The conservation biology of the leopard *Panthera pardus* in Gabon: Status, threats and strategies for conservation

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Tag der mündlichen Prüfung:

In loving memory of Marion Andresen

Abstract

The leopard (*Panthera pardus*) has the greatest geographic distribution of the wild cats, and is the most abundant large felid in Africa. Tropical rainforests comprise a large part of the leopard's range in Africa, and the forests of the Congo Basin in particular have long been considered an important stronghold for the species. While known leopard prey ranges in size from arthropods to the largest ungulates, recent studies suggest that leopards preferentially prey upon species within a weight range of 10-40 kg. In the rainforests of the Congo Basin, species within this weight range are also strongly preferred by bushmeat hunters, creating the possibility that leopards and humans are in direct competition for the same prey. However, baseline knowledge of leopard ecology and responses to human disturbance in African rainforests remain largely unknown.

In the present study I investigate how leopard populations respond to competition for prey with hunters. My two principal hypotheses are that (1) leopards exhibit a functional response at hunted sites and switch to smaller, less preferred prey where larger prey species have been depleted; (2) leopards exhibit a numerical response at hunted sites and occur at lower population densities where larger prey species have been depleted. To test this, I collected leopard scats and camera trap data in four rainforest sites in central Gabon exposed to varying levels of anthropogenic disturbance. Hunting intensity is generally highest in the vicinity of settlements, and my four study sites were therefore situated at varying distances from settlements. I analysed camera trap data using capture-recapture models to estimate leopard densities, and employed occupancy modelling to investigate the factors affecting leopard distribution.

Mean leopard prey weight and leopard population density were positively correlated to distance from settlements. Occupancy modelling revealed that leopard use of an area increased with prey abundance and distance from settlements. The results of this study imply that leopards in the African rainforest exhibit a strong functional and numerical response to competition with hunters for prey, and that leopards are absent in the direct vicinity of settlements where hunting is most intense. I present a simple geographic leopard population model to identify priority areas for leopard conservation in the Congo Basin.

Acknowledgements

This study would not have been possible without the help of a multitude of different individuals, whose help along various stages of this study I want to acknowledge here. First of all I would like to thanks my parents, for instilling a profound love for nature in me at a very early stage, and for their distinct interest in my work and their continued support for it, despite the fact that it resulted in long periods of separation from them. Furthermore, I am grateful to Günther Merz for inspiring my interest in working in Gabon, and Pauwel de Wachter for giving me my first job in this extraordinary country. My PhD supervisor, Michael Mühlenberg, became an immediate supporter when I told him about my plans to study leopards in Gabon for my degree, and I greatly appreciate all his help, his amicable supervision and strong interest in my study.

In Gabon, Kate Abernethy, my field supervisor, and Lee White were equally enthusiastic to kick-start this study on leopards, and I am deeply grateful for their friendship and their permanent support during my years in Gabon. Stays at the Station d'Etudes des Gorilles et Chimpanzés (SEGC) in Lopé and all the long discussions we had there were extremely inspiring and motivating, and I am very grateful that I had this opportunity. Lee, as the director of the Wildlife Conservation Society (WCS) Gabon Program, also invited me into the WCS-Gabon family (when it still was one), which guaranteed me the vital logistical support so dearly needed for the functioning of this study. For the permission to work in Gabon and its spectacular national parks I want to express my gratitude to Gabon's Ministry of Forestry, Water and Fishing, and in particular to Adrien Noungou, Director of Wildlife and Hunting, as well as to the country's National Parks Board, and in particular its then permanent secretary, René Hilaire Adiahéno.

In Ivindo NP, Nigel and Isabelle Orbell welcomed me into their home whenever I came through the park's HQ, and their friendship and wonderful company made my stay in this fantastic park an even better one. Their door (including the one of their fridge) was always open for me after lengthy stays in one of my field camps, and I likewise want to thank their fantastic kids, Claire and Michael, for accepting me as their "foster-brother". Nigel organized all my logistics in Ivindo, and I am extremely grateful for the incredible support he managed to provide under the very demanding logistical conditions. Also in Ivindo, Thomas Gilbert joined me as a voluntary research assistant for a couple of months, and I greatly appreciate his enthusiastic and professional help and pleasant company.

NY to secure funding for my study, in a time where other species of big cats are more critically endangered than the leopard, and for a region where almost all conservation work has traditionally been focused of forest elephants, gorillas and chimps. Against many odds, she managed to convince people that leopards in the Congo Basin rainforest might disappear unnoticed from large tracts of forest due to uncontrolled hunting, as did tigers all across tropical Asia, and that there is a need to invest funding now to gather crucial evidence for this alarming trend. Justina also aided in the design of the study, and I am extremely grateful for all her help and support during the early stages of this study. When Justina moved to her new position with WCS in Canada, Luke Hunter "inherited" me from her, and has been an incredible help since then. Nobody has read more draft versions of my various reports, articles and thesis chapters, and I extremely grateful for all the constructive comments, and for his time and patience. Luke and Panthera, NY, also secured funding for the surveys on lions mentioned in this thesis, and I also want to thank Nicole Williams from Panthera for her help in organizing those surveys and in other issues. I am also grateful to Matt Hayward, for inviting me to present a talk at his symposium on large carnivore reintroduction at the SCB meeting in Port Elizabeth. The chapter 4 of this thesis based on this talk, and I want to thank Matt for all his comments on earlier drafts.

During the writing-up stages, I have received guidance, help and, sometimes even more important, distraction, from a large number of people. In Göttingen, I would like to thank my supervisor, Michael Mühlenberg, and Matthias Waltert, both from the Center for Nature Conservation (CNC) at Göttingen University. In Cologne and surroundings, I thank my parents and my sister with her lovely family, and all my friends there, and especially Wolfgang, who housed me all this time. In Stirling, I want to thank Kate for all her help, and Vicki and Michelle for looking after me. Thank You also to Fernanda, for her love and all her patience with me.

Finally, I'd like to thank a very close friend, with whom I share practically the same passions and interests. Thomas Breuer and I studied at university together, at a time where neither of us was quite so sure where to move and what exactly to do. Our first joint trip to Gabon was definitely an eye-opener and paved the way for this study as well. Our constant discussions about our work have always very positively influenced me and reassured me in what I've been doing over the last years.

This thesis is based on the following publications:

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HENSCHEL, P., Hunter, L. & Mühlenberg, M. (submitted) Leopards in the African rainforest: the impact of bushmeat hunting on population status as revealed by camera trapping.

HENSCHEL, P. (in press) The status and conservation of leopards and other large carnivores in the Congo Basin, and the potential role of reintroduction. Reintroduction of Top-Order Predators (eds M. W. Hayward & M. Somers). Blackwell Publishing, Oxford.

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Chapter 1: General introduction

Some notes the ecology of leopards and their role in the African rainforest

The leopard (*Panthera pardus*) has the greatest geographic distribution of the wild cats (Nowell and Jackson, 1996), and, in Africa, it is the most abundant large felid (Hunter et al., in press). This success appears to be rooted in its wide habitat tolerance, occupying hyper-arid areas and rainforests alike (Hunter *et al.*, in press), and its versatility as a generalist predator (Nowell and Jackson, 1996). Bailey (1993) noted a minimum of 92 prey species used by leopards in sub-Saharan Africa, and known prey ranges in size from arthropods (Fey, 1964) to adult male elands (Kingdon, 1977). Yet despite this apparent ability to successfully exploit prey spanning such an enormous size range, leopard diet is generally dominated by medium-sized ungulates (e.g. Bailey, 1993, Owen-Smith and Mills, 2008). Recent analysis of 33 studies on leopard feeding ecology revealed that leopards preferentially prey upon species within a weight range of 10–40 kg, even if prey outside this weight range is more abundant (Hayward et al., 2006a).

In areas where their preferred ungulate prey is scarce, however, leopards have been recorded to switch to smaller-bodied prey (Nowell and Jackson, 1996). In Comoé National Park in Ivory Coast for example, leopards were found to prey predominately on medium-sized (5-20 kg) to large (>20 kg) ungulates over a three-year period, but when populations of these taxa dwindled due to heavy poaching, leopard predation on large rodents and birds and reptiles increased significantly (Bodendorfer et al., 2006). What remains unknown, is how density and life history parameters of leopard populations are affected when they are constrained to prey on sub-optimal prey for prolonged periods. Predator species exceeding 21.5 kg, and particularly so canids and felids, tend to specialize on larger vertebrate prey near the predator mass (Carbone *et al.*, 1999), and it has been suggested that sub-optimal predation in large carnivores may be an early indicator for a population at risk of extinction (Hayward, in press).

In the Congo Basin rainforest, leopard feeding ecology has been studied in detail at four different field sites, where they showed a relatively broad diet, using a minimum number of 17-32 different prey species per site (Hart et al., 1996, Ososky, 1998, Ray and Sunquist, 2001, Henschel et al., 2005). Leopard diet was uniformly dominated by ungulate prey, occurring in 44.9-53.5 % of analyzed scats, followed by primates, large rodents,

pangolins and small carnivores (Hart et al., 1996, Ososky, 1998, Ray and Sunquist, 2001, Henschel et al., 2005). The mean prey weight, however, varied considerably among study sites, and the respective estimates were 7.3 kg (Ray and Sunquist, 2001), 17.0 kg (Ososky, 1998), 24.6 kg (Hart *et al.*, 1996) and 29.2 kg (Henschel *et al.*, 2005). At the sites with the highest recorded mean prey weights, red river hogs (*Potamochoerus porcus*) and medium-sized forest duikers (*Cephalophus spp.*) were the most important prey (Hart et al., 1996, Henschel et al., 2005), whereas at the two remaining sites the much smaller blue duiker (*Cephalophus monticola*) was the most frequently recorded prey item (Ososky, 1998, Ray and Sunquist, 2001). This heavy use of an ungulate species well below the preferred weight range might have been indicative of a depauperate base of medium-sized prey at these two sites, but this assumption could not be tested as data on prey abundances was not available for these sites (Ososky, 1998, Ray and Sunquist, 2001).

Leopard ranging and hunting behaviour in the African rainforest has so far received little scientific attention. While these aspects of leopard ecology are relatively well studied in different savannah ecosystems of southern and eastern Africa (e.g. Bothma and le Riche, 1989, Bailey, 1993, Bothma et al., 1997, Stander et al., 1997, Mizutani and Jewell, 1998), only three individuals have ever been radio-collared in the African forest biome (Jenny, 1996). Jenny (1996) placed radio collars on one male and two female leopards in the Taï National Park, Ivory Coast, and found that the home range was 86 km^2 for the male, and for the females 29 km^2 and 22 km^2, respectively. Leopards at this rainforest site were chiefly diurnal and crepuscular hunters, who followed the activity pattern of their prey (Jenny and Zuberbühler, 2005).

The leopard is the apex predator of the African rainforest, and the only other felid that occurs sympatrically with leopards in this habitat is the substantially smaller African golden cat (*Felis aurata*). As the sole large mammalian predator in the forest biome, leopards are likely to assume an important ecological role. According to Terborgh (1990), large felids might structure prey communities in the stable environments of tropical forests by reducing numbers of prey, especially for the highly productive prey species. Many of these species are important predators of seeds, seedlings and saplings, and by limiting their numbers, large felids might indirectly facilitate forest regeneration (Terborgh, 1988). At a rainforest site in Malaysia for example, densities of native wild pigs (*Sus scrofa*) are 10–100 times greater than historical levels due to the local extinction of feline predators, and the high-density pig population is a major source of sapling mortality, and is considered to cause

substantial shifts in tree community composition (Ickes et al., 2005). There have been anecdotal reports about very similar phenomena in southern Central Africa, where African bush pigs (*Potamochoerus larvatus*) have increased greatly in numbers following the destruction of leopards by people (Grzimek, 1975).

Current knowledge on status of leopards in the Congo Basin rainforest

The status of the leopard in Africa has been a matter of debate since 1973 when the species was first listed under CITES Appendix I, and several attempts have since then been made to determine the leopard's status (Nowell and Jackson, 1996). In the most recent attempt the sub-Saharan population was estimated at 714 000 (Martin and de Meulenaer, 1988), and although there was a general consensus among leopard authorities that this figure most likely represented an overestimate when it was published almost two decades ago (Jackson, 1989), it is still widely used as it represents the most practical and quantitative attempt to date to estimate potential leopard numbers across a large geographic area (Nowell and Jackson, 1996). The authors of the status survey developed a population model for the leopard, which they used in combination with a regression linking leopard densities with annual rainfall to predict numbers of leopard in the region (Martin and de Meulenaer, 1988).

While it is widely accepted that in savannas ungulate biomass is positively correlated with rainfall (Coe et al., 1976, East, 1984) and that in these open habitats leopard density is linked with prey biomass (Marker and Dickman, 2005, Hayward et al., 2007), it has to be understood that although ungulate biomass increases with rainfall it decreases with forest cover, as a high proportion of the primary productivity is in the canopy and only available to relatively small arboreal mammals (Robinson and Bennett, 2004). Yet it is rainforest habitat that was considered optimal leopard habitat by Martin & de Meulenaer in their 1988 status survey, who considered the forests of the Congo Basin an absolute stronghold for the species that would harbour and estimated 40 % of Africa's leopards, and predicted extremely high population densities for this habitat type of up to 40 individuals/100 km^2 (Martin and de Meulenaer, 1988). These population density estimates have since been used to produce population size estimates for central African countries, but the results were widely considered to be exaggerated (e.g. Jackson, 1989, Norton, 1990). Bailey (1993) and Jenny (1996) are among several authorities who have argued that since terrestrial mammalian prey biomass is lower in rainforest than in savannah environments, leopard densities should be

correspondingly lower. Perhaps most importantly, Martin and de Meulenaer's model failed to account adequately for reduction of wild prey as a factor lowering leopard density, which could lead to overestimates especially in the Congo Basin, where forest wildlife suffers from a high demand for wild game for both local and commercial use (Wilkie and Carpenter, 1999). However, the figures published by Martin and de Meulenaer (1988) are still quoted today, and remain the chief source of information for African governments proposing to open or raise harvest quotas for trophy hunting of leopards.

Why the concern for leopards in the Congo Basin rainforest

Today, the rainforests of the Congo Basin are witnessing what is widely referred to as the 'Bushmeat Crisis', a phenomenon which is generally characterized by unsustainable levels of hunting even in remote forest areas, driven by an ever-increasing demand for wild game, or bushmeat, in the growing urban centres of Central Africa (Wilkie and Carpenter, 1999, Robinson and Bennett, 2000). Recently, marked reductions in ungulate biomass have been documented even in more remote sites and those adjacent to protected areas, and hunting off-takes were unlikely to be sustainable for most of the larger species (Noss, 1998, Muchaal and Ngandjui, 1999, Fimbel et al., 2000). In north-eastern Gabon, comparisons between hunted and unhunted forest sites revealed a 43–100% decline for bushmeat species in hunted areas (Lahm, 2001).

Recent studies have shown that prey depletion can be more important than poaching or habitat loss in reducing populations of large cats (e.g. Karanth and Stith, 1999). That populations of forest felids may decline as a direct consequence of competition with humans hunting for subsistence has already been suggested for pumas and jaguars in the Neotropics (e.g. Jorgenson and Redford, 1993), and in Central Africa, leopards have disappeared from large tracts of otherwise intact rainforest, possibly under pressure from bushmeat harvests. For example, a large-scale survey covering 47 randomly selected forest patches in south-eastern Nigeria found evidence of leopards in only two of the surveyed sites (Angelici et al., 1998). Similarly in south-western Cameroon, hunters confirmed the local extinction of leopards in the area around Banyang-Mbo Wildlife Sanctuary in the mid 1970's (Willcox, 2002), and around Kilum-Ijim Forest in the early 1980's (Maisels et al., 2001). This border region between Nigeria and Cameroon is characterized by a relatively dense human population (>80 inhabitants/km^2), and comprehensive market surveys estimated that

>900,000 reptiles, birds and mammals, or around 12,000 tonnes of wild meat are sold annually in this region (Fa et al., 2006). Interestingly, using data from Kenya, Woodroffe (2000) established a critical human density of above 900 inhabitants/km^2 at which logistic regression predicted a 50% probability of leopard extinction. However, leopards across large parts of south-western Cameroun became extinct 20-30 years ago at human densities more than one order of magnitude lower (Maisels et al., 2001, Willcox, 2002). An obvious explanation for the difference might be that most rural people in Kenya rely on livestock whereas rural populations in Central Africa rely primarily on bushmeat to meet their protein requirements (Wilkie and Carpenter, 1999), and do consequently exclude leopards through intensified competition for prey. While human population density is generally low across most of the Congo Basin, the bushmeat trade is ubiquitous and results in tremendous volumes of wildlife extracted annually (e.g. Wilkie and Carpenter, 1999), and it appears logical that this unsustainable harvest has a marked effect on leopard populations.

The objectives of this study

Earlier attempts to use leopard data from savannah habitats for predictions on leopard population density and numbers in the African rainforest (Myers, 1976, Martin and de Meulenaer, 1988) have delivered unsatisfactory results (e.g. Norton, 1990), and failed to account adequately for reduction of wild prey as a factor (Bailey, 1993). Similarly, predictions about the critical human density leopards can sustain until threatened with local extinction, appear to possess little descriptive power if datasets originating from eastern Africa (Woodroffe, 2000) are applied to Central Africa (see above).

In the present study, I seek to establish how leopard populations respond to competition for prey with humans hunting for bushmeat, by comparing leopard diets and leopard population densities between hunted and protected rainforest sites in central Gabon. My two principal hypotheses are that (1) leopards exhibit a functional response at hunted sites and switch to smaller, less preferred prey where larger prey species have been depleted; (2) leopards exhibit a numerical response at hunted sites and occur at lower population densities where larger prey species have been depleted. To test this, I collected leopard scats and camera trap data in four rainforest sites in central Gabon exposed to varying levels of anthropogenic disturbance. Bushmeat hunting intensity is generally highest in the vicinity of settlements (Fimbel et al., 2000, Laurance et al., 2006b), and my four study sites were

therefore situated at varying distances from settlements. I reconstructed leopard diet by determining prey remains in the collected leopard scats (Putman, 1984), and estimated leopard population density by applying capture-recapture models to camera trap data (Karanth and Nichols, 2002). I employed camera trap-based abundance indices (O'Brien et al., 2003, Johnson et al., 2006) to assess the relative abundance of principal leopard prey species and the relative intensities of human hunting at the 4 study sites. Camera trap data was pooled from all sites to investigate the factors that determined leopard area use via occupancy modelling (MacKenzie et al., 2002). The occupancy modelling results were then applied in a larger-scale geographic leopard population model, which I used to predict leopard landscape use across Gabon and neighbouring countries. The model predictions on leopard occurrence in individual protected areas in this region are compared to available information on leopard presence/absence at the respective sites. Recommendations are made regarding areas with high priority for leopard conservation in this region, and strategies for conservation are discussed.

As aforementioned, leopards are the apex predator of the African rainforest, and the only large mammalian carnivore occupying this habitat. It is less widely known that, historically, also lions (*Panthera leo*), African wild dog (*Lycaon pictus*) and spotted hyenas (*Crocuta crocuta*) occurred within the Congo Basin, in an extensive forest–savannah mosaic which is today geographically isolated. Parallel to my work on leopards, I collected any available anecdotal information in the status of the large savannah carnivores in this forest–savannah mosaic, and I was also able to carry out a number of field surveys in this region. Additional information will be presented in this thesis on the current status of the large savannah carnivores in Gabon and neighbouring Republic of Congo.

The structure of this thesis

In chapter 2, I investigate how competition with humans hunting for bushmeat impacts leopard feeding ecology in Congo Basin rainforest. I employ scat analysis to study leopard feeding ecology at four rainforest sites in central Gabon, which differed in the intensity of hunting they received.

In chapter 3, I investigate how bushmeat hunting impacts leopard population densities in Congo Basin rainforest. I use camera trap data to estimate leopard population

density and area use, and the abundance of principal leopard prey species at four rainforest sites in central Gabon, which differed in the intensity of hunting they received.

In chapter 4, I elaborate how the data on leopard area use presented in chapter 3 were employed to construct a simple geographic leopard population model, and the results of this model are presented. This chapter also contains information on the current known status of the larger savannah carnivores in the Congo Basin, and presents recommendations for the conservation of the large carnivores in this region.

Following chapter 4, I present a small set of conclusions drawn from this work.

Chapter 2: Leopard prey choice in the Congo Basin rainforest and competition with hunters

Abstract

The leopard (*Panthera pardus*) has the greatest geographic distribution of the wild cats, and is the most abundant large felid in Africa. The species owes its success to its wide habitat tolerance, and its versatility as a generalist predator. Known leopard prey ranges in size from arthropods to the largest ungulates, but recent studies suggest that leopards preferentially prey upon species within a weight range of 10-40 kg. In the Congo Basin rainforests, species within this weight range are targeted by bushmeat hunters, and current rates of exploitation are widely regarded as unsustainable. In this study we investigate how leopard populations respond to competition for prey with hunters. Our hypothesis is that leopards will exhibit a functional response at hunted sites, and switch to smaller prey where larger species have been depleted. To test this, we employed scat analysis to study leopard feeding ecology at four rainforest sites in central Gabon, which differed in the intensity of hunting they received. Hunting intensity is generally highest in the vicinity of settlements, and our four study sites were therefore situated at varying distances from settlements.

No leopard scats were found at the study site nearest to a settlement, but 32-83 scats were collected and analyzed from the remaining sites. Mean leopard prey weight ranged from 19.8 to 31.6 kg, and increased with the site's distance from settlements, as did the proportion of large prey (>20 kg) in leopard diet (range: 20.3-39.2%), and the biomass contribution of ungulate prey (range: 67.2-90.6%). At hunted sites, leopards showed higher use of rodents and smaller primates, as the proportion of ungulates in their diet decreased. Our results demonstrate that leopards exhibit a strong functional response to competition with hunters for prey, and the implications of this finding are discussed.

9

Introduction

The leopard (*Panthera pardus*) has the greatest geographic distribution of the wild cats (Nowell and Jackson, 1996), and, in Africa, it is the most abundant large felid (Hunter et al., in press). This success appears to be rooted in its wide habitat tolerance, occupying hyper-arid areas and rainforests alike (Hunter *et al.*, in press), and its versatility as a generalist predator (Nowell and Jackson, 1996). Bailey (1993) noted at least 92 prey species used by leopards in sub-Saharan Africa, and known prey ranges in size from the much-cited dung beetle (Fey, 1964) to adult male elands (Kingdon, 1977). Yet despite this apparent ability to successfully exploit prey spanning such an enormous size range, leopard diet is generally dominated by medium-sized ungulates (e.g. Bailey, 1993, Owen-Smith and Mills, 2008). Recent analysis of 33 studies on leopard feeding ecology revealed that leopards preferentially prey upon species within a weight range of 10–40 kg, even if prey outside this weight range is more abundant (Hayward et al., 2006a). The optimum prey weight for leopards derived from this analysis is 23 kg, based on body mass estimates of significantly preferred prey species (Hayward et al., 2006a). In the Serengeti, each species of larger carnivore, including the leopard, uses prey outside their preferred size range, but is inefficient at catching such prey (Sinclair et al., 2003). Leopards have best returns for time spent hunting for medium-sized prey, rather than smaller or excessively large species (Bailey, 1993). In areas where their preferred ungulate prey is scarce, however, leopards have been recorded to switch to smaller-bodied prey (Nowell and Jackson, 1996). In Comoé National Park in Ivory Coast for example, leopards were found to prey predominately on medium-sized (5-20 kg) to large (>20 kg) ungulates over a three-year period, but when populations of these taxa dwindled due to heavy poaching, leopard predation on large rodents and birds and reptiles increased significantly (Bodendorfer et al., 2006). What remains unknown, is how density and life history parameters of leopard populations are affected when they are constrained to prey on sub-optimal prey for prolonged periods. Predator species exceeding 21.5 kg, and particularly so canids and felids, tend to specialize on larger vertebrate prey near the predator mass (Carbone *et al.*, 1999), and it has been suggested that sub-optimal predation in large carnivores may be an early indicator for a population at risk of extinction (Hayward, in press).

In the Congo Basin rainforest leopards are the apex predator, and their feeding ecology has been studied in detail at four different field sites, where they showed a relatively broad diet, using a minimum number of 17-32 different prey species per site (Hart et al.,

1996, Ososky, 1998, Ray and Sunquist, 2001, Henschel et al., 2005). Leopard diet was uniformly dominated by ungulate prey, occurring in 44.9-53.5 % of analyzed scats, followed by primates, large rodents, pangolins and small carnivores (Hart et al., 1996, Ososky, 1998, Ray and Sunquist, 2001, Henschel et al., 2005). The mean prey weight, however, varied considerably among study sites, and the respective estimates were 7.3 kg (Ray and Sunquist, 2001), 17.0 kg (Ososky, 1998), 24.6 kg (Hart *et al.*, 1996) and 29.2 kg (Henschel *et al.*, 2005). At the sites with the highest recorded mean prey weights, red river hogs (*Potamochoerus porcus*) and medium-sized forest duikers (*Cephalophus spp.*) were the most important prey (Hart et al., 1996, Henschel et al., 2005), whereas at the two remaining sites the much smaller blue duiker (*Cephalophus monticola*) was the most frequently recorded prey item (Ososky, 1998, Ray and Sunquist, 2001). This heavy use of an ungulate species well below the preferred weight range might have been indicative of a depauperate base of medium-sized prey at these two sites, but this assumption could not be tested as data on prey abundances was not available for these sites (Ososky, 1998, Ray and Sunquist, 2001).

However, anecdotal evidence suggests that leopard populations in the Congo Basin rainforest might be negatively affected by the depletion of their prey base, through intensifying competition with humans hunting for bushmeat (Hart et al., 1996, Ray, 2001). Similar mechanisms had been previously described in the Neotropics, where populations of big cats show a high degree of dietary overlap with human hunters, and are expected to decline in numbers where they are sympatric with humans hunting for subsistence (Jorgenson and Redford, 1993). The potential for such competition is enormous in the Congo Basin rainforest, as the rural population in this region relies primarily on bushmeat to meet their protein requirements (Wilkie and Carpenter, 1999, Robinson and Bennett, 2000). Conservative estimates indicate that above one million metric tons of wild meat are traded annually in the Congo Basin (Wilkie and Carpenter, 1999). The hunters in this trade appear to target the larger-bodies species where possible (Willcox, 2002, Fa et al., 2005), and the extraction rates were considered to be unsustainable especially for these larger (>5 kg) species in the majority of studies on bushmeat exploitation (e.g. Noss, 1998, Muchaal and Ngandjui, 1999, Fimbel et al., 2000). The result is generally a sharp decline in numbers of medium-sized and large ungulates and larger primates in the vicinity of settlements, where hunting is most intense (Fimbel et al., 2000, Laurance et al., 2006b). As a consequence, rodents gain in importance in urban markets, most likely because ungulate species have been depleted in nearby forests (Fa et al., 1995), and the ratio of ungulates to rodents found in

bushmeat markets has been suggested as a rough index of bushmeat over-exploitation (Wilkie and Carpenter, 1999).

In the present study we seek to establish how leopard feeding ecology changes in response to the intensifying competition for prey with humans hunting for bushmeat. Our principal hypothesis is that leopards will exhibit a functional response to competition with human hunters (Solomon, 1949), and switch to smaller, less preferred prey where larger species have been deleted by bushmeat hunting. To test this hypothesis, we determined leopard feeding habits at four rainforest sites inside and adjacent to Ivindo National Park (NP), by means of scat analysis (e.g. Putman, 1984). Hunting intensity varied across sites owing to their differing protection status and accessibility, and data on the relative abundance of medium-sized and large prey was readily available for all sites from a camera trapping study (see chapter 3). We compared the results on leopard prey choice to hunter return data collected at the same site (Coad, 2007), or at sites with comparable degrees of anthropogenic disturbance (Muchaal and Ngandjui, 1999, Fa et al., 1995), to investigate dietary similarities and niche overlap between leopards and human hunters.

Methods

Study Areas

The four study sites were located within the same block of contiguous rainforest in central Gabon that contains both Ivindo NP and Lopé NP (Figure 2.1). The human population density in this central part of Gabon is particularly low with 1.5-2.0 inhabitants/km^2 (WNN, 2006), and 95-97% of the region is still covered in forest. The forest in central Gabon has been characterized as mature lowland semi-evergreen rainforest, and the terrain in the region is undulating with elevations ranging between 100 and 1000 meters (White and Abernethy, 1997, Vande weghe, 2006). The climate is equatorial, with two rainy seasons and two seasons that are predominantly dry, and annual precipitation varies between 1300 and 2000 mm (Vande weghe, 2006). The temperature is relatively stable throughout the year, with a monthly minimum of 21.7°C in July and a monthly maximum of 25°C in April (Vande weghe, 2006). The mammalian fauna of the region has been particularly well-studied in the northern part of Lopé NP (e.g. White, 1994), and 45 species of medium-sized and large mammals have been identified in this area, among which fourteen were primates, twelve were ungulates, and eleven were carnivores (Tutin et al., 1997). The mammalian

fauna is less well-studied in Ivindo NP, but species composition for medium-sized and large mammals appears almost identical to Lopé (Vande weghe, 2006), with the only known exceptions that both mandrills (*Mandrillus sphinx*) and sun-tailed guenons (*Cercopithecus solatus*) only occur in Lopé NP, and reach the eastern limit of their respective distributions just east of this park (Brugière and Gautier, 1999, Abernethy et al., 2002).
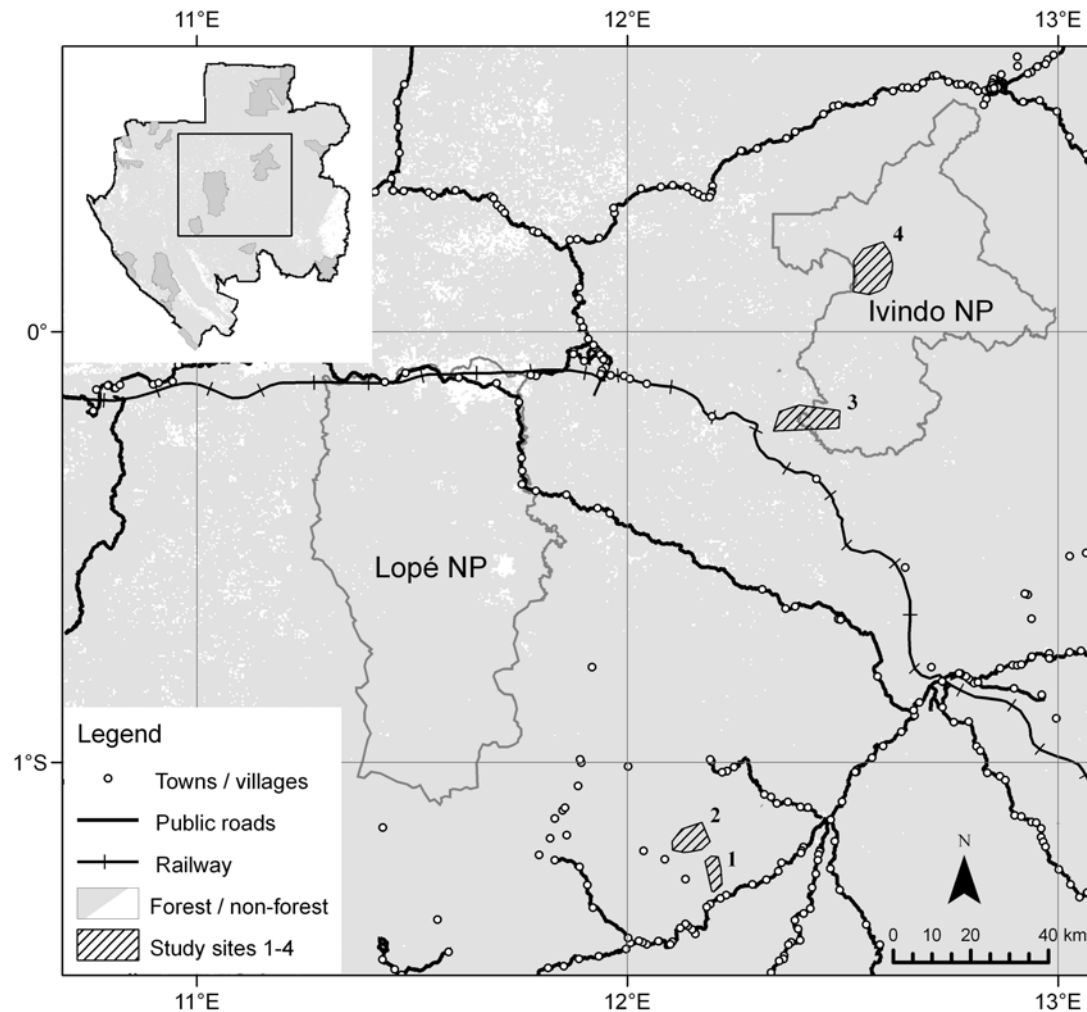
Figure 2.1. Location of the four study sites in central Gabon relative to villages, public roads, railway tracks and protected areas

Both, Ivindo and Lopé were officially declared national parks in late 2002, but had in part been exploited for tropical timber before this legal protection. The forest outside the two national parks is to a large part managed by timber companies, and logging is the only form of habitat conversion occurring in this region, apart from small-scale slash-and-burn agriculture in the direct vicinity (<3 km radius) of settlements. In Gabon, clear-cutting is the exception, and commercial logging is predominantly a low-intensity, selective exploitation of a few timber species, which causes about 10 percent canopy loss on average (Wilks, 1990,

White, 1992). Studies on the mammal community in Lopé prior to and after logging suggest that there is no simple relationship between logging history and mammalian biomass for most species (White, 1992, White and Tutin, 2001), and therefore we selected our four study areas based chiefly on the anticipated intensity of hunting at each site, and irrespective of the logging history of the area. Prior studies have shown that hunting intensity is highest in the direct vicinity of settlements (Fimbel et al., 2000, Laurance et al., 2006b), and the distance to the nearest road or railway station is also a key factor, because they represent points of market access which facilitate the commercialisation of local bushmeat hunting (e.g. Wilkie and Carpenter, 1999). Access to such transportation has been shown to be a crucial step in driving unsustainable levels of hunting (Wilkie and Carpenter, 1999). The study sites were therefore chosen based on their distance from the nearest settlement and point of market access. Two sites were at least partly inside Ivindo NP, and the remaining two sites were located about 100 km to the south between both parks, close to a public road linking two provincial capitals (Figure 2.1). Details on all four study sites are provided in Table 2.1.

Table 2.1. Characteristics of each study area, describing the study period, the predominant form of land-use, the legal status of hunting in the area, and distance from the nearest settlement and point of market access.

Study site	Study period	Land-use type / legal status of hunting	Distance from settlement (km)	Distance from road/railway (km)
1	9-10/2004	Village hunting territory / permitted	2-12	2-12
2	4-5/2005	Inactive logging concession / tolerated	3-14	14-21
3	8-10/2003	National park / prohibited	13-20	13-20
4	5-6/2004	National park / prohibited	19-29	49-63

Determination of leopard diet at the study sites

Leopard feeding habits were reconstructed through the analysis of leopard scats (Putman, 1984). The leopard is the only large mammalian carnivore in the African rainforest, and leopard scats can be readily distinguished from faeces deposited by other species occurring in the region, based on their size, shape, odor and adjacent field sign (Stuart and Stuart, 2003). Scats of African golden cats (*Felis aurata*) can be similar in appearance but are substantially smaller, and were distinguished from leopard scats based on their diameter, using 21 mm maximum width as a cut-off point (Hart et al., 1996, Ray and Sunquist, 2001).

At each study site fieldwork lasted 2-3 months (Table 2.1). During this period leopard scats were collected along prominent game trails and abandoned logging roads, which were regularly patrolled to inspect remote camera traps, distributed at these sites to determine leopard population density and prey abundance (see chapter 3). For every collected scat we recorded the GPS position, the date of collection, and the maximum diameter of the scat. Scats were then air-dried and stored in air-tight plastic bags until further examination. The examination of scat content followed the protocol by Henschel et al. (2005). Scats were carefully rinsed over a 1 mm sieve, and prey remains such as hair, quills, finger nails and hooves, bone fragments and teeth were retained and air-dried. Scat content was compared to a reference collection of African rainforest taxa at the Station d'Etudes des Gorilles et Chimpanzés (SEGC) in Lopé NP (Henschel et al., 2005). Prey hair from scats was examined macroscopically, using criteria like coloration, shape and thickness to discriminate between prey species, or microscopically, following methods described by Perrin and Campbell (1980) and Clement et al. (1980), if macroscopic examination did not permit species identification. Bone fragments, teeth, finger nails and hooves found in scats were used to support the results from hair analysis.

Individual large carnivore scats often contain remains of multiple prey species (Karanth and Sunquist, 1995, Henschel et al., 2005). As the quantity of meat consumed of a given species will decrease when the number of prey species represented in one scat increases, it has to be taken into account how many different prey items were found in one scat. A corrected frequency of occurrence was obtained by counting each prey items as 1/2, if two prey items occurred in one scat, as 1/3, if three species occurred, and so forth (Karanth & Sunquist, 1995). When prey sizes are highly variable in the diet of a predator, the importance of smaller prey species for predator this can be considerably overestimated using scat analysis, if only the frequency of occurrence of prey species in the scat samples is considered (Ackerman et al., 1984). We therefore used a correction factor developed for mountain lions (*Puma concolor*) (Ackerman et al., 1984), to convert our frequency of occurrence estimates to the relative biomass consumed by leopards, assuming that the digestive system of the two felids is comparable. Ackerman et al. (1984) conducted feeding trials and found a linear relationship between ingested biomass per deposited scat (Y), and the live weight of the prey species (X). The resulting linear relationship,

$$Y = 1.98 + 0.035X,$$

can be applied in the form of a correction factor, to convert frequency of occurrence to relative biomass consumed (Ackerman et al., 1984). This correction factor is not applied for small prey species with <2 kg body weight, because each occurrence is assumed to represent a whole individual (Ackerman et al., 1984). All live weights for prey species were taken from White (1994). Our taxonomy follows (Kingdon, 1997).

Analysis of dietary composition and cross-site comparison

To determine if the composition of leopard diet was significantly different between study sites, we compared the corrected frequencies of occurrence across sites using Fisher's exact test. Dietary niche breadth for leopards was calculated separately for each study site using the niche breadth (B) index (Levins, 1968). The actual niche breadth, B, was calculated as:

$$B = 1 / \Sigma p_i^2,$$

where p_i is the proportion of prey taxon i in the predator's diet, based on percent frequency of occurrence (Levins, 1968). B ranges from 1, to the number of prey species used, and we calculated a standardized dietary niche breadth, B_{sta} (Colwell and Futuyma, 1971) to permit comparisons between sites where different numbers of prey species were present. The standardized dietary niche breadth was calculated as:

$$B_{sta} = (B_{obs} - B_{min}) / (B_{max} - B_{min}),$$

where B_{obs} is the observed dietary niche breadth (B), B_{min} is the minimum dietary niche breadth (= 1), and B_{max} is the maximum dietary niche breadth (number of prey species used) (Colwell and Futuyma, 1971). B_{sta} ranges between 0 and 1, where a B_{sta} of 1 means that all prey species used by a predator are taken at equal proportions, while a value approximating 0 signifies that a few species were taken at disproportionately higher frequencies than the remainder. We also calculated the dietary niche breadth for human hunters using study site 1. Hunter return data was collected at this site at the time of our study, and a sample of 1242 hunter kills was available, 1119 of which were mammals (Coad, 2007). No hunter return data was available for our remaining study sites.

We calculated the dietary niche overlap between leopard populations at our respective study sites, and between the leopard populations and humans hunting for bushmeat at study site 1 (Coad, 2007), and at four additional rainforest sites from the

literature, which exhibited degrees of anthropogenic disturbance comparable to our sites (Fa et al., 1995, Muchaal and Ngandjui, 1999). The dataset collected by Fa et al. (1995) represents market data from a site in Rio Muni, Equatorial Guinea, with easy road access and commercial hunting, comparable to our site 1 (Table 2.1). Muchaal and Ngandjui (1999) collected hunter follow data at three zones within the Dja Reserve, Cameroon, which were situated at 0-10, 10-30 and 30-40 km from a relatively remote village, and their zones are similar in spacing to our sites 2-4 respectively. Dietary niche overlap was calculated using Pianka's (1973) index, according to the formula:

$$\text{Niche overlap} = (\Sigma \; P_{ia} \times P_{ib}) \times [(\Sigma \; P_{ia}^{2}) \times (\Sigma \; P_{ib}^{2})]^{-1/2},$$

where P_{ia} was the relative proportion of prey type i in the diet of carnivore species a, and P_{ib} the relative proportion in the diet of carnivore species b. Pianka's (1973) index of dietary niche overlap varies from 0 (exclusive food niches) to 1 (complete dietary overlap).

Results

Leopard diet at the study sites

No leopard scats were found at site 1, and 32-83 scats were found at the remaining three study sites, containing 39-93 different prey items (Table 2.2). The number of scats collected per site increased with distance from settlements (cf. Tables 2.1 and 2.2). Across sites, 99.1% of prey items in scats could be identified to genus level, and only the medium-sized duikers could not be identified to species level. Hair of the Peter's duiker (*C. callipygus*), Ogilby's duiker (*C. ogilby*) and bay duiker (*C. dorsalis*) could not be differentiated based on either macroscopic differences in hair structure, or microscopic differences in cuticular scale patterns (e.g. Perrin and Campbell, 1980), and these species were therefore grouped as 'red' duikers (*Cephalophus spp.*). The hair of chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) is very similar in its macroscopic appearance, but could be distinguished microscopically based on its medullary configuration (Clement et al., 1980). A minimum of 8-18 prey taxa were identified at sites 2-4, and at these sites leopards exclusively used mammalian prey. At the three sites where scats were found, 'red' duikers were the most frequently used prey taxon, followed by brush-tailed porcupine (*Atherurus africanus*) at site 2, and red river hog at sites 3 and 4 (Table 2.2). In terms of the relative biomass consumed, 'red' duikers were the single most important prey taxon at sites 2 and 3,

whereas at site 4 red river hogs were more important, accounting for almost 50% of the biomass consumed (Table 2.3).

Table 2.2 Composition of leopard diet in three of the four study sites in central Gabon; no leopard scats were found in site 1.

Scientific name	Common name	Corrected frequency of occurrence[a]		
		Site 2 (n=32)[b]	Site 3 (n=65)[c]	Site 4 (n=83)[d]
Ungulates				
Neotragus batesi	Bates' pygmy antelope	-	-	1.2
Cephalophus monticola	Blue duiker	3.1	3.8	-
Hyemoschus aquaticus	Water chevrotain	-	0.8	-
Cephalophus spp.	'Red' duikers	34.4	36.9	49.4
Cephalophus silvicultor	Yellow-backed duiker	-	4.6	-
Tragelaphus spekii	Sitatunga	-	1.5	-
Potamocherus porcus	Red river hog	20.3	16.2	36.7
Syncerus c. nanus	Forest buffalo	-	0.8	-
Primates				
Cercopithecus nictitans	Putty-nosed guenon	-	10.0	1.8
Cercopithecus cephus	Moustached guenon	-	2.3	2.4
Lophocebus albigena	Grey-cheeked mangabey	-	1.5	0.6
Colobus satanus	Black colobus	4.7	-	-
Mandrillus sphinx[e]	Mandrill	6.3	-	-
Pan t. troglodytes	Central African chimpanzee	-	3.1	2.4
Gorilla g. gorilla	Western lowland gorilla	-	5.4	-
Rodents				
Atherurus africanus	Brush-tailed porcupine	23.4	6.9	1.8
Unknown small rodent	Unknown small rodent	1.6	0.5	-
Carnivores				
Genetta servalina	Servaline genet	-	1.3	1.2
Atilax paludinosus	Marsh mongoose	6.3	-	0.6
Pangolins				
Uromanis tetradactyla	Long-tailed pangolin	-	0.8	0.6
Phataginus tricuspis	African tree pangolin	-	3.6	1.2

[a] Corrected for the occurrence of multiple prey items (see text).

[b] 32 scats, containing 39 prey items (1.22 items per scat).

[c] 65 scats, containing 81 prey items (1.25 items per scat).

[d] 83 scats, containing 93 prey items (1.12 items per scat).

[e] Mandrills do not occur at sites 3 and 4 (see text).

Table 2.3. Estimates of the of relative biomass consumed by leopards at three of four study sites in central Gabon; no leopard scats were found at site 1.

Species	Body weight (kg)[a]	Correction factor (kg/scat)[b]	Relative biomass consumed (%)		
			Site 2 (n=32)	Site 3 (n=65)	Site 4 (n=83)
Ungulates					
Neotragus batesi	3.8	2.11	-	-	0.8
Cephalophus monticola	3.9	2.12	2.5	2.8	-
Hyemoschus aquaticus	10.4	2.34	-	0.6	-
'Red' duikers	15.5	2.52	32.8	32.2	40.4
Cephalophus silvicultor	56.7	3.96	-	6.3	-
Tragelaphus spekii	62.8	4.18	-	2.2	-
Potamocherus porcus	61.9	4.15	31.9	23.2	49.4
Syncerus caffer nanus	118.8	6.14	-	1.6	-
Total ungulates			**67.2**	**68.9**	**90.6**
Primates					
Cercopithecus nictitans	3.2	2.09	-	7.2	1.2
Cercopithecus cephus	2	2.05	-	1.6	1.6
Lophocebus albigena	4.1	2.12	-	1.1	0.4
Colobus satanus	8.4	2.27	4.0	-	-
Mandrillus sphinx[c]	10.2	2.34	5.5	-	-
Pan t. troglodytes	38.7	3.33	-	3.6	2.6
Gorilla g. gorilla	78.1	4.71	-	8.8	-
Total primates			**9.6**	**22.3**	**5.8**
Rodents					
Atherurus africanus	2.3	2.06	18.3	4.9	1.2
Unknown small rodent	0.1	0.1[d]	0.1	0.1	-
Total rodents			**18.3**	**5.0**	**1.2**
Carnivores					
Genetta servalina	1.6	2.05	-	0.9	0.8
Atilax paludinosus	3	2.09	4.9	-	0.4
Total carnivores			**4.9**	**0.9**	**1.2**
Pangolins					
Uromanis tetradactyla	2.3	2.06	-	0.6	0.4
Phataginus tricuspis	1.9	1.9[d]	-	2.4	0.7
Total pangolins			**0.0**	**2.9**	**1.1**

[a] Estimated mean live weight (kg) from White (1994).

[b] Correction factor calculated following Ackerman et al. (1984) (see text).

[c] Mandrills do not occur at site 3 and 4 (see text).

[d] No correction factor (see text).

At the three sites ungulates made up the bulk of the biomass consumed, contributing 67.2-90.6% to the overall biomass consumed (Table 2.3). At site 2 rodents were the second most important prey group, accounting for 18.3% of the biomass consumed at this site, while at sites 3 and 4 rodents only accounted for a small proportion of the biomass consumed, with 5.0 and 1.2%, respectively (Table 2.3). At the latter two sites primates were more heavily used, contributing 22.3% of biomass consumed at site 3, and 5.8% at site 4 (Table 2.3).

Dietary comparison across sites

The frequency of occurrence of prey items differed significantly between sites (Fisher's exact test, $P < 0.0001$, Table 2.2). When we divided prey taxa into small prey (<5 kg), medium-sized prey (>5 kg, <20 kg) and large prey (>20 kg), use of medium-sized prey did not differ significantly between sites (Fisher's exact test, $P = 0.766$), whereas for small prey (Fisher's exact test, $P = 0.002$) and large prey (Fisher's exact test, $P = 0.01$) there were significant differences. Leopard use of small prey increased at sites in proximity to settlements, whereas the use of large prey decreased at these sites, and was highest at the remotest site 4 (Figure 2.2a). Hunter return data from site 1 showed that hunter catch almost exclusively consisted of small-bodied prey (Coad, 2007) (Figure 2.2a). Similar patterns applied to the hunter return data from Rio Muni and Dja Reserve (Fa et al., 1995, Muchaal and Ngandjui, 1999), where hunter use of small-bodied prey showed a similar increase at the sites more proximal to settlements (Figure 2.2b). In these studies, however, large prey > 20 kg was rarely recorded, and hunters mainly used medium-sized prey, even in the most remote zone 3 in Dja Reserve (Figure 2.2b). Grouping prey species according to taxonomic origin, showed that ungulates dominate both leopard and hunter catch in the remotest sites, whereas primates and particularly rodents gain in importance at the sites in proximity to settlements (Figure 2.3a,b).

Amongst our four study sites in central Gabon, the highest mean prey weight was recorded at site 4 with 31.6 kg, and mean prey weight decreased in the proximity to settlements (Coad, 2007) (Table 2.4). For leopards, the standardized dietary niche breadth (B_{sta}) was smallest at the most remote site 4, and increased at the sites more proximal to settlements (Table 2.4). The standardized dietary niche breadth for hunters at site 1 (Coad, 2007) was intermediate compared to the estimates for leopard niche breadth (Table 2.4).

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Table 2.4. Number of mammalian prey species, mean weight of mammalian prey, dietary niche breadth (B) and standardized dietary niche breadth (B_{sta}) for leopards** and hunters* in four study sites in central Gabon. Data sources: Sites 1, Coad (2007); Sites 2-4, this study.

	Site 1*	Site 2**	Site 3**	Site 4**
Number of mammalian prey taxa	22	8	12	18
Mean weight of mammalian prey (kg)	5.0	19.8	26.5	31.6
B[a]	5.88	4.43	5.34	2.62
B_{sta}[b]	0.29	0.49	0.27	0.15

[a] Dietary niche breadth (Levins, 1968).

[b] Standardized dietary niche breadth (Colwell & Futuyuma, 1971).
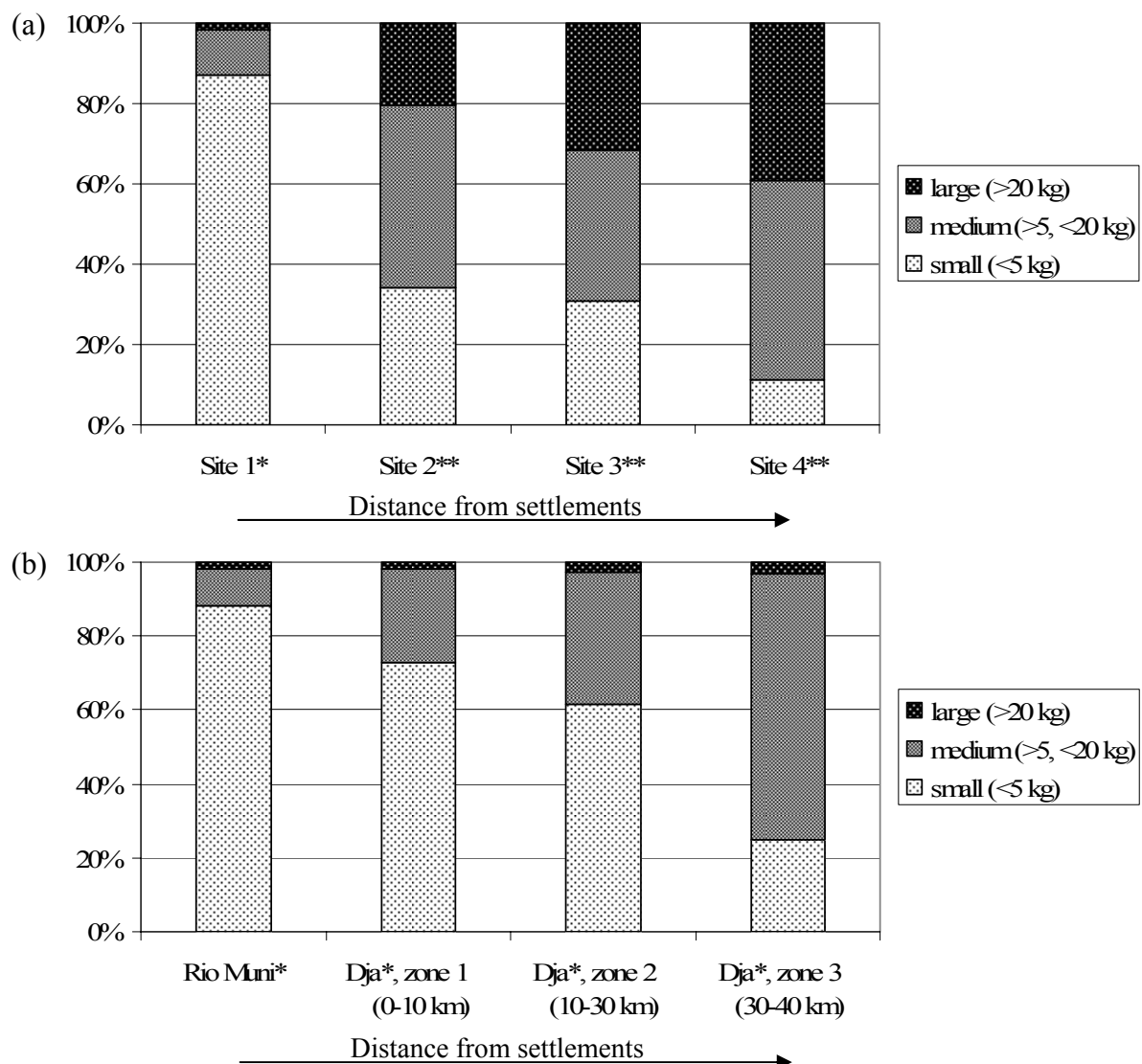
Figure 2.2. Representation of different prey size classes in leopard diet** and hunter return* data at four study sites in central Gabon (a), and in hunter return* data from Rio Muni, Equatorial Guinea, and Dja Reserve, Cameroon (b). Data sources: Sites 1, Coad (2007); Sites 2-4, this study; Rio Muni, Fa et al. (1995); Dja, Muchaal and Ngandjui (1999).

The dietary niche overlap was highest between pairs of sites with similar degrees of remoteness, and this pattern was valid irrespective of predator species (Table 2.5). Leopards at our most remote site 4 for example showed higher niche overlap with leopards at site 3 than at the less remote site 2. When compared to humans, leopards at site 4 had the highest overlap with hunters at Muchaal and Ngadjui's (1999) most remote zone 3, and the lowest overlap with the hunters operating at site 1 and in Rio Muni, in close proximity to settlements (Table 2.5).
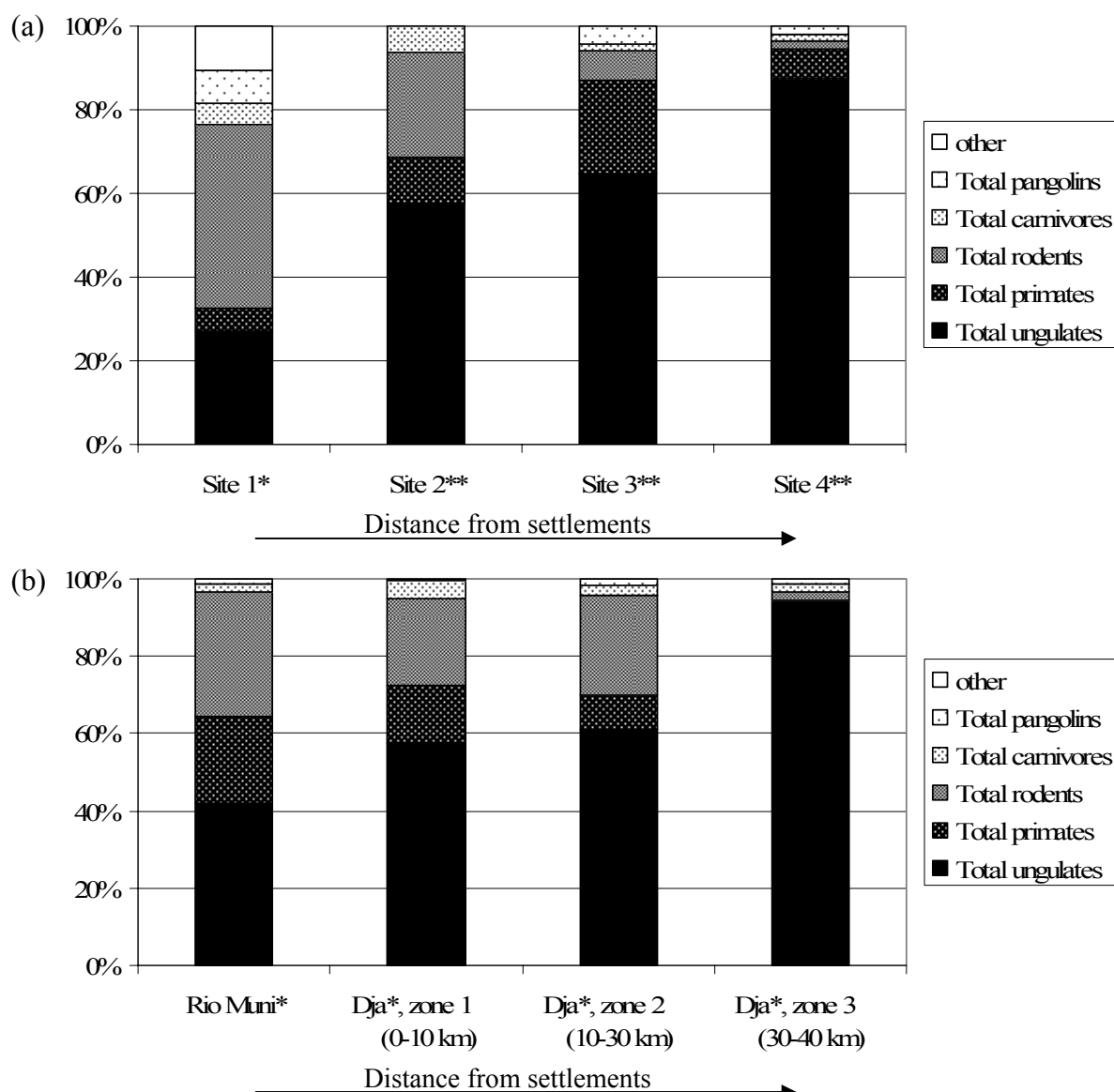

Figure 2.3. Representation of different prey taxa in leopard diet** and hunter return* data at four study sites in central Gabon (a), and in hunter return* data from Rio Muni, Equatorial Guinea, and Dja Reserve, Cameroon (b). Data sources: Sites 1, Coad (2007); Sites 2-4, this study; Rio Muni, Fa et al. (1995); Dja, Muchaal and Ngandjui (1999).

Table 2.5. Food niche overlap between leopards** and hunters* at eight rainforest sites in the Congo Basin. Data sources: Sites 1, Coad (2007); Sites 2-4, this study; Rio Muni, Fa et al. (1995); Dja, Muchaal and Ngandjui (1999).

Study site (n)	Site 1*	Site 2**	Site 3**	Site 4**	Rio Muni*	Dja*, zone 1	Dja*, zone 2	Dja*, zone 3
Site 1* (1242)	X							
Site 2** (32)	0.64	X						
Site 3** (65)	0.42	0.88	X					
Site 4** (83)	0.25	0.86	0.92	X				
Rio Muni* (6440)	0.83	0.51	0.42	0.21	X			
Dja*, zone 1 (189)	0.74	0.65	0.63	0.46	0.91	X		
Dja*, zone 2 (120)	0.78	0.81	0.75	0.61	0.81	0.94	X	
Dja*, zone 3 (89)	0.35	0.75	0.84	0.80	0.35	0.68	0.82	X

Discussion

Leopard response to competition with hunters

In accordance with our hypothesis, leopards exhibited a strong functional response to competition with hunters in the vicinity of settlements, where they showed a significantly higher use of small-bodied prey than at our most remote site 4. In earlier studies on leopard feeding ecology in the African rainforest, it had been suggested that leopards might show higher use of smaller-bodied prey at certain sites due to the high abundance and/or profitability of this prey at the site (Ray and Sunquist, 2001). While this possibility cannot be ruled out for certain, camera trap data from our four study sites strongly suggests that leopards switched to smaller prey at sites in proximity to settlements because the abundance of large (>20 kg) prey was significantly lower at these sites (see chapter 3, Table 3.5). The camera trap data also appeared to confirm that leopards did not appear to occur at site 1, as no leopard photograph was obtained at this site during two months of camera trapping (see chapter 3). While the absence of a species can never be fully established, it appears highly unlikely that resident leopards occurred at this site at the time of the study, considering that no sign of their presence was detected despite the high survey effort with two months of intense fieldwork (Henschel and Ray, 2003). At the remaining study sites, leopard population densities were estimated at 2.7-12.1 leopards/100 km^2, and density increased with distance from settlements (see chapter 3, Table 3.4). These camera trap results suggest that besides the observed functional response in diet, leopards also exhibit a marked numerical response to the competition with human hunters (see chapter 3).

Dietary niche overlap between leopards and hunters

Interestingly, human hunters in the Dja Reserve, Cameroon, exhibit a very similar functional response at sites in proximity to settlements, where they showed a steep increase in the use of small-bodied prey (Figure 2.2b). Particularly rodents and primates were captured at significantly higher frequencies closer to settlements (Figure 2.3b), and density estimations for prey species revealed that this was a direct response to the lowered availability of medium-sized ungulates at these sites (Muchaal and Ngandjui, 1999), rather than a response to increased abundance of the smaller prey. This trend to target small-bodied prey and particularly rodents near settlements is even more pronounced at site 1, and at the study site in Rio Muni (Figures 2.2 and 2.3), where bushmeat hunting occurred at a commercial scale. While no data on the abundance of prey was available for the Rio Muni site, camera trap data from site 1 revealed that medium-sized and large prey was extremely scarce at this site (see chapter 3, Table 3.5). Considering that both hunters, leopards and humans, show a very similar reaction to the depletion of larger-bodied prey, it is not surprising that dietary niche overlap between the two species was high at sites with comparable degrees of remoteness (Table 2.5). Logically, leopards at the very remote site 4 show a very low dietary niche overlap with hunters using the commercially hunted site 1, as several prey species used by leopards at site 4 were no longer recorded at site 1 (see chapter 3, Table 3.5). But when both species have access to a prey base comparable in species composition and abundance, as appears to be the case at the remoter sites 3 and 4 (this study) and Zone 3 in Dja (Muchaal and Ngandjui, 1999), and at site 2 (this study) and Zone 2 in Dja (Muchaal and Ngandjui, 1999), the dietary niche overlap between leopards and hunters can be very high. Unfortunately, there are no datasets on simultaneous prey use by leopards and human hunters from the same site, but as both species exhibit similar prey choice and the same functional response to depletion of larger-bodied prey, dietary niche overlap and thus competition for prey must certainly be high where both species are sympatric.

The extremely narrow standardized niche breath for leopards at the remote site 4 (Table 2.4) stems from the leopard's high preference for a small number of medium-sized to large ungulates at this site (Table 2.2). Where these larger species become less abundant, like at site 2 (see chapter 3, Table 3.5), leopards become less specialized, use a higher number of species at near-equal proportions (Table 2.2), and dietary niche breadth increases (Table 2.4). This observation is in accordance with Emlen (1966), who suggested that dietary niche

breadth is indicative of resource availability, with niche contraction related to increases in prey abundance. The dietary niche breadth for hunters at site 1 was also relatively narrow (Table 2.4), but it appears unlikely that this was a result of hunters specializing in certain prey species, and is much rather a consequence of the impoverished prey community at this site (see chapter 3, Table 3.5).

Comparison to prior studies on prey choice in large felids at disturbed sites

This study marks the first attempt to investigate how competition with human hunters impacts leopard populations in the African rainforest. Prey choice in larger felids at evidentially disturbed sites, however, has been subject to a number of studies, and patterns showed similarities across sites. Leopards in the Comoé NP, Ivory Coast, preyed predominately on medium-sized (5-20 kg) to large (>20 kg) ungulates over a three-year period, but when populations of these taxa dwindled due to heavy poaching, leopard predation on large rodents and birds and reptiles increased significantly (Bodendorfer et al., 2006). Conversely, Weckel et al. (2006) documented that the mean prey weight and the proportion of larger ungulates used increased in a population of jaguars in the Cockscomb Basin in Belize, after the area received protection from hunting. While these two studies recorded a functional response in big cat predation following changes in the abundance of preferred prey, one study from southern India also revealed evidence of a numerical response to changes in prey abundance (Ramakrishnan et al., 1999). Leopard feeding habits and population densities were studied in two protected areas in southern India, one of which was known to have recently experienced declines in larger ungulate numbers following habitat conversion (Ramakrishnan et al., 1999). Leopard diet was similar in both parks regarding species composition, but the mean prey weight and the proportion of large ungulates in leopard diet were markedly lower at the recently disturbed site, and leopard population density was found to be twice as high in the undisturbed protected area (Ramakrishnan et al., 1999). While it cannot be ruled out that this was at least partly a consequence of direct persecution of leopards at the disturbed site, it is well established that population densities of large felids are positively correlated to the biomass of their prey (e.g. Van Orsdol et al., 1985, Stander et al., 1997, Karanth et al., 2004b). Hayward et al. (2007) recently reanalysed relationships between the population densities of large African predators and the biomass of their prey, and discovered that the relationships are even more robust and can deliver greater explanatory power if only preferred prey species or species within the respective predator's

preferred weight range are considered. Among the large African predators, the relationship between abundance of preferred prey and predator density showed the highest significance and explained the greatest amount of variability in density estimates in the case of the leopard (Hayward et al., 2007). These findings imply that leopards depend heavily on the prey species in their preferred weight range of 10-40 kg, and that a depletion of prey within this weight range will invariably lead to a decrease in leopard population density.

Conservation implications

Modelling of the impact of commercial bushmeat hunting on multi-prey communities in the Congo Basin rainforest, has shown that unsustainable hunting first leads to the disappearance of larger-bodied species ('red' duikers, red river hogs and large primates), and that these extinctions are followed by a relatively stable phase, where smaller species such as blue duiker and brush-tailed porcupine are still relatively abundant, and can be exploited by hunters at relatively high rates (Rowcliffe et al., 2003). Finally, at even higher exploitation rates, only the large rodents are still extant, as these are capable of sustaining very high off-takes (Rowcliffe et al., 2003). At our study site 1, brush-tailed porcupines and blue duikers were by far the most important prey species for human hunters (Coad, 2007), and the current state of exploitation at site 1 appears to correspond to the stable phase described by Rowcliffe et al. (2003) which follows the disappearance of larger-bodied prey species. Our data on leopard feeding ecology and population density (see chapter 3) suggests that leopards are not capable of subsisting entirely on the small-bodied prey species that persist at intensively hunted forest sites, but do depend on a prey-base of medium-sized and large ungulates such as 'red' duikers and red river hogs for their survival. Considering that the human population in the Congo Basin is rapidly growing (UN, 2005), and that substitutes for bushmeat are unavailable for the majority of the rural population, it can be expected that larger-bodied prey species will be extirpated from all areas of forest proximal to population centres (Wilkie and Carpenter, 1999). Larger and relatively remote parks and reserves are therefore most likely the only places where leopards in the Congo Basin have the chance for long-term survival.

Chapter 3: Leopards in the African rainforest: the impact of bushmeat hunting on population status as revealed by camera trapping

Abstract

Tropical rainforests comprise a large part of the leopard's (*Panthera pardus*) habitat in Africa, but baseline knowledge of leopard ecology and responses to human disturbance in African forests remain largely unknown. Because of low visibility in forested environments, study methods developed for leopards in open habitats are impractical, but recent advances in the application of camera trapping techniques to monitor tigers in India allowed this first systematic study on leopard abundance and distribution in the African rainforest environment. To assess the impact of bushmeat hunting on leopards, camera trap data was collected in four rainforest sites in central Gabon exposed to varying levels of anthropogenic disturbance. We analysed these data using capture-recapture models to estimate leopard densities, and employed occupancy modelling to investigate the factors affecting leopard distribution. Over survey periods of 39-62 days, 15-31 camera trap stations were sampled that effectively covered 119-232 km^2 of leopard habitat. No leopards were photographed at the most heavily hunted site, and 24-46 leopard photographs were obtained in the remaining areas, representing 4-15 different individuals. Population densities were estimated at 2.7-12.1 leopards/100 km^2, and occupancy modelling suggested that leopard use of an area increased with prey abundance and distance from settlements.

Introduction

The leopard (*Panthera pardus*) is widely recognised as one of the most adaptable and resilient of large felids. It has the broadest geographic distribution of all wild cats, and a very wide habitat tolerance; within Africa, it is the only felid occupying both desert and tropical rainforest (Nowell and Jackson, 1996). However, the prevailing view of the leopard as a successful generalist has been shaped by decades of research in open savannah and woodland habitats in eastern and southern Africa where the species is relatively easy to study (e.g. Schaller, 1972, Bertram, 1982, Bothma and le Riche, 1984, Norton and Henley, 1987, Bailey, 1993, see Hunter et al., in press for a review). Furthermore, in these regions the majority of studies have been carried out within protected areas where the species reaches its highest densities (but see Mizutani and Jewell, 1998, Marker and Dickman, 2005).

Little information exists on the effect of direct persecution or the reduction of wild prey on leopard numbers, but both are likely to exert a strong effect. Leopard population density is known to be positively correlated with biomass of their preferred prey across their range in eastern and southern Africa (Stander et al., 1997, Marker and Dickman, 2005), a pattern demonstrated elsewhere with other large cats (Karanth et al., 2004b). The same principles are likely to apply for leopards in the African rainforest, but baseline knowledge of leopard ecology and responses to human disturbance in forests remain largely unknown.

The only aspect of rainforest leopard biology relatively well-known is feeding ecology; medium-sized ungulates such as red river hogs (*Potamochoerus porcus*) and various species of forest duikers are the most important prey, followed by primates and large rodents (Hoppe-Dominik, 1984, Hart et al., 1996, Ososky, 1998, Ray and Sunquist, 2001, Henschel et al., 2005). The same species are also strongly preferred by bushmeat hunters across Central Africa (for a review, see Robinson and Bennett, 2000), creating the possibility that leopards and humans are in direct competition for the same prey. That populations of big cats may decline as a direct consequence of competition with humans hunting for subsistence has already been suggested for pumas and jaguars in the Neotropics (Jorgenson and Redford, 1993), and in Central Africa, leopards have disappeared from large tracts of otherwise intact rainforest under pressure from bushmeat harvests. For example, a large-scale survey covering 47 randomly selected forest patches in south-eastern Nigeria found evidence of leopards in only two of the surveyed sites (Angelici et al., 1998). Similarly in south-western Cameroon, hunters confirmed the local extinction of leopards in the area around Banyang-Mbo Wildlife Sanctuary in the mid 1970's (Willcox, 2002), and around

Kilum-Ijim Forest in the early 1980's (Maisels et al., 2001). This border region between Nigeria and Cameroon is characterized by a relatively dense human population (>80 inhabitants/km^2), and comprehensive market surveys estimated that >900,000 reptiles, birds and mammals, or around 12,000 tonnes of wild meat are sold annually in this region (Fa et al., 2006). While human population density is generally lower across most of the Congo Basin, the bushmeat trade is ubiquitous and results in tremendous volumes of wildlife extracted annually (e.g. Wilkie and Carpenter, 1999). Recently, marked reductions in ungulate biomass have been documented even in more remote sites and those adjacent to protected areas, and hunting off-takes were unlikely to be sustainable for most of the larger species (Noss, 1998, Muchaal and Ngandjui, 1999, Fimbel et al., 2000).

In this study we seek to assess the impact of bushmeat hunting on leopard population densities in African rainforest. Our principal hypothesis is that leopard populations will exhibit a numerical response where the species is competing with human hunters for prey, and that, accordingly, densities will be highest in remote areas where hunting pressure is least, and lowest in the direct vicinity of settlements where hunting pressure is most intense. We tested our hypothesis in four study areas inside and adjacent to Ivindo National Park (INP) in central Gabon that received varying levels of anthropogenic disturbance, owing to their differing degrees of remoteness. We estimated leopard population density in these four sites by applying capture-recapture models to camera trap data (Karanth and Nichols, 2002), and pooled camera trap data from all sites to investigate the factors that determined leopard area use via occupancy modelling (MacKenzie et al., 2002). We employed camera trap-based abundance indices (O'Brien et al., 2003, Johnson et al., 2006) to assess the relative abundance of principal leopard prey species and the relative intensities of human hunting at the 4 study sites.

Methods

Study Areas

Gabon is characterized by a low human population of approximately 1.3 million at the time of the study, with 84% of the population living in urban areas (UN, 2005) and 40% residing in the capital alone (WNN, 2006). The human population density in the central part of Gabon (Ogooué-Lolo and Ogooué-Ivindo Provinces) is particularly low with 1.5-2.0 inhabitants/km^2 (WNN, 2006) , and 95-97% of the region is still covered in forest, about

55% of which are currently gazetted as logging concession areas (GFW, 2000). Large-scale clear-cutting is an exception in Gabon's timber industry, and commercial logging is predominantly a low-intensity, selective exploitation of a few timber species, which causes about 10 percent canopy loss on average (Wilks, 1990, White, 1992).

Studies on the mammal community in the former Lopé Reserve prior to and after logging suggest that there is no simple relationship between logging history and mammalian biomass for most species (White, 1992), and accordingly, we selected study areas based chiefly on the anticipated intensity of hunting at each site, and irrespective of the logging history of the area. We assumed hunting intensity was determined by the relative remoteness of the site, as it has previously been shown to be strongly and negatively correlated with distance to the nearest settlement (Barnes et al., 1991, Laurance et al., 2006b). The distance to the nearest road or railway station is also a key factor, because they represent points of market access which facilitate the commercialisation of local bushmeat hunting. Access to such transportation has been shown to be a crucial step in driving unsustainable levels of hunting (Wilkie and Carpenter, 1999).

The study sites were therefore chosen based on their distance from the nearest settlement and point of market access, and without prior knowledge on the occurrence of leopards at the sites. All sites were situated within the same contiguous block of forest that contains both INP and Lopé National Park, and while two sites were at least partly inside INP, the remaining two sites were located about 100 km to the south between both parks, close to a public road linking two provincial capitals (Figure 2.1). This forest block has been characterized as mature lowland semi-evergreen rainforest, and the terrain is undulating with elevations ranging between 100 and 1000 meters (for a detailed description, see White and Abernethy, 1997, Vande weghe, 2006). The climate is equatorial, with two rainy seasons and two seasons that are predominantly dry, and annual precipitation varies between 1300 and 2000 mm (Vande weghe, 2006). The temperature is relatively stable throughout the year, with a monthly minimum of 21.7°C in July and a monthly maximum of 25°C in April (Vande weghe, 2006). The forest outside the two national parks is to a large part managed by logging companies exploiting timber at low intensity, and in the direct vicinity of settlements people engage in slash-and-burn agriculture. No other forms of large-scale habitat conversion currently occur in this part of Gabon, and besides logging, the only economical exploitation of the forest consists of bushmeat hunting and the collection of non-timber forest products by local people, and low-scale nature tourism in parts of both national parks.

INP was officially gazetted as national park in late 2002, and at the time of the study anti-poaching activities had not been initiated. It was therefore believed that the protection status of the study sites did not have a significant effect on our results. Sites 2-4 had been subject to logging prior to the study, but no timber exploitation occurred at the time of the study, nor were there any tourism operations or other research activities ongoing at the study sites inside INP. Details on all four study sites are provided in Table 3.1.

Table 3.1. Summary of the physical characteristics, land cover and land use of the four camera trap study sites in central Gabon.

Study site	Camera trap area (km^2)	Habitat and land use type	Distance from settlement/road (km)[a]	Elevation range (m)	Crown cover (%)
1	29	Primary lowland rainforest; village hunting zone	6.6 / 6.6	404-612 (mean: 486)	95-100 (mean: 100)
2	51	Primary-secondary lowland rainforest, formerly logged; inside logging concession	8.7 / 17.0	395-670 (mean: 500)	84-100 (mean: 99)
3	89	Primary-secondary lowland rainforest, formerly logged; partially inside Ivindo NP	15.6 / 15.6	237-580 (mean: 373)	11-100 (mean: 84)
4	106	Primary-secondary lowland rainforest, formerly logged; inside Ivindo NP	23.9 / 54.0	443-560 (mean: 502)	18-100 (mean: 89)

[a]Measured from the geographic center of each study area

Camera trapping

Individual leopards can be identified relatively easily by means of their unique spot pattern (Figure 3.1), and this natural marking permits the application of capture-recapture models for this species, as recaptured individuals can be readily recognized. Because direct sightings of leopards are exceedingly rare in the tropical forest, reliable identification of individuals is only possible using remote photography. Photographic capture-recapture estimates of the abundance of a large cat were first obtained for tigers in India (Karanth, 1995, Karanth and Nichols, 1998, Karanth and Nichols, 2002), and like tigers, forest leopards regularly use game trails and roads for their movements (Henschel and Ray, 2003). Placing camera traps in strategic positions along these travel routes delivers photographic captures of individual leopards using the study area, and while it is highly unlikely that one can capture all individual leopards using a certain area, capture probabilities and population

sizes can be estimated mathematically if some of the animals can be individually identified and periodically recaptured (White et al., 1982).

An important assumption for the application of capture-recapture models is that none of the individuals present has a zero chance of being captured (Karanth and Nichols, 2002), and it is therefore crucial to the sample design that the whole study area is evenly covered with traps, without leaving gaps large enough to contain an individual's movements. The individuals with the smallest home ranges in a population of leopards are adult females, and in the rainforest of Taï National Park, Ivory Coast female ranges measured 25.4 km^2 on average (Jenny, 1996). However, bushmeat hunting was recorded at this site (Jenny, 1996), and we anticipated that female ranges might be smaller in our remote study areas. In prey-rich forest habitat in Thailand an adult female home range can be as small as 9 km^2 (Grassman, 1999), and we therefore placed at least 2-3 traps in an area of this size, which translated to a trap spacing of ca 1.5-2 km (Figure 3.2). Variation in trap spacing has been shown to have a strong impact on density estimates in a cross-site comparison (Dillon and Kelly, 2007), and, experimentally, by omitting data from a subset of traps (Wegge et al., 2004), and trap spacing was therefore kept constant across all four study sites, although home ranges could be expected to be larger at the hunted sites.

We restricted the duration of the camera trapping to two months at our sites, because the capture-recapture models applied in this study assume demographic closure of the study population, and in prior studies on large cats it was suggested that trapping periods of 2-3 months would be sufficiently short to assume no population changes occurred during the study (Karanth, 1995, Karanth and Nichols, 1998, Silver et al., 2004).

Camera trapping was conducted in the driest months of the year, as heavy rain was found to result in technical failures of the units (Henschel and Ray, 2003). At each site we used 35 Camtrakker (Cam Trak South Inc., GA, USA) camera traps which are triggered by heat and motion sensors. All camera trap stations were set up along abandoned logging roads, large game trails (often located on ridges and besides rivers), and other features that showed high use by leopards in a series of pilot studies in protected and hunted rainforest sites in Gabon (Henschel and Ray, 2003). Although it is generally desirable to place two cameras per station and photograph both flanks simultaneously to obtain a positive identification for the animal (Karanth, 1995), we used single cameras per station at our sites in INP to increase our sampled area. Of necessity, this was a trade-off with logistical constraints given that all field work took place on foot, and we were unable to carry in twice

as many cameras for paired stations due to a lack of manpower. At the unprotected sites, our sampled areas were smaller to ensure we sampled an area with homogenous hunting pressure and we placed cameras in pairs. All cameras were mounted at a height of 40-45 cm, and were at least 1.5 meters away from the trail. Cameras were programmed to function continuously, day and night, and with a five minute delay between successive photographs, to prevent the unit from being repeatedly triggered by large groups of animals passing in front of the sensor, or by forest elephants (*Loxodonta africana cyclotis*) feeding in the vicinity. Camera traps were loaded with ASA 100 film and were visited every 6-14 days to change film and batteries. Each camera was programmed to leave a stamp with the date on each photograph, and additionally each roll of film was labelled with a unique identifier for the study area, trap site and film number when retrieved.

Estimating leopard population density

For each site, all leopards were identified using their unique spot pattern (Figure 3.1) and we created a capture history for each individual by assigning either "1", or "0", depending on if the individual was captured on each occasion, where each trap day represented a separate capture occasion. Capture histories were stored in a so-called 'X-matrix' for each site and were analyzed using the computer program CAPTURE (Rexstad and Burnham, 1991). CAPTURE offers seven different estimators of population size to account for differences in capture probability between different individuals and sampling occasions, variations over time or as a reaction to prior capture, and several combinations of these. It is also possible to select all estimators of population size, and CAPTURE will assign scores between 0.0-1.0 to each potential model, where the highest score represents the best fit (Otis et al., 1978). For each selected model CAPTURE produces an estimate of capture probability and a resulting population size with confidence limits and standard error. The actual population density is then obtained by dividing the resulting population size by the size of the effectively sampled area. This is defined as the area covered with camera traps plus a boundary strip around the outer traps (Figure 3.2), to account for an additional area from which individuals may enter the trapping polygon (White et al., 1982). The width of this strip should be equivalent to the radius of an average home range, and for trapping studies the mean maximum distance moved (MMDM) by animals that were captured on more than one occasion can be used as an approximation of home range diameter (Wilson & Anderson, 1985). Consequently, the ½ MMDM has been used to define boundary strip width
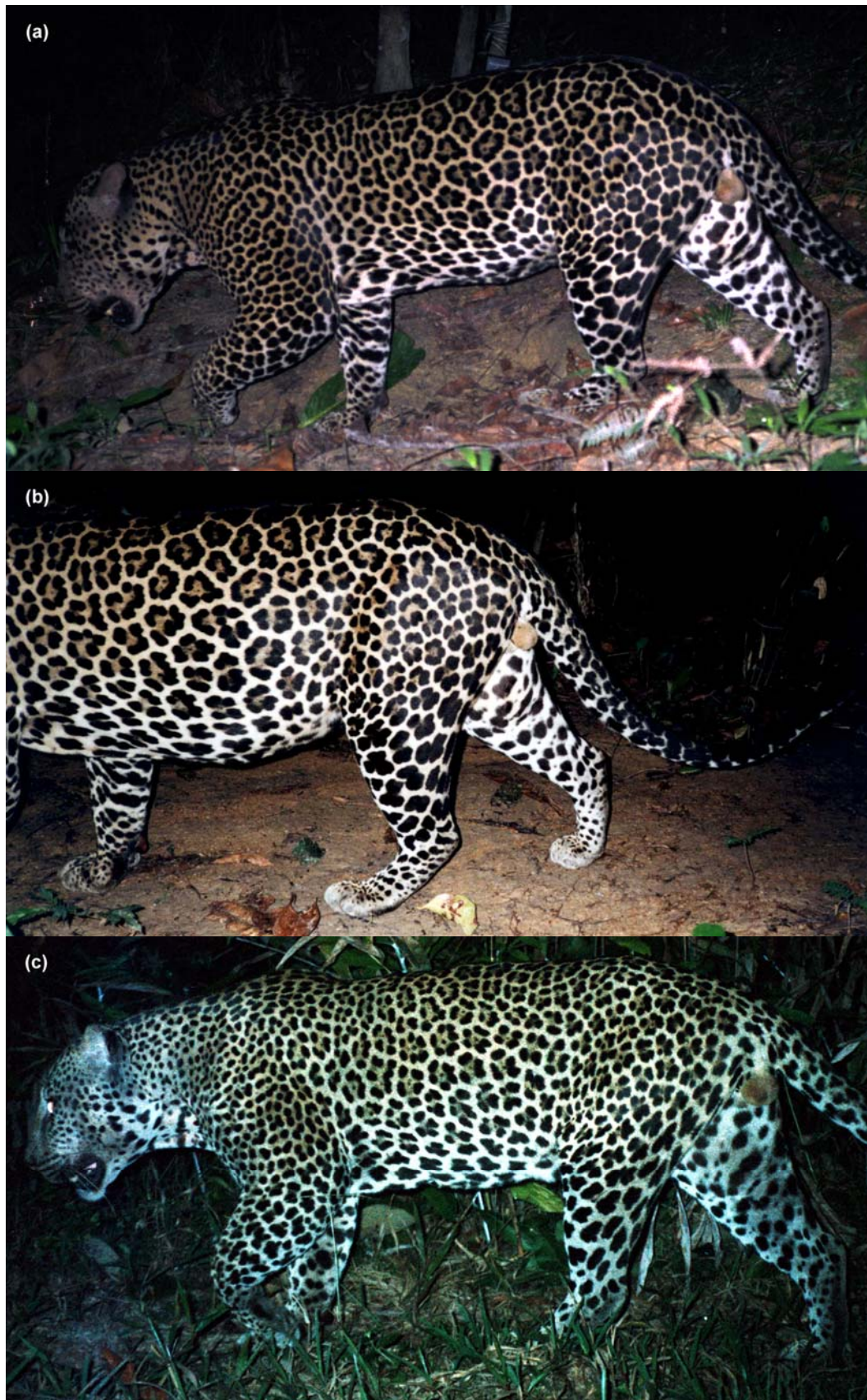
Figure 3.1. Example for the identification of individual leopards based on their characteristic pattern of spots and rosettes. Fig. 2 a) and b) show the same adult male SE-M01, whereas c) shows a second male DI-M02. Note the difference in size and shape of the rosettes, and the usefulness even of partial photographs.
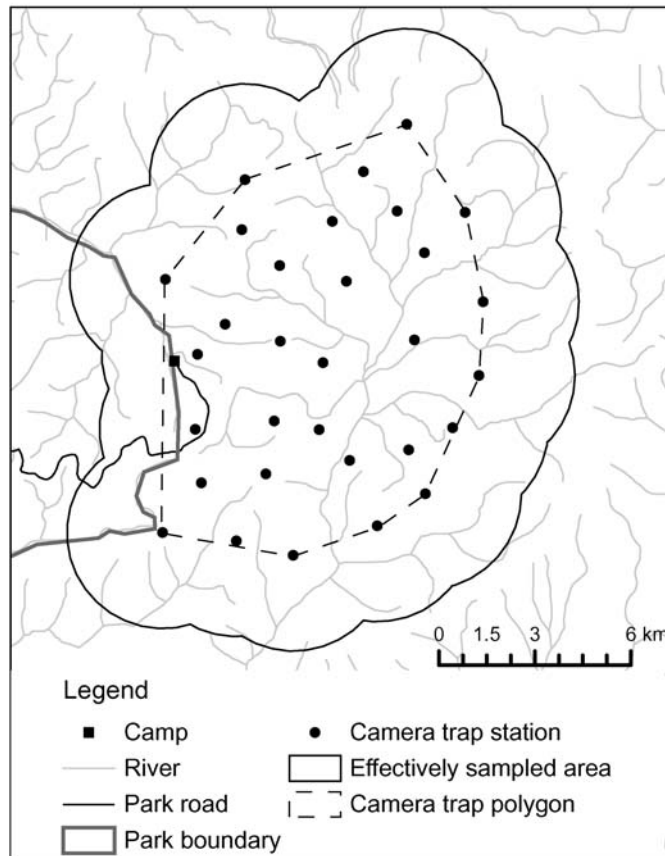
Figure 3.2. Map of study site 4 in Ivindo National Park, central Gabon, showing the camera trap locations, the trapping polygon and the effectively sampled area.

Figure 3.3. Two hunters filmed on the southern edge of Ivindo National Park at the site 3, when illegally entering the park; note their firearms and backpacks. This was the only photograph taken of hunters inside any of the formally protected study sites.

in a number of camera trap studies on big cats (e.g. Karanth and Nichols, 1998, Karanth et al., 2004a, Silver et al., 2004, Kelly et al., 2008, Balme et al., in press-a), and we also adopted this method here. While the accuracy of this approach has recently been disputed (Soisalo and Cavalcanti, 2006), it certainly appears to perform well if trapping polygons are large enough to capture the study animals' true maximum distances moved (Maffei and Noss, 2008).

Investigating the factors that determined leopard area use

Occupancy surveys are commonly used to describe geographic ranges of species and to test hypotheses about factors affecting species' distribution (MacKenzie et al., 2004). However, the nondetection of a species at a specific landscape unit does not imply that the species is definitely absent from this unit, and it is generally advisable to use detection history data from a set of landscape units to estimate detection probability, and the probability that a sample unit is occupied (MacKenzie et al., 2002). These probabilities can be computed using likelihood-based functions, which can further be employed to model covariates that might influence detection probability and occupancy (MacKenzie et al., 2002). One of the assumptions of this method is that all landscape units are closed to changes in occupancy during the study (MacKenzie et al., 2002), however, MacKenzie et al. (2006) subsequently suggested that this assumption could be relaxed to rather estimate the 'use' of an area by a wide-ranging species. In this study our interest was not to estimate the overall proportion of area occupied by leopards across our study sites, but to identify the covariates that had the highest influence in shaping the apparent leopard land-use pattern captured by our camera traps.

We constructed leopard detection histories for each camera trap station which we pooled across study sites, and imported into PRESENCE v.2 software (Proteus Wildlife Research Consultants, New Zealand; http://www.proteus.co.nz). Because the model in PRESENCE tends to provide biased results for detection probabilities below 0.3 (MacKenzie et al., 2002), we condensed seven trap-days into one sampling occasion to increase the detection probability per occasion. As study duration varied slightly across sites, we used detection data from the first seven weeks from each site representing seven sampling occasions in our analysis. For each camera trap station, seven covariate parameters were extracted and imported into PRESENCE; these were distance from water, distance from

public roads, distance from settlements, elevation, percent forest cover, and the relative abundances of hunters and leopard prey. Coverage containing digitized rivers, roads and settlements were provided by the Wildlife Conservation Society Gabon Program, and distances were analyzed using ArcGIS 9.1 software (ESRI Inc., Redlands, CA). Elevation data was freely available for this region at 90 m resolution (Jarvis et al., 2006), and percent forest cover at 500 m resolution (Hansen et al., 2007). Relative abundance estimates for hunters and prey were derived from camera trap data (see below).

Due to the high number of covariates, we used a step-wise approach and identified a parsimonious model for detection probability prior to performing model selection with respect to area use (MacKenzie, 2006). Models were ranked based on their Akaike Information Criterion (AIC) values (Burnham and Anderson, 2002), and to assess the relative influence of each covariate on area use, computed model weights were summed over all models containing the particular covariate (MacKenzie, 2006).

Estimating prey abundance and hunting pressure

We assessed the relative abundance of potential leopard prey for each site by using a camera trap-based abundance index used previously in studies on tigers and their prey in Asia (O'Brien et al., 2003, Johnson et al., 2006). For this, we identified each photograph to species level and rated it as a dependent or independent capture. Independent captures were defined as consecutive photographs of different individuals of the same or different species, or as nonconsecutive photos of individuals of the same species (O'Brien et al., 2003). We calculated the number of independent photographic captures of leopard prey for each site, and produced a relative abundance index (RAI) which we defined as the number of frames taken per 100 trap-days. Species were categorized as prey and non-prey based on dietary analyses at the four study sites (see chapter 2) and one other forest site in Gabon (Henschel et al., 2005). Prey species were grouped as medium-sized prey (<20 kg) and large prey (>20 kg). Some small prey species (<5 kg) such as arboreal primates and large terrestrial rodents are also preyed upon by leopards, but these species were very rarely photographed owing to their small size and/or arboreal habits, and could therefore not be included.

At each study site we also calculated an RAI for hunters, who are easily recognized as they always carried guns and/or cable-snares and traditional rucksacks for the transport of meat (Figure 3.3). Villagers engaged in activities other than hunting were only photographed

at site 2 in an area visited by villagers for artisanal gold-panning; they did not carry guns or snares and we excluded them from the calculation of the hunter RAI. We did not lose any cameras to theft or vandalism during our surveys, nor did we find evidence that hunters actively avoided traps (for example, by their tracks skirting around cameras), so we are confident that our hunter RAI represents an accurate measure of hunter use of an area. Our taxonomy follows (Kingdon, 1997).

Results

We operated 87 camera trap stations across all four study sites over periods of 39-62 days (Table 3.2). Of the resulting 4060 trap-days, camera traps recorded events for an absolute minimum of 3555 trap-days (87.6%). It was in most cases impossible to determine the exact date a unit had stopped functioning, and therefore the date on the last frame exposed before the failure was noted as the last day the trap was fully functional, and subsequent days up to the date the unit was checked were subtracted from the total count of trap-days. The resulting figure is certainly an overestimate of the true failure rate exhibited by the units, and the projected average failure rate of 2.6 units/study site can be regarded as an absolute maximum, and is unlikely to have biased trapping results, given the tight trap spacing. Camera traps failed in most cases because either the camera or the entire unit malfunctioned, which happened predominantly in periods of increased humidity following rainfall. Damage to units by forest elephants occurred but was uncommon, and we recorded no case of units being stolen or damaged by hunters.

Table 3.2. Camera trap sampling effort at four study sites in central Gabon.

Study site	Dates	Duration (days)	# camera stations	Trapping polygon size (km^2)	Minimum # trap-days	Trapping intensity (# trap-days/km^2)
1	9-10/2004	45	15	29	581	19.9
2	4-5/2005	39	18	51	679	13.2
3	8-10/2003	62	23	89	1131	12.7
4	5-6/2004	46	31	106	1164	11.0

Leopards were photographed 167 times in total, representing 108 independent photographic captures of individually identifiable leopards (Table 3.3). For the study sites where we deployed single camera traps, we used subsets of photographs for individual identification of leopards that showed either the right or the left flank, whichever side was represented more often.

Table 3.3. Camera trapping results for four study sites in central Gabon, showing leopard captures and recaptures with estimated capture probability (p) per sampling occasion (using model M_h), and the results of the closure test.

Study site	# captures + recaptures	# individuals	# individuals recaptured	P	Closure test	
					Z	P
1	0	0	0		-	-
2	24	4	3	0.12	-1.54	0.06
3	38	8	6	0.06	-0.34	0.37
4	46	15	6	0.04	-0.08	0.47

No leopards were captured in the village hunting zone of site 1, and 24-46 captures were obtained at the remaining sites, representing 4-15 individual leopards (Table 3.3). The closure test results confirmed that population closure occurred at all sites (Table 3.3). The mean maximum distances moved (MMDM) were fairly constant across sites but showed a slight increase in the areas that were less remote (Table 3.4). In the CAPTURE model choice function model M_h scored highest (1.0) for sites 3 and 4, and only at site 2 it was model M_{bh} that scored highest (1.0). Both models assume heterogeneity in capture probabilities among individual leopards, but model M_{bh} also suggests a behavioural response of the animal after first capture, and only initial captures and no recapture events are used to estimate population size. For site 2 CAPTURE failed to produce an estimate with model M_{bh}, and thus model M_h was used for all sites. The estimated population size at the respective study areas ranged from 5 ± 1.51 (95% CI of five to 12) individuals at site 2 to 28 ± 8.26 (95% CI of 20 to 55) leopards at the remotest site 4, with corresponding population densities ranging from 2.7 ± 0.94 leopards/100 km^2 at site 2 to 12.1 ± 5.11 leopards/100 km^2 at site 4 (Table 3.4).

Table 3.4. CAPTURE results for four study sites in central Gabon, showing population size (using model M_h), the boundary strip width as determined by the mean maximum distance moved (MMDM), and the resulting leopard population density.

Study site	Population size ± SE	95% confidence interval	½ MMDM (km) ± SE	Effectively sampled area (km^2)	Density (per 100 km^2) ± SE
1	-	-	-	-	-
2	5 ± 1.51	5 – 12	3.59 ± 0.49	186	2.69 ± 0.94
3	10 ± 2.17	9 – 19	2.99 ± 0.97	218	4.58 ± 2.58
4	28 ± 8.26	20 – 55	2.90 ± 0.65	232	12.08 ± 5.11

We obtained 2343 independent photographic captures of a minimum of 28 different species, 26 of which were mammals. Of these, 12 species were known leopard prey (Henschel et al., 2005, chapter 2). These species represented 1221 photographic captures or

52.1% of all frames. Larger carnivores and larger prey species were never captured at site 1, and the highest number of larger species was recorded at the remoter sites 3 and 4 (Table 3.5). The RAI did not vary significantly across sites for larger carnivores (Kruskal–Wallis χ = 5.60, d.f. = 3, P = 0.133) and medium-sized prey species (Kruskal–Wallis χ = 1.05, d.f. = 3, P = 0.788), whereas for large prey the differences were significant (Kruskal–Wallis χ = 14.42, d.f. = 3, P = 0.002), with higher relative abundances recorded at the remoter sites (Table 3.5). The mean relative abundance of hunters was significantly higher at sites 1 and 2 than at the remoter sites 3 and 4 (Mann–Whitney U, Z = -5.31, n = 85, P < 0.0001) (Table 3.5).

Table 3.5. The relative abundance index (RAI) values (number of photographic captures per 100 trap-days) for the most commonly captured mammals at four study sites in central Gabon, including hunters.

Scientific name	Common name	RAI (# photographs/100 trap-days)			
		Site 1	Site 2	Site 3	Site 4
Larger carnivores					
Civettictis civetta	African civet	-	-	1.4	0.9
Felis aurata	African golden cat	-	-	0.2	0.4
Panthera pardus	Leopard	-	5.7	5.0	6.3
Medium-sized prey (< 20 kg)					
Cephalophus spp.	Medium-sized duikers (4 species)	0.3	20.9	12.1	14.4
Mandrillus sphinx, Cercopithecus solatus[a]	Smaller primates (2 species)	1.2	1.0	-	-
Large prey (> 20 kg)					
Pan t. troglodytes	Central African chimpanzee	-	0.9	1.3	2.9
Gorilla g. gorilla	Western lowland gorilla	-	-	1.8	0.9
Cephalophus silvicultor	Yellow-backed duiker	-	0.6	12.3	15.2
Potamocherus porcus	Red river hog	-	0.7	6.6	6.1
Syncerus c. nanus	Forest buffalo	-	2.4	9.5	5.8
Tragelaphus euryceros	Bongo	-	-	-	2.3
Total medium-sized prey		1.5	21.9	12.1	14.4
Total large prey		-	4.6	31.5	33.2
Non-prey					
Loxodonta a. cyclotis	Forest elephant	9.8	20.5	16.8	35.7
Homo sapiens	Hunter	4.8	0.9	0.1	-

[a] Mandrills and sun-tailed guenons do not occur at sites 3 and 4 (see chapter 2).

Among the seven covariates tested, none improved model fit of our parsimonious model when used as a variable for detection probability. Therefore we kept detection probability constant during the subsequent modelling of leopard area use. The relative abundance of prey and distance from settlements were the most important variables for determining use (Table 3.6). The summed model weights for these variables were 89% and

70%, respectively, while the summed model weights for the remaining variables were 35% for distance from roads and 31% for forest cover. It is interesting to note that leopard area use was positively related to prey abundance and the distances from settlements and roads, but negatively related to percent forest cover. A strong, positive relationship existed between the relative abundance of prey and distance from settlements (Pearson correlation $r = 0.6$, $n = 85$, $P < 0.0001$).

Table 3.6. Summary of model-selection results for the probability of leopard use (w*) of 85 camera trap sites from four study areas in central Gabon. The modelled covariates are distance to settlements (DS), distance to public roads (DR), percent forest cover (FC), and the relative abundance of prey species (PREY). Only the top 12 models are shown.

Model	Model AIC	ΔAIC	K	W
w*(DS + PREY) p(.)	550.46	0	3	28%
w*(DS + DR + PREY) p(.)	551.83	1.37	4	14%
w*(DS + FC + PREY) p(.)	552.17	1.71	4	12%
w*(PREY) p(.)	552.24	1.78	2	11%
w*(DR + PREY) p(.)	553.11	2.65	3	7%
w*(FC + PREY) p(.)	553.19	2.73	3	7%
w*(DS + DR + FC + PREY) p(.)	553.67	3.21	5	6%
w*(DS) p(.)	554.01	3.55	2	5%
w*(DR + FC + PREY) p(.)	554.27	3.81	4	4%
w*(DS + DR) p(.)	554.39	3.93	3	4%
w*(DS + FC) p(.)	555.36	4.9	3	2%
w*(.) p(.)	559.77	9.31	2	0%

ΔAIC is the relative difference in AIC values compared to the top-ranked model, K is the number of parameters in the model, and W is the AIC model weight.

Discussion

This was the first systematic attempt to estimate leopard status in the African rainforest, and as for large felids in prior studies, the use of camera traps was well-suited to estimate the population density of a cryptic carnivore in dense forest habitat. The results of the closure test (Table 3.3) suggested that the maximum capture period of two months was sufficiently short to meet the assumption of a closed population during the survey period. Furthermore, capture probabilities produced by CAPTURE for leopards were similar to results from studies on tigers and jaguars (e.g. Karanth et al., 2004a, Silver et al., 2004). Notably, capture probabilities were twice as high at site 2 compared to the remaining sites where leopards were detected (Table 3.3), however, this difference was linked to the fact that only subsets of photographs showing either the right or the left flank were used at the remaining sites that were operated with single cameras. The overall RAI for leopards was almost identical at all three sites where leopards were detected (Table 3.5).

Although it would have been desirable to use paired cameras at each study site, we do not believe that the lower capture probabilities from sites trapped with single-camera stations resulted in biased estimates of population size. Parameters reported to lead to biased estimates of population size in camera trap studies when not kept constant across sites, are trap spacing (Dillon and Kelly, 2007) and relative sampling effort (Wegge et al., 2004). In the present study those two variables were not subject to significant change, and the resulting trapping intensity, measured as the number of trap days per square kilometre, was very similar across sites (Table 3.2). The only parameter that changed considerably among sites in the present study was the total size of the trapping polygon (Table 3.2), and results from prior camera trapping studies suggest that bias may occur if trapping polygons are too small to capture animals' true maximum distances moved (Maffei and Noss, 2008). In the present study however, MMDM was very similar across sites irrespective of trapping polygon size (Table 3.4), suggesting that the smaller polygons were large enough to capture leopard movements during the survey period.

Another potential source of bias was the degree of anthropogenic disturbance that varied amongst sites, which might have led to leopards avoiding camera trap exposure at the sites frequented by hunters. An indicator for such trap avoidance might have been the high score of capture model M_{bh} at the unprotected site 2, which suggests a behavioural response of the animal after first capture, yet even at this site three of the four identified leopards were recaptured (Table 3.3). Furthermore, the computation of leopard capture data in PRESENCE did not reveal any effects of distance from settlements or hunter RAI on leopard capture probability at a given camera station, which strongly suggests that leopards did not actively avoid camera traps or the trails on which they were placed in areas also used by hunters.

Photographs of larger prey species were too rare at the hunted sites to test if individuals seemed to actively avoid trails where hunters were also photographed, which might have led to an underestimate of the relative abundance of large prey in the unprotected areas. However, data on forest ungulates in southeast Asia suggests that relative abundance indices derived from camera trap data are directly related to independent density estimates even in areas where poaching occurs (O'Brien et al., 2003), and camera trap-based abundance indices have consequently been used in a number of studies to measure the impact of hunting on populations of large carnivores and their prey (e.g. Johnson et al., 2006, Datta et al., 2008).

Leopard population densities and the factors determining them

Our results are the first rigorous estimates of rainforest leopard densities using capture-recapture models applied to camera-trap data. Estimates for our protected study sites are comparable to Jenny's (1996) calculation from Taï National Park, Ivory Coast of 7.1-11.1 leopards/100 km^2, based on telemetry results from three collared leopards. Significantly, even at our most remote and intact site 4, leopard density (12.08 ± 5.11 leopards/100 km^2) was greatly below the frequently-cited estimates of 33-40 leopards/100 km^2, suggested for rainforest habitat in Africa by Martin & de Meulenaer (1988).

In accordance with our hypothesis, leopard showed a strong numerical response to competition with hunters, and leopard population density increased with growing distance from permanent settlements. Likewise, leopard area use was positively correlated with the relative abundance of prey and distance from settlements. The fact that leopards did not actively avoid areas used by hunters, suggests that direct persecution of leopards was generally uncommon in the study areas, and that the respective absence and low density of leopards at the hunted sites 1 and 2 was much rather a consequence of the low availability of larger prey at these sites, as had been documented for tigers in India (Karanth and Stith, 1999, Ramakrishnan et al., 1999).

At our most heavily hunted site 1, there were 67 hunters operating from the nearest village at the time of the study, and about half of them were active north of the road throughout our study area, where each hunter worked with a mean number of 77 ± 17.9 illegal cable snares (Coad, 2007). Of the 1242 animals killed by hunters over a period of 14 months, 78% were taken in cable snares and most of the remainder was killed with gunshots during night-hunts (Coad, 2007). Larger prey was not recorded at this site (Table 3.5), and the entire village hunting territory which extends up to 12 km north of the village is not believed to support a resident population of leopards.

Relative to our other study areas, site 1 represents an extreme case for leopards but a pattern of competitive effects of hunting prey species is manifested in other ways across all sites. The mean prey weight of leopards declined from 31.6 kg at our least impacted site 4 to 19.7 kg at site 2 (see chapter 2, Table 2.4). Ungulates comprised 91% of biomass consumed by leopards at site 4 whereas this dropped to 69% and 67% at sites 3 and 2, respectively. At site 3, leopards switched more to primates to supplement their diet whereas large rodents were more important to leopards at the more impacted site 2 (see chapter 2, Table 2.3). This

diet data and the abundance indices for larger species (Table 3.5) reflect the progressive loss of larger taxa under increasing intensity of human hunting. For example, Wilkie & Carpenter (1999) demonstrated that the ratio of ungulates to rodents was highest in remote sites and lowest near urban markets in densely settled areas, and suggested the utility of this ratio as an index of bushmeat over-exploitation.

In Gabon's rainforests, leopards are rarely sought by local hunters with firearms, partly because direct encounters with the species are extremely rare in the dense forest habitat. There is a regional market however for leopard skins, claws and canine teeth, which are widely used in traditional medicine across the Congo Basin, and if presented with the opportunity to kill a leopard, most hunters will probably seize it. One male was thus shot by villagers south of our study site 1, after it had been repeatedly encountered by a group of hunters during night-hunts in the same area. But in general, leopards are more likely to be killed unintentionally in illegal cable snares. We know of at least two adult males killed by snares during the course of the study, and in both cases the individual was captured on the edge of a national park, where leopards naïve to humans come into contact with illegal snare-lines. It is evident that such removal of individual leopards is more common at the edge of protected areas than in remote areas of parks, and might partially explain the reduced density of leopards at site 3 compared to the more remote site 4. Woodroffe & Ginsberg (1998) suggested that high mortality rates of wide-ranging carnivore species on reserve borders could transform those areas into population sinks. Furthermore, for small protected areas with a high proportion of edges, the existence of a protected area alone might not be sufficient for large carnivore conservation if mortality in adjacent areas is not reduced (Ferreras et al., 1992).

Conservation implications

Our data emphasize the very significant problems with earlier estimates of forest leopard densities, which omitted anthropogenic factors and prey availability. This has been noted by earlier authors (Norton, 1990, Marker and Dickman, 2005, Hunter et al., in press) but our study presents the first rigorous density estimates using mark-recapture models. Notably, estimates from the model developed by Martin & de Meulenaer (1988) remain the chief source of information for African governments proposing to open or raise harvest quotas for trophy hunting leopards.

In West and Central Africa, trophy hunting of the species is only permitted in the Central African Republic though there are proposals to open hunting more widely in the region in rainforest habitat (Balme et al., in press-b). Given the low densities of rainforest leopards compared to their savannah-woodland counterparts and their vulnerability to effects of bushmeat hunting in forested habitat as demonstrated here, we caution against the introduction of trophy hunting in rainforest. Before considering any level of harvest, at very least we strongly recommend first calculating density estimates by applying mark-recapture models and incorporating a measure of hunting intensity.

More immediately, our data are alarming as they clearly show that leopards disappear from areas exposed to high levels of bushmeat hunting where direct persecution of the species may not be evident. We (and others; e.g. Coad, 2007) chose site 1, the hunting territory of the village Dibouka, for this study because it is regarded as an average Gabonese roadside village representative of much of rural forested Gabon (Coad, 2007). Relative to our other sites, the hunting intensity at site 1 represents a threshold at which leopards cannot survive, a situation which likely applies for approximately 64.9% of the Congo Basin rainforest, which is the proportion of rainforest habitat that lies within 10 km of towns and roadside villages (Blake et al., 2007). Using data from Kenya, Woodroffe (2000) established a critical human density of above 900 inhabitants/km^2 at which logistic regression predicted a 50% probability of leopard extinction. However, leopards across large parts of south-western Cameroun became extinct 20-30 years ago at human densities more than one order of magnitude lower (Maisels et al., 2001, Willcox, 2002, Fa et al., 2006) and our data from site 1 strongly suggests the absence of leopards and larger prey in an area of primary rainforest where human population density is only 1-2 inhabitants/km^2. The obvious explanation for the difference is that most rural people in Kenya rely on livestock whereas rural populations in Central Africa rely primarily on bushmeat to meet their protein requirements (Wilkie and Carpenter, 1999), and do therefore exclude leopards through intensified competition. Human population across the region is likely to double in 25–30 years (UN, 2005), and if per capita demand for bushmeat remains constant and effective substitutes remain unavailable, it can be expected that larger bushmeat species will be extirpated from all areas of forest proximal to population centres (Wilkie and Carpenter, 1999), and that the larger, more remote parks and reserves are likely to be the only places where leopards in the Congo Basin have the chance for long-term survival.

Chapter 4: The status and conservation of leopards and other large carnivores in the Congo Basin, and the potential role of reintroduction

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Abstract

The Congo Basin contains the world's second largest expanse of tropical rainforest, and yet also within the catchment lies an extensive, geographically isolated forest–savannah mosaic. While the forests in this region have long been considered an important stronghold for the leopard (*Panthera pardus*), the apex predator in this habitat, the forest–savannah mosaic also once harboured important populations of lions (*Panthera leo*), African wild dogs (*Lycaon pictus*) and spotted hyenas (*Crocuta crocuta*). Uncontrolled hunting by man, however, has led to a dramatic decrease in ungulate populations, especially in the more accessible open habitats. Today, lions and African wild dogs are almost certainly regionally extinct, while spotted hyenas have been reduced to one small and isolated population in the Republic of Congo. In remote forest regions, wildlife populations have remained less severely affected, but in densely populated areas where demand for wild game is high, intensive commercial hunting has led to a widespread disappearance of leopards, even from within protected areas. Conservation efforts directed towards leopards and spotted hyenas should promote rigorous protection of remaining populations and their prey to prevent any further range loss. Owing to the present geographical isolation of their former range within this region, however, any effort to re-establish lions or African wild dogs would inevitably need to involve reintroduction. Most suitable habitat is currently without protection and wild prey is scarce, so potential reintroductions would need to be preceded by the creation of sufficiently large protected areas and their restocking with prey, provided that government and local support for such a proposal could be acquired and guaranteed for the long term.

Introduction

The Congo Basin: Habitat and fauna

The rainforest of the Congo Basin represents the world's second-largest expanse of dense humid tropical forest, surpassed in size only by the Amazon. Climatic changes have dictated the extent of this forest throughout its geological history, leading to its fragmentation in arid phases and, during 80%–90% of the past 800,000 years, the African rainforest was less extensive and more fragmented than at present (Maley, 2001). During the last glacial maximum (~18,000 BP), hyper-arid conditions caused the retraction of the forest to a series of refuges, which were mainly riparian or mountain forests, and palynological data suggest that the remainder of the Congo Basin was covered by a forest–savannah mosaic dominated by open, grass-rich vegetation (Dupont et al., 2000, Maley, 2001). The discovery of 7000-year-old molars of a black rhinoceros (*Diceros bicornis*), a species not recorded in this region in historical times, in a rock shelter in southern Congo (van Neer and Lanfranchi, 1985), suggests that a more diverse savannah fauna existed during this period than at present. Other larger savannah taxa might have likewise disappeared from this region during the last hyper-humid phase between approximately 9000 and 4000 BP, which was characterized by maximum forest extension and an extreme reduction of open habitat (Maley, 2001).

Today, within the Congo Basin, there remains a single important expanse of natural open habitat, which has been classified as a distinct terrestrial ecoregion and termed the Western Congolian forest–savannah mosaic (Olson et al., 2001). It stretches north and south from the lower reaches of the Congo River (Figure 4.1a). Its northern part, in Gabon and the Republic of Congo (hereafter, termed "Congo"), is isolated from the southern part in the Democratic Republic of Congo (DRC) and Angola by the Congo River. It is separated from the Northern Congolian forest–savannah mosaic of Cameroon and the Central African Republic (CAR) by a wide band of contiguous rainforest. It is not known when the Western Congolian forest–savannah mosaic became isolated from the surrounding grasslands, but the presence of southern reedbuck (*Redunca arundinum*) in this region has led to the early assumption that the most recent connection existed towards the south, and not towards the Northern Congolian forest–savannah mosaic, which harbours the Bohor reedbuck (*Redunca redunca*), (Malbrant and Maclatchy, 1947). This assumption has recently been corroborated by two genetic studies on the biogeography of lion (*Panthera leo*) and bushbuck
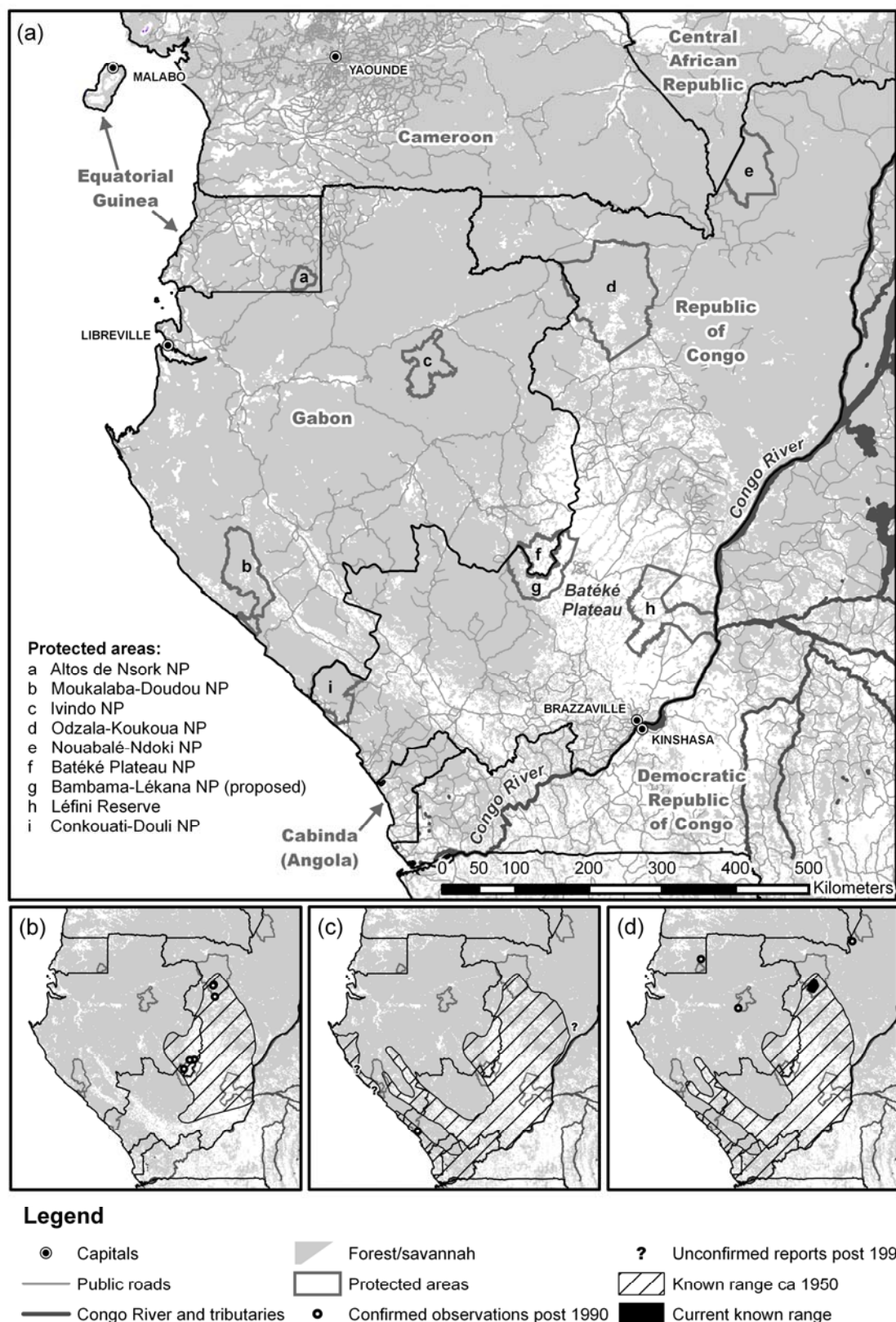
Figure 4.1. The distribution of open habitat in the western proportion of the Congo Basin (a) and the historical range, recent records and current known range of the larger savannah carnivores (b) lion; (c) African wild dog; and (d) spotted hyena. Only protected areas mentioned in the context of savannah carnivores are shown.

(*Tragelaphus scriptus*), which confirmed that samples for the two species collected in Gabon and Congo shared the same haplotypes as populations from south of the Congo River, and were more genetically distinct from populations in the Northern Congolian forest–savannah mosaic (Barnett et al., 2006, Moodley and Bruford, 2007).

The isolated northern part of the Western Congolian forest–savannah mosaic consists of roughly 200,000 km^2 of open grasslands, interspersed with wooded savannah and dense gallery forest along the deeper river valleys. In colonial times, it harboured a range of species that are characteristic of the African savannah, including lion, African wild dog (*Lycaon pictus*), spotted hyena (*Crocuta crocuta*), defassa waterbuck (*Kobus ellipsiprymnus defassa*), southern reedbuck, bushbuck and common duiker (*Sylvicapra grimmia*) (Malbrant and Maclatchy, 1949). Larger Alcelaphinae, Antilopinae and Hippotraginae grazers, however, were never recorded in this landscape, and neither was the cheetah (*Acinonyx jubatus*) (Malbrant and Maclatchy, 1949). The larger fauna in this landscape was instead comprised of several species that are characteristic of the rainforest, such as forest elephant (*Loxodonta africana cyclotis*), forest buffalo (*Syncerus caffer nanus*), yellow-backed duiker (*Cephalophus silvicultor*) and red river hog (*Potamochoerus porcus*), which were all widely distributed across the Western forest–savannah mosaic (Malbrant and Maclatchy, 1949). While several forest species, such as forest buffalo and red river hog, actually reach their highest densities in this mosaic of habitats (Tutin et al., 1997), there are only isolated observations of savannah species from within the contiguous forest (Malbrant and Maclatchy, 1949, Juste and Castroviejo, 1992, Henschel and Ray, 2003, Henschel, 2006), underlining the unsuitability of this habitat for savannah species. The only large carnivore that appears equally adapted to both the contiguous forest and the Western forest–savannah mosaic is the leopard (*Panthera pardus*), and the species has been subject to a number of studies in the Congo Basin over the past decades. The savannah carnivores in this region have received little scientific attention to date.

Large carnivores in the Congo Basin: historical distribution, recent decline and current status

Leopards – historical distribution and numbers

As a habitat generalist, the leopard occurs in all major vegetation types found within the Congo Basin, including lowland and mountain forest, logged secondary forest, the open

habitat of the Western Congolian forest–savannah mosaic and even inundated forests and swamp systems (Hunter et al., in press). Consequently, it seems safe to assume that leopards once had a continuous distribution across the Congo Basin and, in the two most recent Africa-wide status surveys on the species, this region was considered a stronghold for the species in Africa (Myers, 1976, Martin and de Meulenaer, 1988). This assumption was based on the vast amount of unaltered and seemingly prey-rich forest habitat still available to leopards and their role as the apex predator therein, which was suspected to result in extremely high leopard population densities in this habitat. Although the Congo Basin represented only 12% of the leopard's range in Africa at the time of the latest status survey, it was estimated in 1988 that this region harboured an approximate 40% of Africa's leopards (Martin and de Meulenaer, 1988). Leopard population density had never been determined in rainforest habitat, however, and several authorities in the field criticised these estimates, arguing that the biomass of potential prey is generally lower in forests compared to savannah, which should result in correspondingly lower leopard densities in this biome (Jackson, 1989, Bailey, 1993).

Leopards – recent decline

The figures published by Martin and de Meulenaer (1988) are still quoted today, and remain the chief source of information for African governments proposing to open or raise harvest quotas for trophy hunting of leopards. However, evidence is mounting that leopards have already disappeared from a number of forest sites on the fringes of the Congo Basin (e.g. Angelici et al., 1998, Andama, 2000, Maisels et al., 2001). While the reasons for these local extinctions are not fully understood, they occurred in two of the most densely populated regions of Central Africa, the Cross River region between Cameroon and Nigeria, and the Albertine Rift Mountains (Burgess et al., 2007).

Across the Congo Basin, "bushmeat" constitutes the primary source of animal protein for the majority of the rural population, and the bulk of the species captured by hunters in these rural areas consists of medium-sized ungulates, such as forest duikers and red river hogs (Wilkie and Carpenter, 1999). Interestingly, a first study on leopard feeding habits in a forest reserve in DRC revealed that leopard prey was likewise dominated by medium-sized ungulates (Hart et al., 1996). These results were corroborated in subsequent studies on leopard feeding habits from protected areas throughout the Congo Basin (Ososky, 1998, Ray

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and Sunquist, 2001, Henschel et al., 2005), and correspond well with data on leopard prey preferences from across their range (Hayward et al., 2006aa). In densely populated areas and urban markets across the Congo Basin, however, rodents have recently gained importance as food items, and this is seen as a sign that duikers and other larger-bodied species have become depleted in nearby forests (Wilkie and Carpenter, 1999).

That populations of big cats may decline as a direct consequence of exploitation competition with human hunters, has already been suggested for felids in the Neotropics (Jorgenson and Redford, 1993) and also for leopards in the Congo Basin (Hart et al., 1996, Ray, 2001). Since leopard population density is known to be positively correlated with the biomass of their preferred prey across their range in eastern and southern Africa (Marker and Dickman, 2005, Hayward et al., 2007), the same principles are likely to apply for leopards in the Congo Basin rainforest. It therefore appears logical that the bushmeat harvest and consumption across the Congo Basin – estimated to be in excess of 1 million metric tons per annum (Wilkie and Carpenter, 1999) – has had a marked effect on leopard populations, and it is possible that the local extinctions of leopards in parts of the Cross River region and the Albertine Rift may be a result of this intensified competition for prey with human hunters.

Leopards – a new dataset from Gabon

To investigate the exact manner in which the bushmeat harvest affects leopard populations in the Congo Basin, hunting intensity, leopard population density and diet, and the abundance of preferred leopard prey was recently determined in four rainforest sites in central Gabon. The sites were located at varying distances from settlements (range 6–24 km, measured from the centre of the site), and two of them were inside a protected area and two were village hunting zones (see chapter 2 for a detailed description). The results revealed a clear pattern: hunting was most intense near settlements, and signs of hunting were only rarely detected beyond 12 km from settlements. No leopards were photographed at one commercially hunted study site, and population densities at the remaining sites varied between 2.7 and 12.1 leopards/100 km^2 (Table 3.4). Leopard population density and area use increased significantly with distance from settlements. While no leopard scats were found at the commercially hunted site, mean leopard prey weight varied between 19.8 and 31.6 kg at the remaining sites (see chapter 2, Table 2.4), and both mean prey weight and the proportion of ungulate prey in leopard diet increased with distance from settlements. No larger prey

species were detected at the commercially hunted site and, across sites, the abundance of larger ungulates increased with distance from settlements (Table 3.5). These data suggest that there is a strong correlation between commercial bushmeat hunting near settlements and the local disappearance of leopards.

Across the Congo Basin, roads, major rivers and, occasionally, railway lines represent points of market access which facilitate the commercialization of local bushmeat hunting. Access to transportation is a crucial step leading to unsustainable levels of hunting (Wilkie and Carpenter, 1999). Consequently, the distance from public roads was a strong predictor of forest elephant and duiker abundance, human presence and levels of poaching (Blake et al., 2007, Laurance et al., 2006b). Similarly, variation in area use by leopards across the four study sites in central Gabon was best explained by the distance from settlements when occupancy modelling was used to analyse camera trap data; the most likely model indicated that leopard area use increased with distance from settlements (Table 3.6).

The same patterns are likely to apply across the Congo Basin, but reliable data on leopard occurrence from this region are too sparse to allow regional priority-setting exercises similar to those conducted for jaguars (Sanderson et al., 2002) and tigers (Wikramanayake et al., 1998), or to construct more sophisticated spatially explicit habitat models (e.g. Schadt et al., 2002). Besides a larger set of reliable leopard presence/absence data from sites across the Congo Basin, a realistic leopard population model for this region would need to incorporate data on habitat type and quality, its connectivity and productivity, forms of land use, and infrastructure and human population density. However, since leopard area use in central Gabon was best explained by the distance from settlements and, to a minor degree, public roads (Table 3.6), it seems reasonable to construct a simple geographic population model to predict leopard occurrence based on the distribution of these features.

Accurate geographic datasets containing both public and logging roads and settlements were available for the western proportion of the Congo Basin (provided by Global Forest Watch World Resources Institute, Washington, DC, United States). Based on leopard data from Gabon, all suitable leopard habitat within the Congo Basin was divided into three different strata. These widths of individual strata were defined based on camera trap data from study sites in central Gabon (Henschel and Ray, 2003, and chapter 3), and information on hunter area use (Coad, 2007). The first stratum comprised areas that were unlikely to support any resident leopards, and was defined by a buffer of 10 km around roadside settlements and of 5 km around settlements with no road and market access, and

thus no commercial hunting. Secondly, an intermediate stratum was defined that extended 5 km beyond the first "leopard-free" stratum and probably still experiences a degree of hunting but is likely to support leopards at reduced densities. Thirdly, a remote stratum was defined at a minimum distance of 15 km from roadside settlements or 10 km from settlements with no road access, which represents core leopard areas that receive little hunting pressure. All geographic data were imported into an ESRI ArcGIS 9.1 software package (Redlands, California, United States), and strata were mapped with the "Buffer Wizard" extension, whereby isolated core areas of less than 50 km^2 were excluded. While this simple stratification model cannot be expected to reliably predict leopard occurrence across the Congo Basin, it can draw attention to areas where leopards are seemingly extirpated or where there could be large populations that might merit focused conservation effort.

The model results were supplemented by any available information on leopard occurrence from field surveys in potential leopard habitat, almost all of which were conducted in the larger protected areas across the region. Leopards or other carnivores were among the researched species at only a few sites, and information on the occurrence of leopards comes mainly from general wildlife surveys. These surveys generally rely on the detection of spoor for terrestrial species, as direct observations are rare in rainforest habitat. Inside protected areas in Gabon and CAR, signs of leopard are usually encountered on a daily basis and, even in hunted areas, the presence of leopards in a given area becomes relatively unlikely if no evidence is encountered during several weeks of fieldwork (Henschel and Ray, 2003). Survey results were utilized only where the survey methods were appropriate to detect signs of leopard, and sites with no surveys or an inappropriate survey protocol were categorized as "data deficient". Accurate geographic coverage of roads, settlements and data from wildlife inventories were not available for large parts of both DRC and CAR, and therefore data on the status of leopards are presented only for the western proportion of the Congo Basin (Table 4.1; Figure 4.2).

Leopards – current status

In Gabon and Congo, leopards are still widely distributed and were detected in all but one (Mwagné National Park in Gabon) of the larger protected areas that were surveyed in these two countries (Table 4.1; Figure 4.2). Survey effort was extremely low at this site and local hunters reported the species as present (Maisels et al., 2004).

Table 4.1. Larger protected areas in the western proportion of the Congo Basin, with their current classification, IUCN protected area category, size and location, and data on the presence/absence of leopards at the site. Presence/absence of leopards at any given site was predicted using a geographic population model based on field data from Gabon (see text for details), and supplemented with field survey data from the respective protected area. Numbers in the first column refer to protected area locations shown in Figure 4.2.

Id	Name	IUCN PA category[a]	Size (km^2)	Country	Population model prediction	Leopard status at site indicated by surveys	Source (personal communication or reference)
1	Cross River NP	II	3650	Nigeria	Present	Confirmed present	(Okon, 2005)
2	Korup NP	II	1300	Cameroon	Present	Not detected	(C. Astaras)
3	Mont Cameroun FR	None	650	Cameroon	Absent	Not detected	(Forboseh et al., 2007)
4	Takamanda FR	None	600	Cameroon	Present	Not detected	(Sunderland-Groves and Maisels, 2003)
5	Banyang-Mbo WS	IV	700	Cameroon	Present	Not detected	(Willcox, 2002)
6	Douala Edéa FR	IV	1700	Cameroon	Present	Not detected	(Ngandjui and Blanc, 2000)
7	Ebo Forest	None (II)	1400	Cameroon	Present	Not detected	(B. Morgan)
8	Campo Ma'an NP	II	2600	Cameroon	Present	Confirmed present	(Matthews and Matthews, 2006)
9	Mpem et Djim NP	II	1050	Cameroon	Present	No data	
10	Mbam et Djerem NP	II	4300	Cameroon	Present	Confirmed present	(Maisels et al., 2000)
11	Dja Reserve	IV	5900	Cameroon	Present	Confirmed present	(Williamson and Usongo, 1995)
12	Boumba Bek-Nki	None (II)	5600	Cameroon	Present	Confirmed present	(Madzou and Ebanega, 2006)
13	Lobéké NP	II	2150	Cameroon	Present	Confirmed present	(Ekobo, 1998)
14	Dzanga-Sangha NP and Reserve	II + IV	1250+ 3100	CAR	Present	Confirmed present	(Ray and Sunquist, 2001)
15	Nouabalé-Ndoki NP	II	4100	Congo	Present	Confirmed present	(Ososky, 1998)
16	Odzala-Kokoua NP	II	13600	Congo	Present	Confirmed present	(Henschel, 2008)
17	Bambama-Lékana	None (II)	3900	Congo	Present	Confirmed present	(Aust and Inkamba Nkulu, 2005)

Table 4.1. Continued.

18	Léfini Reserve	IV	6650	Congo	Present	Confirmed present	(Mathot et al., 2006)
19	Conkouati-Douli NP	II	5050	Congo	Present	Confirmed present	(H. VanLeeuwe)
20	Moukalaba-Doudou NP	II	4450	Gabon	Present	Confirmed present	(Boddicker, 2006)
21	Loango NP	II	1550	Gabon	Present	Confirmed present	(Boddicker, 2006)
22	Birougou NP	II	700	Gabon	Present	Confirmed present	(Aba'a Nseme and Bezangoye Ndoukoue, 2007)
23	Batéké Plateau NP	II	2050	Gabon	Present	Confirmed present	(Bout, 2006)
24	Waka NP	II	1050	Gabon	Present	Confirmed present	(Abitsi, 2006)
25	Lopé NP	II	4950	Gabon	Present	Confirmed present	(Henschel et al., 2005)
26	Wonga-Wongué Reserve	IV	4950	Gabon	Present	No data	
27	Pongara NP	II	850	Gabon	Present	Confirmed present	(Latour, 2006)
28	Ivindo NP	II	3000	Gabon	Present	Confirmed present	(this study)
29	Mwagné NP	II	1150	Gabon	Present	Not detected	(Maisels et al., 2004)
30	Monts de Cristal NP	II	1200	Gabon	Present	Confirmed present	(Aba'a Nseme, 2006)
31	Minkébé NP	II	7550	Gabon	Present	Confirmed present	(W.W.F. Minkébé, unpublished data)
32	Altos de Nsork NP	II	400	Equatorial Guinea	Present	Not detected	(Larison et al., 1999)
33	Estuario del Muni Reserve	IV	700	Equatorial Guinea	Absent	No data	
34	Monte Alén NP	II	2000	Equatorial Guinea	Present	Confirmed present	(Nchanji et al., 2005)
35	Rio Campo Reserve	IV	350	Equatorial Guinea	Absent	Not detected	(Larison et al., 1999)

[a]IUCN categories listed in parentheses are the levels that will be assigned once the areas are upgraded; these sites have been proposed as national parks. IUCN categories: (II) National Park; (IV) Habitat/Species Management Area.

CAR, Central African Republic; Congo, Republic of Congo; FR, forest reserve; IUCN, International Union for the Conservation of Nature and Natural Resources; NP, national park; PA, protected area, WS, wildlife sanctuary.
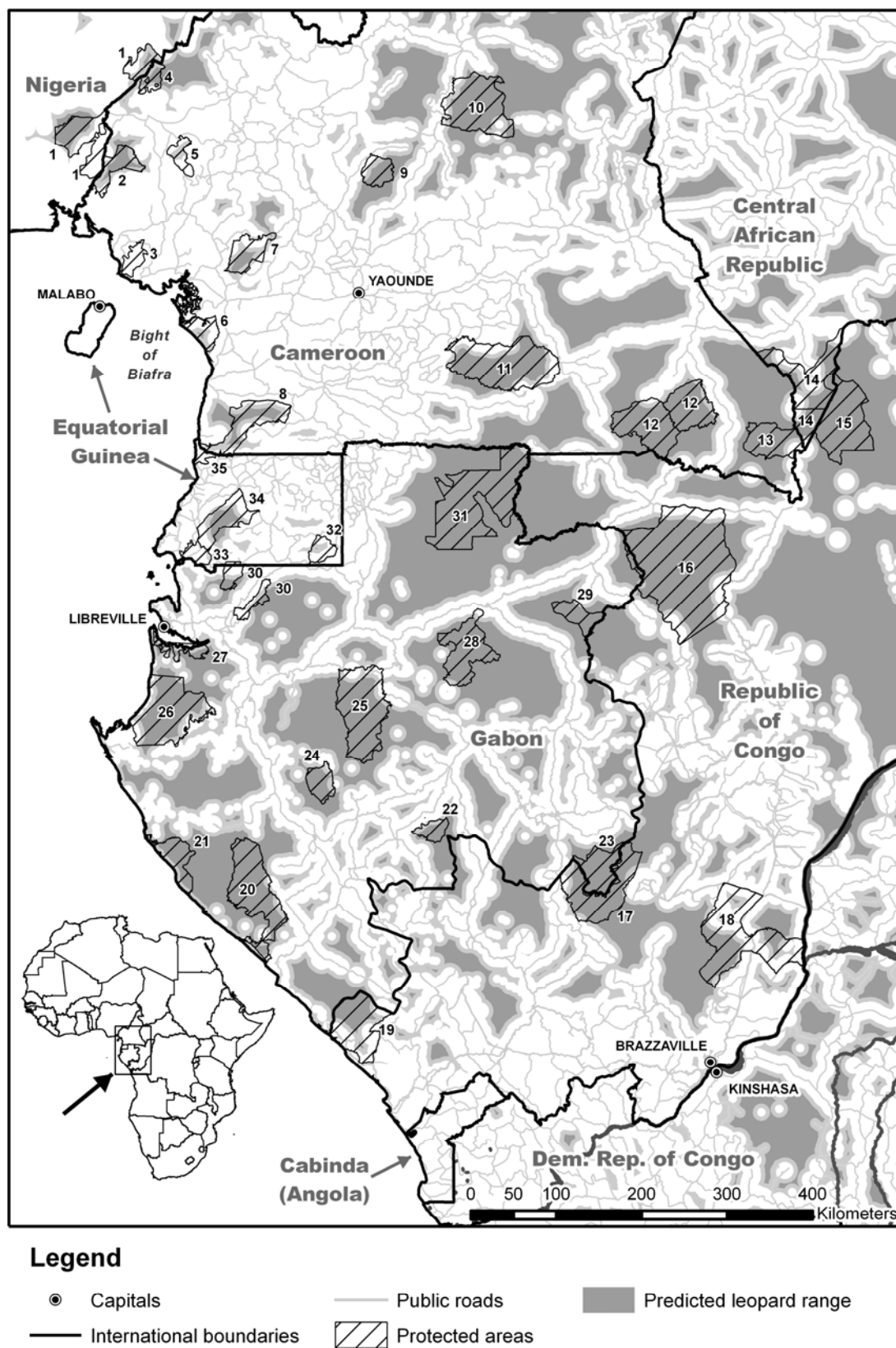
Figure 4.2. Predicted distribution of leopard in the western proportion of the Congo Basin (arrow in insert). Numbers refer to protected areas listed in Table 4.1.

In Equatorial Guinea, leopards appear largely absent across the country and were only confirmed for the Monte Mitra Forest inside Monte Alén National Park (Nchanji et al., 2005), where the species survives in an isolated population (Table 4.1; Figure 4.2). In the rainforests of southern Cameroon, leopards still have a wide distribution in the east, where they occur in all protected areas. In the more densely populated south-western part of the country, leopards have almost completely disappeared, and isolated populations can only be found in Campo Ma'an National Park, on the border with Equatorial Guinea (Matthews and Matthews, 2006), and possibly in Korup National Park in the Cross River region (Table 4.1; Figure 4.2). Although signs of leopard were never detected in the Korup area despite extensive fieldwork (e.g. Forboseh et al., 2007, Astaras et al., 2008), local hunters report the species as present, and leopard tracks were recently confirmed across the border in the southern section of Nigerian Cross River National Park (Okon, 2005). For southern Nigeria, this represents the only recent record for the species' presence, and leopards can be regarded as virtually extinct there (Angelici et al., 1998).

The leopard population model predicted leopards to be absent in only two of the 32 protected areas with available survey data, and no leopards were detected during field surveys at these sites (Table 4.1). Signs of leopard presence were equally not detected at an additional seven protected areas that contained core leopard areas according to model predictions (Table 4.1; Figure 4.2), suggesting either that the model was inappropriate or too optimistic, or that leopards do in fact occur at these sites and were simply not detected in surveys. Interestingly, all protected areas that had no confirmed records of leopard presence were smaller than 2000 km[2,] and most of these were situated in south-western Cameroon or Equatorial Guinea whereas, in Gabon, leopards were recorded in almost all sites irrespective of their size (Table 4.1). In Gabon, leopards occur widely even outside protected areas, and populations in the smaller parks and reserves form part of larger, contiguous populations. In south-western Cameroon and Equatorial Guinea (Figure 4.2), however, the species' range has contracted to small, isolated populations, and this might already have led to local extinctions in the smaller forest reserves.

Large savannah carnivores – historical distribution

Historically, lions, African wild dogs and spotted hyenas probably occupied all suitable open habitat within the northern part of the Western Congolian forest–savannah

mosaic, yet missionaries documented the local disappearance of lions from the coastal savannahs of today's Congo and Cabinda as early as 1750. Likewise, du Chaillu (1861) did not encounter lions when he explored the grasslands behind the coast of today's Gabon, where he recorded only leopards, African wild dogs and spotted hyenas. Further inland, however, in the extensive grasslands north of the Congo River, explorers and ethnologists alike still described lions as locally common around 1900 (e.g. Guiral, 1889, Dusseljé, 1910).

The first comprehensive study on the fauna in this part of Africa was conducted almost 50 years later, by naturalists Malbrant & Maclatchy (1949), and their contribution remains the only attempt so far to map the distribution of the larger carnivores in this region. By the time of their study, lions had disappeared from the savannahs of southern Congo around Brazzaville (Figure 4.1b), whereas African wild dogs and spotted hyenas had suffered no apparent range loss and were still widely distributed (Figure 4.1c,d). Lions appeared most abundant in the Léfini Reserve and Odzala-Kokoua National Park (Figure 4.1a), while African wild dogs and spotted hyenas were described as locally common in many localities, including the coastal savannahs (Malbrant and Maclatchy, 1949), along which African wild dogs in particular had penetrated deeply into Gabon (Figure 4.1c).

Large savannah carnivores – recent decline

The dramatic range loss that occurred over the following decades is very poorly documented, but seems to be tied to a massive reduction in wild prey and an increased persecution of the carnivores themselves. Pastoralism was never extensively practised by the inhabitants of the Western Congolian forest–savannah mosaic, and the wild game that constituted the major source of animal protein was traditionally killed in well-organized net-hunts (Dusseljé, 1910). Larger species like forest buffalo and forest elephants were reportedly not very vulnerable to this form of hunting (Dusseljé, 1910). Hunting with guns gradually replaced the traditional net-hunting, however, and the larger species soon disappeared from densely populated landscapes (Malbrant and Maclatchy, 1949). This trend continued, and today the forest buffalo is largely absent from southern and central Congo and south-eastern Gabon, and the largest remaining population in the Western Congolian forest–savannah mosaic is thought to occur in the remote Odzala-Kokoua National Park in northern Congo (East, 1999). Similarly, waterbuck and southern reedbuck have lost much of

their former range, and both species might be extinct in Congo, whereas their range in Gabon is restricted to the band of savannah extending south from Moukalaba-Doudou National Park on the coast (East, 1999). The extreme scarcity of wild prey has also led to an increase in human–carnivore conflict, particularly in the surroundings of newly established cattle ranches (Malbrant and Maclatchy, 1949). It is these cattle ranches which precipitated the initiation of programmes that relied on professional hunters (e.g. de Baleine, 1987), as well as on poisoning, to eradicate large carnivores (Henschel, 2006). No official records are available stating the number of large carnivores killed in these programmes, but accounts by villagers document that lions were still present in the region of the Léfini Reserve around 1960 (Sautter, 1960), and that entire prides were poisoned by ranch owners in neighbouring Gabon in the 1970s (Henschel, 2006).

Large savannah carnivores – current status

By 1990, it was believed that lions had disappeared from Léfini and that the only population in Congo survived in a hunting reserve that is today incorporated into the Odzala-Kokoua National Park (Dowsett, 1995). In 1994, two male lions were shot in this reserve after they attacked and killed a worker at the reserve's headquarters. These two individuals were considered to be "two of Congo's last lions" (Dowsett, 1995). Following this incident, very few substantiated records of lion presence were obtained at this site, and most occurred within a few months after the killing (Dowsett and Dowsett-Lemaire, 1997). A comprehensive large-carnivore survey at the site in 2007 did not produce any signs of lion presence (Henschel, 2008). In neighbouring Gabon, one male lion accompanied by a female was shot north of the Batéké Plateau National Park in 1995 (Figure 4.1b), and one female was observed in the same area 1 year later (Henschel, 2006). Two lion surveys in this part of Gabon in 2001 and 2003, respectively, did not produce any evidence of lion presence (Henschel, 2006); however, one set of felid tracks identified as lion was detected by a team conducting wildlife monitoring inside the Batéké Plateau National Park in 2004 (Bout, 2006). This single set of tracks remains the sole convincing evidence of lion presence found within the Congo Basin in more than one decade, and it therefore seems reasonable to assume that lions are effectively extinct in this northern part of the Western Congolian forest–savannah mosaic.

The data on African wild dogs are extremely scarce. While the species was listed as extinct in this region in the most recent status survey (Sillero-Zubiri et al., 2004), it was acknowledged in a prior status survey that there are still occasional rumours of their presence in coastal Gabon (Woodroffe et al., 1997). The rumours and occasional unconfirmed sightings persist in one region west of Moukalaba-Doudou National Park in Gabon (L. White, Wildlife Conservation Society; personal communication), and similar reports originate from one area in north-eastern Congo (Figure 4.1c). The last confirmed sighting dates back to 1991, when one individual was observed in a savannah south of Conkouati-Douli National Park in coastal Congo (Dowsett and Dowsett-Lemaire, 1991). While it cannot be ruled out that a few individuals persist in one of the aforementioned areas, there is no recent field evidence suggesting the presence of a resident population of African wild dogs anywhere within this northern part of the Western Congolian forest–savannah mosaic.

Spotted hyenas also experienced an extreme collapse of their former range within the Congo Basin but, until recently, two resident populations persisted in Congo – one on the coast in Conkouati-Douli National Park and one in the north in Odzala-Kokoua National Park (Mills and Hofer, 1998). While no additional signs of hyena presence were found in Conkouati-Douli National Park in the past decade (H. van Leeuwe, Wildlife Conservation Society; personal communication), the species was still locally abundant in the savannah sector of Odzala-Kokoua National Park in 2007 (Henschel, 2008). Furthermore, in recent years, several individual spotted hyenas have been recorded at different localities within the Congo Basin, deep inside rainforest habitat (Juste and Castroviejo, 1992, Henschel and Ray, 2003, F. Maisels, Wildlife Conservation Society; personal communication) and at distances of between 200 and 420 km from the nearest known hyena population in Odzala-Kokoua National Park (Figure 4.1d). In all cases, these were single individuals that were either found dead (Juste and Castroviejo, 1992, F. Maisels, Wildlife Conservation Society; personal communication), or were recorded only once in an area (Henschel and Ray, 2003). The available information suggests that there is currently just one resident population of spotted hyenas in this northern part of the Western Congolian forest–savannah mosaic, which occupies the savannah sector of Odzala-Kokoua National Park. The observations of individuals recorded at other sites in recent years might represent unsuccessful dispersal events from the Odzala population.

Is there a need for reintroduction?

Leopards

The current status of leopards in the rainforests of central and north-eastern Gabon, northern Congo and south-eastern Cameroon can be regarded as secure. In this sparsely settled region, leopards occur in contiguous populations (Figure 4.2) and large, remote protected areas, such as Minkébé National Park in Gabon and Odzala-Koukoua National Park in Congo, can potentially secure the long-term survival of leopards. In the human-dominated landscapes of Equatorial Guinea, south-western Cameroon and southern Nigeria, however, leopards are absent from most protected areas (Table 4.1; Figure 4.2). There are in fact indicators that in some parts of these so-called Biafran forests (Figure 4.2), leopards had already disappeared several decades ago. Hunter interviews at two forest sites in south-western Cameroon revealed that, at these sites, leopards had not been documented for more than 30 years (Maisels et al., 2001, Willcox, 2002), and this discovery raised concern that the absence of the apex predator of the system might have already led to a localized increase in herbivores and, therewith, associated changes in forest dynamics and composition at these sites (Willcox and Nambu, 2007).

However, evidence of change has been emerging in recent years. The discoveries of remnant populations of highly endangered primate species (e.g. Morgan et al., 2003), and the growing recognition of the Biafran forests as a biodiversity hotspot (Oates et al., 2004) and a centre of endemism (Bergl et al., 2007), has reinvigorated plans to enlarge the protected area network and to increase the protection status at a number of sites (Morgan and Sunderland-Groves, 2006, Bergl et al., 2007, Forboseh et al., 2007). Leopards, as the dominant predator of this forest, should ultimately be restored to re-establish their ecological functionality, which is considered to be one of the central arguments for the restoration of large carnivores (Berger, 2007). However, reintroductions of large carnivores are extremely lengthy, costly and complex processes (IUCN, 1998) and should be avoided if it appears possible to protect and encourage the remnants of an existing population (Yalden, 1993).

The joint results from the geographic population model and wildlife surveys suggest that in the Biafran forest region leopards still persist in at least three protected areas: the southern section of the Cross River National Park in Nigeria, Campo Ma'an National Park in Cameroon and Monte Alén National Park in Equatorial Guinea (Table 4.1; Figure 4.2). For the conservation of leopards in these forests, it should be an absolute priority to strengthen

these three populations and to avert their local extinction. Any such effort should begin with systematic presence/absence surveys in these national parks, in order to map the current occurrence of leopards across the landscapes and to investigate the factors that determine whether they are present. This would allow the identification of core populations and the formulation of strategies for their protection. If properly managed, these parks could potentially harbour 90–120 leopards, based on their size and an average population density estimate of 4.6 leopards/100 km^2 obtained at a protected area in Gabon (see chapter 3).

Closed populations of this size can be expected to suffer from genetic deterioration through inbreeding, and several migrants per generation would need to be translocated between reserves to compensate for these effects (Frankham, in press). This requirement would need to be incorporated into any strategy designed to secure the long-term survival of leopards in these parks. However, costly approaches involving periodic translocations to mimic natural dispersal, which have been used for large carnivores elsewhere (e.g. Gusset, in press), do not seem feasible in the Congo Basin. The major obstacles are poor infrastructure in most protected areas and the lack of expertise needed for large-carnivore reintroductions; most protected areas possess no functional road network and, to date, not a single large carnivore has ever been captured alive and radio-collared anywhere in the Congo Basin.

A more suitable approach would be to design a leopard conservation landscape around the remnant populations of the Biafran forest using cost–distance models, which have found prior use in the management of metapopulations of other species of large cats in human-dominated landscapes (e.g. Wikramanayake et al., 2004). Through rigorous protection of potential dispersal corridors, the populations in Campo Ma'an and Monte Alén could probably be reconnected to populations in northern Gabon, and the Cross River National Park population could potentially expand into the Korup National Park and adjoining forest reserves. Setting aside all financial and logistical constraints, reintroductions of individual leopards into any of these sites would exclusively promote the persistence of one single species. The establishment and maintenance of wildlife corridors between individual protected areas, however, would encourage dispersal for a whole suite of larger mammals.

Spotted hyenas

The status of the spotted hyena in the isolated northern part of the Western Congolian forest–savannah mosaic is critical, with just one resident population remaining in the savannah sector of the Odzala-Kokoua National Park. The loss of this population would represent the local extinction of the species from its former range in Gabon and Congo and, owing to the geographical isolation of the Western Congolian forest–savannah mosaic, the chances for natural recolonization would be minimal. As for the leopard, it should be a priority to secure the conservation of this last, isolated population to avoid the need for reintroduction to restore the species in this region.

Spotted hyenas have been completely protected under Congolese law since 1983 (IUCN, 1989) but, to date, there have been no detailed scientific studies on the species in Congo, and no focused attempt to secure its survival there. Nonetheless, spotted hyenas persist in a small population in the savannah sector of the remote Odzala-Kokoua National Park, but not much is known about the current status of this population. Odzala-Kokoua National Park is the largest protected area in Congo since its extension in 2001, when the park size increased from 2800 km^2 to 13,600 km^2 (Aveling and Froment, 2001). However, open habitat suitable for spotted hyenas can only be found on the southern tip of the park and, in the course of the park extension in 2001, the extent of savannah habitat under protection increased only slightly from 750 km^2 to just above 1000 km^2, despite the existence of an additional 1500 km^2 of uninhabited, open habitat just south of the park. Owing to uncontrolled hunting and the resulting scarcity of prey, these unprotected savannahs are currently not occupied by spotted hyenas. Even inside the park, hyenas appear most common in the remoter savannah areas, and signs of hyena and potential prey are largely absent towards the southern limit of the park where signs of hunters is frequent (Henschel, 2008). Overall, the species currently occupies an area of approximately 500 km^2, and a minimum of 46 individual spotted hyenas were identified from camera trap photographs during an initial large-carnivore survey in 2007 (Henschel, 2008).

The small size of the area currently occupied by the species and the complete isolation of this population make it inevitable that inbreeding and loss of genetic diversity has occurred (Frankham, in press). Consequently, a study should be conducted to assess the genetic diversity of this population and to investigate the need for population supplementation to enhance the genetic diversity.

Irrespective of whether or not an introduction of unrelated individuals into the population of Odzala-Kokoua National Park is deemed necessary, the range and size of this population should be increased. This could be achieved by promoting more rigorous protection of the savannahs towards the southern limit of the park and by including the 1500 km^2 of open habitat into the park limits that are currently without protection and do not support any resident hyenas. Another prospect might be the establishment of a second population of spotted hyenas in the centre of their former range, the Batéké Plateau (Figure 4.1a). The Batéké Plateau National Park in Gabon and the proposed Bambama-Lékana National Park across the border in Congo will together protect almost 6000 km^2 of intact grasslands but, owing to uncontrolled hunting preceding the recent establishment of the Gabonese park, and ongoing hunting on the Congolese side, potential prey is only patchily distributed and numbers are low (Bout, 2006). However, the continued protection of these parks will ultimately lead to an increase in ungulate populations, and the restoration of a hyena population in this landscape would serve two conservation goals simultaneously. Large-bodied and/or social carnivores that are capable of killing comparatively large prey, and reach high population densities, can be expected to have the greatest impact on ecosystem function (Woodroffe and Ginsberg, 2005). The restoration of spotted hyenas in these parks would be an important step towards the restoration of ecological functionality in this landscape, and the establishment of a well-protected population of spotted hyenas would significantly increase the prospects for the long-term survival of this species in this region.

The distance between the current population in Odzala-Kokoua National Park and the Batéké Plateau is 250 km. The records of spotted hyenas in forest sites across this region in recent years (e.g. Juste and Castroviejo, 1992), however, suggest that individuals travel even farther in their search for suitable habitat. While dispersal is usually male-biased in spotted hyenas (Boydston et al., 2005), clan fission and dispersal by females has also been observed when the carrying capacity of the natal home range is reached and when food availability is therefore low (Holekamp et al., 1993). Corridors should be identified and protected to encourage dispersal, and strategically located stepping-stones could be used to increase dispersal success (Wikramanayake et al., 2004). Ultimately, Léfini Reserve could be connected to the Batéké Plateau/Bambama-Lékana National Parks, although its proximity to Brazzaville and the immense demand, originating from the capital, for wild meat has made the protection of this site very challenging in the past.

Lions and African wild dogs

The current situations for lions and African wild dogs in the Congo Basin have certain similarities. Despite persistent rumours about their presence in some areas and occasional unconfirmed reports about sightings of their sign, no material evidence of their presence has been produced for more than a decade, and it seems reasonable to assume that both species are virtually extinct in this northern part of the Western Congolian forest–savannah mosaic. The nearest known populations for both species are in northern Cameroon (Chardonnet, 2002, Sillero-Zubiri et al., 2004) and are separated from the Western Congolian forest–savannah mosaic by a 1000-km wide continuous rainforest belt. Natural reinvasions are therefore highly unlikely, and any effort to re-establish either species would inevitably involve the introduction of captive or wild individuals from outside this region.

Given the high cost and complexity of large reintroduction programmes (IUCN, 1998), a number of factors have to be considered thoroughly when deciding whether or not a reintroduction of a large carnivore should be attempted. These include:

1) The justification for the reintroduction – will it mark a significant contribution to the survival of a species or the functionality of an ecosystem? (IUCN, 1998, Berger, 2007);

2) Biological/technical aspects, such as the availability of protected habitat, prey and a suitable release stock (IUCN, 1998);

3) Organizational aspects, such as the availability of adequate human and financial resources for the reintroduction (Yalden, 1993);

4) Valuational aspects, such as the local perception of wildlife in general, and attitudes towards the reintroduction of a specific large carnivore in particular (Reading and Clark, 1996).

The above factors should all be addressed in an initial feasibility assessment that should precede any well-planned reintroduction programme (IUCN, 1998); however, the reintroduction of a large-carnivore species has never been attempted or even considered in this region, and many of the questions revolving around the feasibility of such a task simply cannot be addressed at this stage. Nonetheless, there appear to be two central factors of disproportionate importance when considering the reintroduction of either lions or African wild dogs into this region: the availability of protected habitat and community attitudes towards the species.

Availability of protected habitat

In the open landscape of this forest–savannah mosaic, prey is scarce outside protected areas as a result of uncontrolled bushmeat hunting, and this can be considered the main cause underlying the initial decline of large carnivores in this region. In a region where bushmeat constitutes the primary source of animal protein for the majority of the rural population, the survival of large carnivores and their prey can most likely only be ascertained through the designation and rigorous protection of sufficiently large protected areas.

The last sightings of African wild dogs occurred in the coastal savannahs in Congo and Gabon (Figure 4.1c), which are also the last refuge for waterbuck and southern reedbuck in this region (East, 1999). Both species of ungulates are in the body-mass range of preferred prey species for wild dogs (Hayward et al., 2006b), and their presence along the coast might have facilitated the persistence of wild dogs in this area. The coastal region, however, is characterized by a relatively dense human population, and there are no protected areas that contain substantial expanses of open habitat, nor is there uninhabited land available which would permit the creation of new ones (Figure 4.1a). The only large expanse of uninhabited and unfragmented open habitat that remains in the Western forest–savannah mosaic is the Batéké Plateau, but prey availability is low and both waterbuck and southern reedbuck no longer occur even inside the protected areas in this landscape (Bout, 2006, Mathot et al., 2006). While prey populations could be increased by protecting these parks and ungulate species could be reintroduced, the size of the current and proposed protected areas will most likely be too small to support a viable, self-sustaining population of African wild dogs. Wild dogs generally occur at low densities even in the absence of larger competitors, and the species is reportedly very vulnerable to anthropogenic mortality (Woodroffe et al., 1997), which can be high even inside protected areas (Rasmussen, 1997). Mortality along reserve borders has a greater effect on population persistence in smaller parks and reserves (Woodroffe and Ginsberg, 1998), and African wild dogs are considered to require protected areas in excess of 10,000 km^2 to maintain viable populations (Woodroffe and Ginsberg, 1999).

Lions, however, are capable of reaching high population densities when preferred prey is abundant, and have good chances of persistence even in comparatively small parks and reserves (Woodroffe and Ginsberg, 2005). As the dominant predator, their numbers in protected areas are determined chiefly by the available biomass of their preferred prey, and a

monitoring of ungulate biomass in the protected areas of this landscape could be used to predict carrying capacity for lions at these sites (Hayward, in press). Furthermore, this technique could help to decide when and if a lion reintroduction would most likely lead to the establishment of viable population.

Attitudes towards carnivores

Any reintroduction of large carnivores needs the consensus of the local human population (Moore, 1992), as a lack of acceptance often leads to the killing of reintroduced individuals (e.g. Breitenmoser et al., 2001). While, in general, reintroduced animals might be relatively safe from direct persecution inside protected areas, large carnivores are wide-ranging, and human-induced mortality on reserve borders has been shown to lead to the extinction of local populations of large carnivores (Woodroffe and Ginsberg, 1998). Lions, in particular, have long been feared by the local population inhabiting the Western forest–savannah mosaic (Guiral, 1889, Dusseljé, 1910, Malbrant and Maclatchy, 1949, Sautter, 1960), but virtually nothing is known about people's attitudes towards spotted hyenas and African wild dogs.

If the attitudes of the local population towards lions were to remain unchanged, any attempt to reintroduce them into this northern part of the Western Congolian forest–savannah mosaic would inevitably fail. A possible incentive to further the acceptance of lions in the local population might the contribution of revenues from wildlife tourism to local communities. For the Gabonese government, a major impetus for establishing new national parks was the prospect of developing a viable ecotourism industry (Laurance et al., 2006a). Creating the possibility for tourists to observe western lowland gorillas Gorilla g. gorilla and lions in one national park has the potential to allow for an increase in ecotourism in areas where the economic incentives to communities are well understood and accepted.

General conclusions

- Leopards exhibited a strong functional response to competition with hunters in the vicinity of settlements, where they showed a significantly higher use of small-bodied prey compared to the remoter study sites. Camera trap data on prey abundance confirmed that large (>20 kg) prey was significantly less abundant at sites in the vicinity of settlements, strongly suggesting that the observed functional response was indeed caused by the local depletion of larger, more preferred leopard prey.

- Leopard equally showed a strong numerical response to competition with hunters in the vicinity of settlements, and leopard population density increased with growing distance from settlements. Leopard area use was positively correlated with the relative abundance of prey and distance from settlements.

- In the immediate vicinity of settlements, leopards were never recorded. The entire village hunting territory at my study site 1, which extends up to 12 km north of the village, is not believed to support a resident population of leopards. Hunters catch at this site is dominated by brush-tailed porcupines and blue duikers (Coad, 2007), and our data on leopard feeding ecology and population density suggests that leopards are not capable of subsisting entirely on these small-bodied prey species that persist at intensively hunted forest sites. Leopards in the Congo Basin rainforests appear to depend on a prey-base of medium-sized and large ungulates such as 'red' duikers and red river hogs for their survival.

- Even at our most remote and intact site 4, leopard density (12.08 ± 5.11 leopards/100 km^2) was greatly below the frequently-cited estimates of 33-40 leopards/100 km^2, suggested for rainforest habitat in Africa by Martin & de Meulenaer (1988), based on their population model linking leopard densities with annual rainfall. This emphasises that extrapolations on leopard numbers, status and resilience in rainforest regions have to be viewed with extreme caution, if the data used in these models has been collected on leopards in a different ecological context (e.g. Martin and de Meulenaer, 1988, Woodroffe, 2000).

- Considering that the human population in the Congo Basin is rapidly growing and that substitutes for bushmeat are unavailable for the majority of the rural population, it can be expected that larger-bodied prey species will be extirpated from all areas of forest proximal

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to population centres (Wilkie and Carpenter, 1999). Larger and relatively remote parks and reserves are therefore most likely the only places where leopards in the Congo Basin have the chance for long-term survival

- However, in the sparsely settled region of central and north-eastern Gabon, northern Congo and south-eastern Cameroon, the current status of leopards can still be regarded as secure. Leopards still occur in contiguous populations and large, remote protected areas, such as Minkébé National Park in Gabon and Odzala-Koukoua National Park in Congo, can potentially secure the long-term survival of leopards in this region.

- In the human-dominated landscapes of Equatorial Guinea, south-western Cameroon and southern Nigeria, leopards are absent even from most protected areas. The few small remnant populations in this so-called Biafran forest region will need immediate conservation efforts to avert their local extinction. These efforts should first concentrate on the protection of leopards and populations of their preferred prey. Ultimately, wildlife corridors could be established to connect the small, isolated remnant populations, and a leopard conservation landscape could be designed in this human-dominated landscape (Wikramanayake et al., 2004).

- Despite persistent rumours about lion and African wild dog presence in some areas, it seems reasonable to assume that both species are virtually extinct in Gabon and the Republic of Congo. Natural reinvasions into this region is highly unlikely owing to the geographical isolation of their former range in these countries, and any effort to re-establish either species would inevitably involve the introduction of captive or wild individuals from outside this region.

- Spotted hyenas survive only in one small population in Odzala National Park in the Republic of Congo. The disappearance of this single population would represent the local extinction of this species in the western Congo Basin. Immediate efforts should be undertaken to increase the size and the range of this population, by rigorously protecting suitable savannah habitat in the vicinity of Odzala, and by promoting hyena dispersal into these areas through the establishment and protection of suitable corridors.

- Immediate needs for further research on leopards include extensive presence/absence surveys in the critical leopard sites identified in this study, such as Cross River National Park in Nigeria, Campo Ma'an National Park in Cameroon, Monte Alén National Park in Equatorial Guinea, and other protected areas in this human-dominated landscape. A larger

set of leopard presence/absence data from a wide range of sites, differing in habitat type and quality, connectivity and productivity, forms of land use, infrastructure and human population density, would also permit us to construct a more sophisticated spatially explicit habitat model (e.g. Schadt et al., 2002) for leopards in this region. Furthermore, demographic data on leopards in the African rainforest environment would be required for the application on population viability analyses in this habitat. Of particular interest in the context of wildlife corridors to link smaller protected areas in the region, would be data on dispersal distances and mortality during dispersal.

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