcher presence resulting in potential predator avoidance of study groups during observation periods [Tutin et al., 1981; Cheney and Wrangham, 1987]. Since direct evidence of primate predation is scarce [Janson, 1998], some authors have dismissed the role of predation in primate sociality [reviewed in Anderson, 1986]. However, low direct evidence of predation does not prove that predation is genuinely low or unimportant. Even if predation rates were accurately measured and found to be low, the size and composition of a primate group could still be significantly affected by only one predation event a year [Janson, 1992].

Studies that focussed on defining and assessing primate responses to predation risk (as opposed to direct predation events) have produced significant insights into the role that predation may play in group size and composition [e.g. Janson and Goldsmith, 1995; Cowlshaw, 1997; Hill and Dunbar, 1998; Hill and Lee, 1998], in signalling and communication [e.g. Treves, 2000; Zuberbühler, 2001; Arnold and Zuberbühler, 2006], and in interspecific associations [e.g. Noë and Bshary, 1997]. Comprehensive models predict that primate social groupings are thus based on a complex network of predation, ecological factors, competition, habitat saturation and infanticide avoidance [Wrangham, 1982; Terborgh and Janson, 1986; Van Schaik, 1989; Sterck et al., 1997; Isbell and Young, 2002; reviewed in Stanford, 2002].

Behavioural adaptations to minimize the chance of death due to predation should be expected even with very low probabilities of predatory events [Van Schaik et al., 1983]. It is imperative to distinguish between lethal predation causing mortality, and predation risk [Hill and Lee, 1998]. Antipredator strategies are thought to evolve from the level of perceived predation risk – defined as the probability of encountering a predator and the perception of attack danger – faced by an individual or a group [Hill and Dunbar, 1998; Hill and Lee, 1998; Hart, 2007].

Here, we present a literature review of non-human predation on great apes, including a discussion of the behavioural modifications of great apes in response to predation risk. More information in this area is required to better evaluate the consequences of ape predation on their socio-ecology. We therefore also present non-invasive research methods that combine the use of remote camera traps, capture-mark-recapture (CMR) statistics and occupancy modelling to study predator-African ape relationships.

Does Large Body Size Protect Great Apes from Non-Human Predation?

Though a vast array of species are known or suspected to prey on primates (i.e. reptiles, raptors, felids, canids, hyaenids and smaller carnivores [Miller and Treves, 2006; Hart, 2007; this special issue]), great apes are thought to be protected from non-human predation pressure due to their large body size [Cheney and Wrangham, 1987] (but see also section on forest leopard predation below). Consequently, many believe

their grouping patterns are the result of feeding and mate competition, and infanticide avoidance [e.g. Wrangham, 1980; Watts, 1996]. However, the importance of predation to ape association patterns has remained largely unexplored [e.g. D'Amour et al., 2006], and their slow life histories combined with a growing inventory of predator-ape incidents suggest that, contrary to traditional thought, predation pressure may strongly affect ape populations [Robbins et al., 2004]. Some studies have, for example, illustrated that lethal predation may be a significant cause of ape mortality [e.g. Boesch, 1991; Zuberbühler and Jenny, 2002; reviewed in Robbins et al., 2004] and that predation risk may shape and increase behavioural flexibility by forcing individuals to adapt their activities in relation to predator patterns [e.g. Boesch, 1991]. In order to achieve maximum fitness, individuals with long lifespans and larger brains are expected to invest in cognitive flexibility; effective antipredator tactics can thus be learned during a prolonged period of dependence [Shultz and Dunbar, 2006].

We conducted a comprehensive literature review, based solely on published accounts of African ape predation incidents (table 1). For this review, we searched internet databases (e.g. Web of Science, Google Scholar) and existing references within relevant articles. We review all lethal (resulting in death) and non-lethal (not resulting in death) predation incidents published on chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and gorillas (*Gorilla* spp.). We focus solely on African apes since little is published on predatory incidents for orang-utans (*Pongo pygmaeus* or *P. abelii*) [Rijksen and Rijksen-Graatsma, 1975; Rijksen, 1978]. Table 1 also reviews published accounts of behavioural reactions to the detection of potential predators, and documents all published occasions where African ape remains were found in predator scat (although note that the possibility of scavenging cannot be ruled out).

Owing to their large body size, accounts suggest that large carnivores, like the leopard and the lion (*Panthera leo*) [Cheney and Wrangham, 1987] are the main predators of African apes. However, pythons are also suspected predators of apes [Goodall, 1968] as are some large raptors [Goodall, 1968], and the crocodile (Crocodylidae) [Parnell, 2002]. Though there may be other predators capable of killing apes such as the hyaena and the African wild dog (*Lycaon pictus*), predation on large primate species will be limited by predator size, strength, geographical home range and hunting strategies (i.e. group or solitary).

It is, however, likely that many accounts of predatory incidents have not been published and many more have gone undetected. A 'complete' data set is currently only available for the Bai Hokou Primate Habituation Camp (hereafter, 'Bai Hokou'), Dzanga-Sangha Protected Areas Complex (DSPAC), Central African Republic, from 1997 to 2012. Research presence was continuous during this time frame. Only 3 (table 1) out of the 8 total detected events have been published. Unpublished events were described as: (1) dead subadult gorilla female found with leopard-like neck bites; (2) injured female gorilla seen with leopard-like wounds; (3) a 2-week-old gorilla baby found abandoned and freshly dead, and traces showed the group potentially fled from a leopard; (4) traces of a leopard were spotted following a gorilla group, and (5) 1 chimpanzee, who was missing a hand due to an old snare injury, was found dead with evidence of leopard attack and there was additional evidence that the leopard had dragged the carcass (all incidents were observed by A. Todd or a Bai Hokou assistant or tracker). Outside this 15-year period, an additional 2 accounts (table 1) have been published from data collected in 1987–1998 when research presence at the site was intermittent [Fay et al., 1995]. Once 'complete' data sets are available for all re-

Table 1. All published incidents of lethal and non-lethal predation of African apes, and behavioural reactions to the detection of potential predators and findings of African ape remains in predator scat

Location	Ape	Predator	Incidents, reactions and remains	Reference
Bai Hokou	<i>G.g.g.</i>	Leopard	Attack on 1 silverback and 1 blackback ♂; not lethal	Fay et al., 1995
	<i>G.g.g.</i>	Leopard	Upon hearing leopard, group silverback quickly gathered group and moved quietly and swiftly out of area	Klailova, 2011 [L. Van der Weyde, pers. commun.]
	<i>G.g.g.</i>	Leopard	Study group's silverback severely injured in suspected attack; not lethal, but his group reduced in size by half	Cipolletta, 2003
Lopé	<i>G.g.g.</i>	Leopard	Gorilla remains found in scat	Tutin and Benirschke, 1991
	<i>G.g.g.</i> and <i>P.t.t.</i>	Leopard	Gorilla and chimpanzee remains found in scat	Henschel, 2005, 2008
Lossi	<i>G.g.g.</i>	Leopard	Blackback death; predation strongly suspected	Robbins et al., 2004
Mbeli Bai	<i>G.g.g.</i>	Crocodile	Upon detection, gorillas either clustered around silverback who led them quickly away, vocalized aggressively until the crocodile left, reacted with fear (screaming), or became more vigilant to crocodile sound	Parnell, 2002
	<i>G.g.g.</i>	Leopard	Silverback in poor health found dead with signs of predation	Robbins et al., 2004
Mongambe	<i>G.g.g.</i>	Leopard	Adult gorilla male chased and attacked; unknown if lethal	Watson, 1999–2000; A. Todd, pers. observation
Ndakan	<i>G.g.g.</i>	Leopard	Gorilla remains found in scat	Fay et al., 1995
Various	<i>G.g.g.</i> and <i>P.t. spp.</i>	Leopard	Gorilla and chimpanzee remains found in scat	Hayward et al., 2006
Virungas	<i>G.g.b.</i>	Leopard	Death of 2–3 adults; anecdotes describe gorillas reacting with fear and fleeing upon detection, but one anecdote described gorillas ignoring leopard in full view	review in Schaller, 1963; review in Pitcairn, 1974
	<i>G.g.b.</i>	Leopard	Attack; heard gorillas screaming, 2 leopards stalking them from nest at night	Johnson, 1931
Idambo	<i>P.t. sp.</i>	Leopard	Female chimpanzees with infant attacked; infant killed	Rahm, 1967
Ituri	<i>P.t. spp.</i>	Leopard	Chimpanzee remains found in scat	Hart et al., 1996
Gombe	<i>P.t.s.</i>	Leopard	Juvenile in tree screamed at evidence of leopard in ravine but mother remained unperturbed	Goodall, 1968
	<i>P.t.s.</i>	Leopard	Chimpanzees ignored coughing leopard 50 yards away	Goodall, 1968
	<i>P.t.s.</i>	Python	Chimpanzees showed fear and avoidance of a nearly dead python	Goodall, 1968
	<i>P.t.s.</i>	Night adder and monitor lizards	Chimpanzees expressed surprise and hit reptiles until reptiles left	Goodall, 1968
	<i>P.t.s.</i>	Small snake	Chimpanzees ignored, were curious or chased off the snake	Goodall, 1968
	<i>P.t.s.</i>	Leopard	Chimpanzee threw branch at lame leopard	Goodall, 1968
	<i>P.t.s.</i>	Leopard	Chimpanzees ran up trees, alarm called, then mobbed leopard	Pierce, 2009
Kasakati Basin	<i>P.t.t.</i>	Leopard	Chimpanzees shook branches and loud called to unperturbed leopard 25 m away in tree	Izawa and Itani, 1966

Table 1 (continued)

Location	Ape	Predator	Incidents, reactions and remains	Reference
Kigoma	<i>P.t.s.</i>	Lion	Chimpanzee threw branches until it ran off	Goodall, 1986 (M. Mbrisho, pers. observation)
Mahale	<i>P.t.s.</i>	Leopard	Chimpanzees in tree threw branches at leopard in undergrowth below	Nishida, 1968
	<i>P.t.s.</i>	Lion	Chimpanzees barked, whimpered, screamed upon detection; mobbed lioness and killed cub	Hiraiwa-Hasegawa et al., 1986
	<i>P.t.s.</i>	Lion	Chimpanzee hairs found in faeces	Inagaki and Tsukahara, 1993
	<i>P.t.s.</i>	Lion	4 deaths; chimpanzees showed little response to lion sound when in trees but fled and hid inside trees when in grassland; also reacted with silence and avoidance	Tsukahara and Nishida, 1990 Tsukahara, 1993;
	<i>P.t.s.</i>	Leopard	Chimpanzees made fearful, alarm calls and scanned environment upon hearing leopard	Kutsukake, 2006
Mt. Assirik	<i>P.t.v.</i>	Leopard	Female chimpanzee with infant chased out of a tree	Gandini and Baldwin, 1978
	<i>P.t.v.</i>	Leopards	Chimpanzees fled, went silent, or loud called upon detection; reaction was dependent on distance of leopard	Tutin et al., 1981
	<i>P.t.v.</i>	Hyaenas	No response to hyaena detection	Tutin et al., 1981
	<i>P.t.v.</i>	Lions	Chimpanzees did not respond, went silent or loud called upon detection; reaction was dependent on distance of lion	Tutin et al., 1981
Ndoki	<i>P.t.t.</i>	Leopard	Chimpanzees remains found in scat	Osofsky, 1998
Petit Loango	<i>P.t.t.</i>	Leopard	Chimpanzee carcass found with evidence of leopard predation, faeces and tracks	Furuichi, 2000
Taï	<i>P.t.s.</i>	Leopard	A lone male repelled leopard without tools	Boesch and Boesch, 1989
	<i>P.t.v.</i>	Leopard	6 chimpanzee deaths, 4 chimpanzee injuries and 22 interactions with leopards occurred in 5 years; 39% of chimpanzee deaths due to leopards, chimpanzees mobbed and chased leopards	Boesch, 1991
	<i>P.t.v.</i>	Leopard ¹	1 leopard moved in the opposite direction of chimpanzees in 6/15 cases of drumming and/or screaming of party 100–125 m away	Jenny and Zuberbühler, 2005
	<i>P.t.v.</i>	Leopard	2 dead juveniles were dragged and consumed; most likely scavenging	Jenny and Zuberbühler, 2005
Ugalla	<i>P.t.s.</i>	Lion	15 chimpanzees driven up trees calling in agitation while lion hid in bush, charged and hit Kano and ran off	Kano, 1972; Itani, 1979
Salonga	<i>P. paniscus</i>	Leopard	Bonobo remains found in scat	D'Amour et al., 2006
Various	<i>P.t. spp.</i>	Leopard	Chimpanzees mobbed leopards, with and without sticks; in other cases chimpanzees reacted by scattering away from leopard; reactions differed according to savannah and forest habitats	Kortlandt, 1962, 1967; Kortlandt and Kooij, 1963; van Zon and van Orshoven, 1967; Kortlandt and van Zon, 1969; Albrecht and Dunnett, 1971

(For table footnote see next page.)

search sites, it may be possible to ascertain basic predation probabilities only if external variables are controlled (e.g. study length, length of researcher presence, number of groups followed, target study species, area size, detection probability).

Behavioural Adaptations of Great Apes to Potential Predation Risk

In this section we discuss adaptations to predation risk over time, rather than detailing behavioural reactions to specific predator-ape incidents (see previous section).

Predator avoidance in apes may be reflected in their nesting patterns. Most apes do not construct night nests in feeding trees which bear ripe fruit [Fruth and Hohmann, 1996]. This may help to avoid restless nights arising from interruptions of nocturnal frugivores (i.e. bats), and it may also diminish the risk of agonistic encounters [Rijsken, 1978] with potential predators. Forest leopards patrol fruit trees [Hart et al., 1996], and these areas often provide excellent cover for predators to attack while prey approach or descend from sleeping spots [Isbell, 1994]. Apes may also nest at different heights according to predation risk. When compared to their Equatorial Guinean counterparts who faced comparatively less predation risk due to the closed nature of the forest canopy, the Mt. Assirik (Senegal) chimpanzees of woodland-savannah and predator-rich habitats nested in more open trees, higher and often in larger groups [Baldwin et al., 1981; Tutin et al., 1983; see Pruett et al., 2008, for similar results from Fongoli, Senegal]. Additionally, exposed environments can be risky due to the lack of trees available as escape routes. Tutin et al. [1983] suggest that it is this risk that causes chimpanzees of all parties at Mt. Assirik – especially mother/infant parties and lone individuals – to prefer more forested environments.

Brownlow et al. [2001] noted that adult male chimpanzees in the Budongo Forest, Uganda, nested lower than females in trees at night. Western lowland gorilla females nested arboreally more often and at higher sites than silverbacks [Tutin et al., 1995; Mehlmann and Doran, 2002]. These may reflect protective positions such that predators (or other extra-unit conspecific adult males) will be forced to confront the

(Table 1 footnote.)

Ape: *G.g.g.* = *Gorilla gorilla gorilla*; *G.g.b.* = *Gorilla gorilla beringei*; *G.g. sp.* = *Gorilla gorilla* species unknown; *P.t.s.* = *Pan troglodytes schweinfurthii*; *P.t.v.* = *Pan troglodytes verus*; *P.t.t.* = *Pan troglodytes troglodytes*; *P.t. sp./spp.* = *Pan troglodytes* species unknown or several species together.

Location: Bai Hokou Primate Habituation Camp, Dzanga-Sangha Protected Area Complex, Central African Republic; Gombe National Park, Tanzania; Idambo, Democratic Republic of Congo; Ituri Forest, Democratic Republic of Congo; Kasakati Basin, Tanzania; Kigoma, Tanzania; Lopé National Park, Gabon; Mahale Mountains National Park, Tanzania; Mbeli Bai, Nouabalé-Ndoki National Park, Republic of Congo; Mongambe Primate Habituation Camp, Dzanga-Sangha Protected Area Complex, Central African Republic; Mt. Assirik, Niokolo Koba National Park, Senegal; Ndakan Camp, Sangha River north of border with Republic of Congo, likely in current Nouabalé-Ndoki National Park; Nouabalé-Ndoki National Park, Republic of Congo; Petit Loango Reserve, Gabon; Salonga National Park, Democratic Republic of Congo; Taï National Park, Côte d'Ivoire; Ugalla, Tanzania; Virunga Volcanoes, Democratic Republic of Congo, Rwanda, Uganda.

¹ Though this example does not describe the behavioural reaction of apes to potential predators, it was included because it illustrates that some leopards may actively avoid chimpanzees. Chimpanzees can viciously attack leopards when threatened, and this may be the reason for some leopards to avoid them entirely.

adult male before they can reach other more vulnerable party members [De Vore and Hall, 1965; see Remis, 1994, for an alternative explanation concerning male weight and tree or branch size]. Remis [1993] also found that smaller and therefore more vulnerable groups of western lowland gorillas were more likely to nest arboreally than larger groups. Yamagiwa and Kahekwa [2001] showed that gorilla groups that did not contain an adult male leader were more likely to nest arboreally. The focal silverback of one single-male habituated group at Bai Hokou was significantly more likely to nest closest to the largest trail than any other group member [Klailova, 2011]. In rain forests, large trails are the main pathways of movement for predatory leopards [Henschel and Ray, 2003].

It has been suggested that parties of chimpanzees minimize predation risk by moving more swiftly, cohesively, quietly and in large numbers when crossing open habitats [reviewed in Tsukahara, 1993]. Rapid, unified movements were also observed in mountain gorillas (*Gorilla gorilla beringei*) crossing a particular open cattle area [Fossey, 1974], most likely rife with poachers during Fossey's tenure. Apes may form unique progressions within their group or party in response to the level of perceived danger and the vulnerability of its individuals [e.g. Schaller, 1963; Itani and Suzuki, 1967; Yamagiwa, 1983; Hockings, 2007]. At Bai Hokou when the focal gorilla group was feeding and therefore dispersed, its silverback was significantly more likely to be located at the back of the group, potentially ensuring that all individuals passed by safely. During periods of heavy rainfall – where movement can be very risky since approaching danger cannot be heard or seen – the focal silverback was significantly more likely to be nearer the 'leading' front of the group [Klailova, 2011].

Chimpanzees at Mt. Assirik appear to respond differently according to the perceived risk of each predator species, and according to predator distance upon detection [Tutin et al., 1981]. Kutsukake [2006] found that chimpanzees with no neighbours at Mahale Mountains National Park, Tanzania, increased vigilance when on the ground where the chance of encountering a leopard was higher. Additionally, standing and gazing at the surrounding environment, as a form of extreme vigilance, was mainly observed when leopards or chimpanzees in neighbouring groups were heard [Kutsukake, 2006].

Though party size is expected to increase with predation pressure [reviewed in Anderson, 1986], large groups may prove detrimental to safety in forest environments. Forest density limits the advantages of having 'many eyes' to detect predators. The noise produced by larger groups in forests may make them less able to hear oncoming danger. Furthermore, this same noise may allow predators to locate larger primate groups more efficiently. From a predation risk perspective, it may pay to remain in smaller, more concealed groups in rain forest habitats. Boesch [1991] showed that chimpanzees at Tai National Park, Côte d'Ivoire, respond to leopard predation risk by decreasing their party size and increasing party types better equipped (i.e. all-male parties) to defend against potential acts of predation. Little is known about the possible behavioural adaptations to predation pressure in bonobos [Hohmann and Fruth, 2002]. Predators are more common at Lomako, Democratic Republic of Congo, than at Wamba, Democratic Republic of Congo [White, 1996]. Interestingly, party sizes are smaller, lone parties are less common and mixed parties are more common at Lomako than at Wamba [Boesch, 1991; White, 1996]. While researchers have attributed these intersite differences to a variety of factors [Hohmann and Fruth, 2002], the potential effects of predation risk may have been overlooked.

Forest Leopard Predation on Apes

Open environments are said to be more dangerous to primates than closed habitats due to the lack of shelter and arboreal escape routes [e.g. Tutin et al., 1983; Parnell, 2002; Klailova, 2011]. However, apes living in rain forests must also navigate through extremely dense, low-visibility habitats that can become useful ambush spots [Isbell, 1994] for highly dangerous predators such as the forest leopard [Jenny and Zuberbühler, 2005]. Forest leopards are the apex predator of non-human primates in African rain forests [Jenny and Zuberbühler, 2005; Henschel, 2008] (table 1). As stated earlier (in the previous section), forest leopards may adopt a sit-and-wait attack technique near favoured feeding spots, popular game trails or at the base of trees while prey feed arboreally [Isbell, 1994; Hart et al., 1996; Jenny and Zuberbühler, 2005; Hayward et al., 2006]. Forest leopards are crepuscular, diurnal hunters known to follow the activity pattern of their prey species and can develop highly specialized prey preferences [Hart et al., 1996; Jenny, 1996; Ososky, 1998; Ray and Sunquist, 2001; Zuberbühler and Jenny, 2002; Henschel et al., 2005; Jenny and Zuberbühler, 2005]. Primates represent a significant portion – approximately 17–25% – of forest leopard diet [reviewed in Henschel et al., 2005].

In relation to the carnivore guild of African rain forests, leopards prey on the largest mammals [Ray and Sunquist, 2001] and take larger prey than savannah leopards even when the relative biomass of each environment is accounted for [Kruuk and Turner, 1967; Fay et al., 1995; Hart et al., 1996]. Though they preferentially hunt medium-sized species in tropical habitats (7–30 kg) [Hart et al., 1996; Ososky, 1998; Ray and Sunquist, 2001; Henschel, 2005], leopards are capable of hunting mammals far larger than themselves. Fay et al. [2005] recorded several leopard hunts of forest buffalo and bongo (*Tragelaphus euryceros*) at Bai Hokou. Leopard predation on a 200 kg okapi (*Okapia johnstoni*) was witnessed in the Ituri Forest, Democratic Republic of Congo [T. and J. Hart, pers. commun. in Fay et al., 2005] where ungulates greater than 45 kg represented 21% of scat remains. While items found in scat may simply reflect scavenging, the large ungulate carcasses found in this study all showed evidence of predation struggle by leopards [Hart et al., 1996]. They have even been known to cache giraffes (*Giraffa camelopardalis*) in trees [e.g. Stevenson-Hamilton, 1947]. Leopards also have a long history of predation on hominids and humans [reviewed in Fay et al., 1995]. If leopards are capable of hunting the animals listed above, predation on apes should not be limited solely by their large body size.

Competition with human hunters for similar prey types in African rain forests coupled with high extraction rates have forced leopards to hunt outside their preferred prey weight range [Ray, 2001; Ray and Sunquist, 2001; Henschel, 2008; Hodgkinson, 2009]. If high levels of competition are experienced by leopards, they may be required to use different resources within their range [Jenny and Zuberbühler, 2005]. As they face direct competition with African golden cats (*Caracal aurata*) for smaller prey species (i.e. rodents) and humans for medium-sized prey [Hart et al., 1996; Ososky, 1998; Ray, 2001; Ray and Sunquist, 2001; Hodgkinson, 2009], hunting larger mammals such as apes may provide an energetically viable alternative [Fay et al., 1995; Hart et al., 1996; Ray and Sunquist, 2001].

While patterns of primate predation are starting to emerge, Anderson [1986], Cheney and Wrangham [1987], Isbell [1994] and Hill and Lee [1998] all emphasize that more field data on this topic are desperately needed if we are to effectively and

confidently understand the impact of predation on ape socio-ecology. Several studies have advocated systematic collection of predator-primate patterns by habituating predators to observers or by working in teams of carnivore specialists and primatologists [Anderson, 1986; Isbell, 1994].

Camera Trapping, Capture-Mark-Recapture, and Occupancy Modelling of Species Co-occurrence Patterns

Camera traps – developed for wildlife research in the early 1980s [Carbone et al., 2001] – are automated cameras equipped with motion and/or infrared sensors. When triggered, they capture photos or take videos of animals passing by. They have been used to inventory elusive species [e.g. Rovero and De Luca, 2007; Tobler et al., 2008], to determine activity patterns and habitat preferences [e.g. Bowkett et al., 2007; Linkie et al., 2007; Henschel, 2008; Harmsen et al., 2009], to study behaviour through videos [e.g. Sanz and Morgan, 2007, 2011] and to estimate population size using CMR sampling techniques [e.g. Karanth and Nichols, 1998; Maffei et al., 2004; Silver et al., 2004; Henschel, 2008; Balme et al., 2009; Rovero and Marshall, 2009].

Camera trapping allows for higher species detection rates than both dung and transect counts [Bowkett et al., 2006] and can detect the most crepuscular and rare species [e.g. Karanth and Nichols, 1998; Rovero et al., 2005] with 100% certainty. Although it has high initial costs [Silveira et al., 2003], it is more cost-efficient than traditional censuses in the long term [Rovero and Marshall, 2009]. It requires less personnel and decreased field time than conventional methods, and the traps can be re-used in future surveys [Rovero and Marshall, 2009]. Camera trapping simplifies data collection by greatly reducing the possibility for human error [Rovero and Marshall, 2009] and by removing potential bias, such as that resulting from poor interobserver reliability [e.g. Mitani et al., 2000]. Camera traps also enable continuous data collection (i.e. both day and night) and can collect additional information on other non-focal species during trapping periods [e.g. Henschel and Ray, 2003; Silveira et al., 2003; Henschel, 2008].

The use of camera traps for density estimation has proven successful when combined with CMR statistical analysis. This technique estimates the size of a population by trapping (photographing) and marking (identifying via photographs) individuals, releasing them, resampling the same population at a later time, and then comparing the proportion of recaptured individuals (i.e. rephotographed identified individuals) with the original number of captured individuals [Karanth and Nichols, 1998]. As with any statistical estimate of abundance, the probability of detection (i.e. non-detection does not necessarily mean true absence) must be accounted for to make accurate inferences [Karanth and Nichols, 1998; Pollock et al., 2002; Mackenzie and Nichols, 2004]. For the CMR technique to be deployable, however, the study species must be individually identifiable through natural markings [e.g. Karanth and Nichols, 1998; Azlan, 2006]. The spotting patterns of leopards make them a perfect subject for such studies [Henschel and Ray, 2003; Henschel, 2008]. However, it is difficult to consistently distinguish individuals from photographs for the majority of medium to large mammals captured by camera traps, including great apes. As a result, camera trapping methodologies have not yet been systematically implemented for use in ape surveys [Kühl et al., 2008], although the methods are currently being tested [L. Wil-

liamson and H. Kühl, pers. commun.; Klailova et al., in progress; Max Planck Institute for Evolutionary Anthropology, in progress; Morgan and Sanz, in progress].

Species spatial occurrence models can also draw inferences about species and community dynamics [Mackenzie and Nichols, 2004]. The study of occupancy – the proportion of an area occupied by a species – offers a promising surrogate to the capture-recapture technique [Mackenzie and Nichols, 2004]. While occupancy does not estimate absolute abundance, presence or detection versus absence or non-detection data can be used to characterize geographic ranges of a species, to study the variables that affect a species distribution and to assess local extinction and colonization probabilities and rates [Mackenzie et al., 2003; Mackenzie and Nichols, 2004]. Likelihood-based methods have been developed for occupancy modelling, which not only take into account imperfect detection probabilities (as with CMR surveys, species may go undetected), but also allow for the addition of environmental covariates [reviewed in Mackenzie and Nichols, 2004]. Since the model can cope with the inclusion of environmental covariates, researchers can assess relationships between various model parameters and site characteristics (i.e. habitat preference in relation to occupancy). Promising results by Linkie et al. [2007] illustrate that occupancy modelling in conjunction with camera trapping can be applied to non-individually identifiable species. They used camera traps in conjunction with a presence/absence survey, and 4 environmental variables to successfully determine sun bear (*Helarctos malayanus*) occupancy in three habitat types with various logging histories.

Camera trapping in combination with occupancy models of species' co-occurrence patterns [MacKenzie et al., 2004] can be used to study the complicated nature of predator-prey relationships between cryptic species, such as those between sympatric forest leopards and apes. Using a modified version of the single-species likelihood-modelling framework described above, interspecific relationships between co-occurring species can be explored via occupancy patterns for each target species [Mackenzie et al., 2004, 2005]. Do the species co-occur independently or does the presence/absence of one species depend on that of the other species? In other words, could a particular presence/absence matrix have occurred as a result of interspecific competition or predator-prey dynamics? Harmsen et al. [2009] used camera traps in conjunction with a basic occupancy framework to illustrate that sympatric individually identifiable jaguars (*Panthera onca*) and plain-coloured pumas (*Puma concolor*) in the Cockscomb Basin of Belize avoid one another more than they avoid conspecifics. It is hypothesized that the pumas may be exhibiting antipredator behaviour since jaguars are known to prey on the smaller puma [review in Harmsen et al., 2009].

Description of the Analytical Framework

The accuracy and precision of any camera trapping study will depend on: (1) study area size; (2) number and placement of cameras; (3) length of survey; (4) the number of 'trapping occasions' at each site/cell grid; (5) environmental and logistical considerations, and (6) the ability of the analytical programme of choice to handle variables which may bias result accuracy and precision.

Areas should be large enough to contain at least parts of the focal species' home ranges. The chance of an 'edge effect' – the likelihood of trapping partial residents [White et al., 1982] – will decrease as study area size increases. However, determin-

ing study area size will often be a compromise between desired size, landscape and logistics. For example: though sampling areas greater than 100 km² may be desirable for species with large home ranges, a researcher will struggle to cover this area if working alone and on foot.

Surveys should be short enough to meet the closed population assumption, where the study population size is not affected by death, birth or emigration/immigration. This is often considered to be 2–3 months for felids [reviewed in Henschel and Ray, 2003, and Henschel, 2008] but can vary appreciably between species and study sites. The study area must be evenly covered with traps so there are no holes in the trapping grid. This ensures that no individual present will have a zero chance of being captured [Karanth and Nichols, 2002]. Each event of sampling a site (i.e. or cell grid) within a survey area is termed a ‘trapping occasion’ [Karanth and Nichols, 1998; Henschel and Ray, 2003]. Results will be more precise, as the number of ‘trapping occasions’ increase [Karanth and Nichols, 1998; Henschel and Ray, 2003]. The length of time needed for one ‘trapping occasion’ will vary according to the detection probability of the target species [Mackenzie et al., 2002; Henschel and Ray, 2003]. Some studies may consider all pictures captured in each day to be separate trapping occasions [e.g. O’Brien et al., 2003], while others facing low detection probabilities may need to pool several days together into one trapping occasion [e.g. Henschel, 2008]. Within each sampling site, capture probabilities will be maximized by placing cameras in areas where focal species have the greatest chance of being detected [Henschel and Ray, 2003]. Camera placement at each site should be changed as often as possible to maximize capture probability, though the number of changes will clearly depend on logistics and area remoteness [Henschel and Ray, 2003; Harmsen et al., 2010]. Environmental conditions must also be considered during survey set-up. For example: periods of increased humidity due to rainfall can cause camera traps to malfunction, therefore avoiding peak wet seasons is advisable.

The basis for both CMR and occupancy analysis is the ‘X-matrix’ [reviewed in Henschel and Ray, 2003]. Each trapping occasion assigns a capture history (where ‘1’ represents captured and ‘0’ represents not captured) to every identified individual, or a detection history to target study species (where ‘1’ represents detected and ‘0’ represents not detected) [Karanth and Nichols, 1998; Henschel and Ray, 2003; Mackenzie et al., 2004]. Capture histories can then be analysed using the CAPTURE program [Rexstad and Burnham, 1991]. Density is calculated using the resulting population size computed by CAPTURE, divided by the area sampled with inclusion of an additional outer boundary strip to take ‘partial residency’ of trapped individuals into account [White et al., 1982] (see above). PRESENCE software [Proteus Wildlife Research Consultants, New Zealand; <http://www.proteus.co.nz>] computes occupancy from detection/non-detection matrices. As previously discussed, both programs cope with imperfect detection probabilities, and allow for the inclusion of environmental covariates (see the preceding section). Here, we have attempted only to provide a general summary of basic methodological principles. For more detailed information of methods, sample design considerations and a mathematical explanation of results computed by CAPTURE and PRESENCE software, see the references listed in this paragraph. Though not discussed here, note also that the application of newly developed spatially explicit CMR modeling (SECR) may perform better statistically than traditional CMR models, and may allow for the relaxation of some CMR

model assumptions; such as the need for geographical closure in the sampled area and the assumption that no individual has a zero probability of being captured in the sampled area [review in Blanc et al., 2012; Sollman et al., 2012].

Additional Methods to Assess Predator-Prey Relationships

Understanding predator-prey relationships can be further illustrated by studying predator scat and, where feasible, assessing changes in prey preferences through time [e.g. Henschel, 2008]. Predator scat can be collected at regular intervals along game trails and roads during remote camera trap patrols. For every scat, reference information can be recorded (i.e. GPS position, diameter of scat, habitat, trail type). Collected scats can then be air-dried and stored in sealed plastic bags until further examination. Prey hair found in scat can be examined microscopically using methods described in Perrin and Campbell [1980] and Clement et al. [1980]. Other remains found in scat (i.e. bone fragments, teeth) can be used to support hair analysis results. Changes in niche overlap through time can then be explored by comparing current results to previous results for the study area. For example: current results from Bai Hokou could be compared to results from the Ray and Sunquist [2001] study done 16–18 years ago in the DSPA. Researchers should be careful when drawing inferences from scat analysis, since prey remains in faecal samples may be due to scavenging rather than direct predation. Nonetheless, assessing scat may be a useful and cost-effective addition to species' co-occurrence studies, since results could further complement camera trap findings.

Future Research

We plan to investigate species co-occurrence patterns in leopards-gorillas, and leopards-chimpanzees at Bai Hokou and the surrounding forests of DSPA in the Central African Republic and the Boé Administrative Sector of the Dulombi/Gabu region in Guinea-Bissau. Bai Hokou is home to two habituated groups and two semi-habituated gorilla groups and several other groups who range in the surrounding area. We will use camera traps to assess leopard density and occupancy in relation to gorilla occupancy and gorilla ranging patterns – ranging data at Bai Hokou is recorded continuously from direct daily follows and traces – of the sympatrically occurring habituated gorilla groups. We aim to use a combination of CMR and occupancy methods to elucidate the interspecific relationships between forest leopards and western lowland gorillas, by studying their spatial variation patterns. Results should allow us to answer questions such as: is interspecific avoidance occurring? And do western lowland gorillas avoid forest leopards? Upon completion of the gorilla-leopard surveys, we aim to assess chimpanzee-leopard relationships – which appear to vary greatly from those with gorillas (table 1) – in Guinea-Bissau. Since camera trapping data will be collected remotely and gorilla ranging data will be collected continuously from day follows (when researchers are present) and night traces (when researchers are absent), we hope to minimize biases resulting from potential predator avoidance of study groups during survey periods. Methods are currently being developed and we aim to test/apply them during a minimum of two 3-month surveys at each study site. Should

methods be applied successfully, we hope to (a) shed more light on the nature of non-human predator-ape relationships and (b) provide researchers with a novel and reliable approach to systematically studying the behavioural modifications of predation risk in apes. We also plan to complement our investigation by conducting a review across African field sites of unpublished predation-ape events (see the section ‘Does large body size protect great apes from non-human predation?’).

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