

Wildlife Monitoring and Conservation in a West African Protected Area

By

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## ABSTRACT

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Global declines in biological diversity are increasingly well documented and threaten the welfare and resilience of ecological and human communities. Despite international commitments to better assess and protect biodiversity, current monitoring effort is insufficient and conservation targets are not being met (e.g., Convention on Biological Diversity 2010 Target). Protected areas are a cornerstone of attempts to shield wildlife from anthropogenic impact, yet their effectiveness is uncertain. In this dissertation, I investigated the monitoring and conservation of wildlife (specifically carnivores and other larger mammals) within the context of a poorly studied savanna reserve in a tropical developing region: Mole National Park (MNP) in the West African nation of Ghana.

I first evaluated the efficacy of the park's long-term, patrol-based wildlife monitoring system through comparison with a camera-trap survey and an assessment of sampling error. I found that park patrol observations underrepresented MNP's mammal community, recording only two-thirds as many species as camera traps over a common sampling period. Agreement between methods was reasonable for larger, diurnal and social species (such as many larger ungulates and primates), but camera traps were more effective at detecting smaller, solitary and nocturnal species (particularly carnivores). Long-term patrol data were also subject to considerable sampling variation that could make interpretation of wildlife trends unreliable, and I suggest ways in which this locally based monitoring program may be improved.

Given the ecological and cultural importance of carnivore species, their propensity for human conflict, and the difficulty with which they are monitored, I assessed their status and vulnerability to extinction in MNP. Only 9 of 16 historically occurring carnivore species were detected in the camera-trap survey (covering 253 stations deployed for 5,469 trap days between October 2006 and January 2009). A hierarchical multi-species occupancy model applied to camera-trap data indicated a low overall likelihood of the presence of undetected species. Results from concurrent sign, call-in, and village surveys, as well as patrol records, provided more

equivocal evidence of carnivore occurrence but supported the conclusion that many carnivores have declined and are likely functionally or fully extirpated from the park, including the top predator, lion (*Panthera leo*). Evidence of local human-carnivore conflict was also documented, including hunting of carnivores for traditional use and in retaliation for livestock depredation. Contrary to expectation, variation in carnivore persistence was not explained by ecological or life-history traits such as body size, home range size or fecundity, thus raising doubt as to the predictability of carnivore community disassembly.

I extended the multi-species occupancy model to test hypotheses about extrinsic influences on carnivore community dynamics in MNP. I derived spatially explicit GIS descriptors of heterogeneity in illegal hunting pressure, law enforcement patrol effort, prey biomass, and habitat productivity, and used a Bayesian modeling framework to assess support for their effects on carnivore occurrence. The framework explicitly accounted for spatial autocorrelation and variation in species- and site-specific detection probabilities. Contrary to my expectation, there was no indication of a consistent, negative effect of illegal hunting activity on spatial patterns of carnivore occurrence. By contrast, occurrence patterns of most species were positively associated with prey biomass, and several species had either positive or negative associations with riverine forest (but not with other indicators of habitat heterogeneity).

I conclude that pressure from hunting and other anthropogenic impacts remains high for West African wildlife, even within protected areas, but that human-wildlife relations are complex and their consequences inadequately predicted by simple models of extinction risk. Existing monitoring programs may generate data unsuitable for strong inference on wildlife community dynamics, and careful attention to objectives and methodology is needed. More attention to the protection and recovery of carnivore populations is also needed, as are further focused and interdisciplinary efforts to inform and improve wildlife conservation in West Africa.

I would like to dedicate this dissertation to the many Ghanaians working to conserve wildlife and find sustainable solutions to poverty alleviation in their country.

*“I can only believe, from somewhere deeper than any logic center of the brain, that a life of incomprehensible loneliness awaits a world where the wild things were, but are never to be again.”*

~ William Stolzenburg (2008)

*“If you look at the science about what is happening on earth and aren't pessimistic, you don't understand the data. But if you meet the people who are working to restore this earth and the lives of the poor, and you aren't optimistic, you haven't got a pulse.”*

~ Paul Hawken (2009)

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# CHAPTER 1

## General Introduction

This dissertation is broadly motivated by two fundamental themes in conservation science. The first is the growing threat to biological diversity imposed by an ever-expanding global human footprint, and the second is the uncertainty inherent to our understanding of ecological responses to this threat. Within these overarching themes, I aim to explore more specific topics, including the effectiveness of protected areas for biodiversity conservation, the challenge of accurate ecological monitoring, the vulnerability of carnivores and other mammals to extinction, and the complexity of conservation in species-rich but economically poor regions. I investigate these themes through a case study of wildlife conservation in a West African savanna protected area—Mole National Park in northern Ghana—and I pursue the following three principal objectives: (i) evaluate the effectiveness of a long-term wildlife monitoring program; (ii) assess patterns of persistence across a community of carnivore species; and (iii) examine the influence of anthropogenic and natural factors on carnivore occurrence. In this opening chapter, I provide an overview of my motivating themes and the study context, and I briefly introduce the three focused studies comprising the core of the dissertation.

### *Threats to biodiversity and the need for conservation science*

The discipline of conservation biology emerged from an increasing awareness, among scientists and society in general, of humanity's unsustainable trajectory of growth (Groom et al. 2006). In North America, early expressions of a conservation ethic—such as the writings of Henry David Thoreau and John Muir—came from a desire to preserve wilderness values in the face of widespread resource exploitation and land degradation (Borgerhoff Mulder & Coppolillo 2005; Mahoney 2009). Influential approaches to conservation and management, rooted in ecological science, were articulated by the likes of Aldo Leopold (1933, 1949), and broader public concern for the environment was galvanized by seminal writings on topics like pesticide toxicity (Carson 1962), overpopulation (Ehrlich 1968), and limits to growth (Meadows et al. 1972). Global concern over anthropogenic threats to biodiversity led to the Convention on Biological Diversity (CBD), a landmark international treaty created in 1992 at the United Nations Conference on Environment and Development in Rio de Janeiro ([www.cbd.int](http://www.cbd.int); Balmford et al. 2005a). In recent years, alarm over anthropogenic climate change has pervaded the public arena, and scientists have made unprecedented efforts to provide to the public consensus-based information on such large-scale threats to human and ecological well-being (e.g., Intergovernmental Panel on Climate Change, IPCC 2001; Millennium Ecosystem Assessment, MEA 2005).

Yet, despite the many professional and public voices decrying the scale of human impact to the biosphere, conservation objectives continue to be marginalized in mainstream society, and international commitments languish from a lack of political will. The “International Year of Biodiversity” is thus marked by a failure to meet CBD targets of slowing biodiversity loss (<http://gbo3.cbd.int>; MEA 2005; Butchart et al. 2010). Furthermore, our ability to accurately assess and monitor the many components of biodiversity remains inadequate (Balmford et al. 2005b; Dobson 2005), and our understanding of complex socio-ecological dynamics and the consequences of global change is sorely deficient (Clark et al. 2001; Gunderson & Holling 2002;

Folke et al. 2005; Liu et al. 2007). There is thus a vital need for strong and interdisciplinary conservation science to improve biodiversity conservation and help guide society in its transition from an “empty world” to “full world” paradigm (Daly & Farley 2004; Balmford & Cowling 2006; Sutherland et al. 2009).

### *Biodiversity monitoring and the challenge of uncertainty*

A pressing need in conservation science is an ability to reliably track the status of biodiversity components, such as populations, species, and ecosystems (Balmford et al. 2003b, 2005b). There has been much recent effort expended on the development of appropriate biodiversity indicators, and promising approaches include the IUCN Red List Index (Baillie et al. 2008; Mace et al. 2008) and the Living Planet Index (Loh et al. 2005; Collen et al. 2009). Nevertheless, considerable uncertainty remains in our knowledge of biodiversity status and vulnerability. Even among mammals (Class Mammalia)—one of the most widely studied and well-known groups—there remains a lack of information for many species, populations, and regions, and new species continue to be discovered (Schipper et al. 2008; Ceballos & Ehrlich 2009). Population losses are a precursor to species extinction, yet the dynamics of local populations are often poorly known (Ceballos & Ehrlich 2002). Where local populations are monitored, sources of sampling error are often ignored (Yoccoz et al. 2001; Pollock et al. 2002). Such uncertainty in species occurrence and abundance at local scales undoubtedly influences the reliability of regional or global biodiversity assessments, yet uncertainty is rarely propagated through aggregated datasets (e.g., Rondinini et al. 2005; Jetz et al. 2008; Craigie et al. 2010). Furthermore, biodiversity monitoring has often ignored socioeconomic variables that underlie threats to biodiversity, even though tracking threats is essential to conservation planning and the evaluation of management effectiveness (Bawa & Menon 1997; Salafsky & Margoulis 1999; Wilson et al. 2005; Carwardine et al. 2008).

### *Promise and pitfalls of protected areas*

Despite the uncertainty inherent in biodiversity assessments, the recent decline and extinction of many species due to human impacts is well documented (Dirzo & Raven 2003; Butchart et al. 2010). One of society’s chief responses to wildlife declines and habitat degradation has been the creation of protected areas (hereafter PAs or parks). Beginning with America’s Yellowstone National Park in 1872, there have been well over 100,000 terrestrial PAs created around the world, covering approximately 12% of the earth’s land surface (Chape et al. 2008; IUCN & UNEP 2009). This exponential increase in officially protected lands represents an enormous global investment and is undoubtedly a sign of conservation achievement. Nevertheless, the success of PAs at achieving their ultimate goal—stemming the tide of biodiversity loss—is far from certain, and their rate of establishment has exceeded the development of capacity to manage and monitor them (Ervin 2003; Chape et al. 2005).

Many parks were established for reasons other than biodiversity protection (such as scenic value), and gap analyses have identified numerous taxa and ecoregions with inadequate coverage in the global PA network (Brooks et al. 2004; Rodrigues et al. 2004). Placement of PAs may also be biased towards areas unlikely to face land conversion pressures (i.e., “rock and ice”, Joppa & Pfaff 2009). The small size and increasing isolation of most parks predisposes them to lose

species, even in the absence of direct human impact, through the process of “faunal relaxation” (Diamond 1975; Soulé et al. 1979; Newmark 1987, 1996). This has led to greater recognition of the need to consider ecological rather than political boundaries, and of the importance of conservation in “matrix” habitats surrounding PAs (e.g., buffers, corridors; Newmark 1985, 2008; Crooks & Sanjayan 2006; Hilty et al. 2006; Hansen & DeFries 2007). Many PAs also lack the capacity to effectively enforce their protective regulations (Brandon et al. 1998; Terborgh et al. 2002; Bruner et al. 2004; Leroux et al. 2010), or the ability to balance conflicting mandates (such as protection and recreation, e.g., Reed & Merenlender 2008). Studies assessing the ecological effectiveness of protected areas are limited and provide mixed results (Gaston et al. 2008), with many relying on indirect methods of evaluation like remote sensing or expert opinion (Bruner et al. 2001; DeFries et al. 2005; Struhsaker et al. 2005; Joppa et al. 2008). While PAs appear to be effective at protecting habitat in many areas, there is mounting evidence of wildlife declines and extinctions within parks (Caro & Scholte 2007; Brashares 2010; Hebblewhite et al. 2010; Karanth et al. 2010). Furthermore, most PAs lack the monitoring data required to properly evaluate their effectiveness (Chape et al. 2005; Parr et al. 2009), so there is a great need to better appraise this prominent approach to conserving biodiversity (Sutherland et al. 2009).

In addition to addressing the ecological effectiveness of PAs, the social impacts of setting aside land for nature require more attention (Brandon et al. 1998; Naughton-Treves et al. 2005; Adams & Hutton 2007). While parks can provide many positive social benefits—including research and education, employment, and cultural or spiritual satisfaction—their detrimental impacts have also been widely noted (West et al. 2006). For instance, park establishment has often come at the expense of disenfranchised local communities, who may have been displaced from their homelands and forcibly denied access to traditional resources (Brockington & Igoe 2006; Cernea & Schmidt-Solau 2006). This antagonistic approach to protectionism (i.e., “fences and fines”) has led to strong critiques of conservation and often caused persistent conflict between park authorities and their neighbors (Peluso 1993; Naughton-Treves 1997; Neumann 1998, 2004; Brockington 2002; Chapin 2004). While the exclusionary approach has its roots in the first North American parks (i.e., “the Yellowstone model”), its impacts are most strongly felt today in developing nations, where wildlife conservation and poverty alleviation have often been at odds (Adams & McShane 1992; Adams et al. 2004; Borgerhoff Mulder & Coppolillo 2005). Efforts to simultaneously achieve both goals—such as through integrated conservation and development projects and community-based conservation—have had limited success to date (Gibson & Marks 1995; Neumann 1997; Agrawal & Gibson 1999; Oates 1999; Newmark & Hough 2000; Hulme & Murphree 2001; Wells & McShane 2004). It is clear that improving the effectiveness of wildlife conservation in and around PAs will require not only better ecological data, but also an enhanced understanding of the complex social, political and economic factors underlying human-wildlife relations.

### *Carnivore conservation and conflict*

Understanding human-wildlife relations is particularly important for species prone to conservation conflict (Woodroffe et al. 2005). Larger mammal species are increasingly dependent on conservation action, and they also evoke strong and varied emotional responses across diverse cultural contexts (Ceballos et al. 2005; Morrison et al. 2007; Schipper et al. 2008).

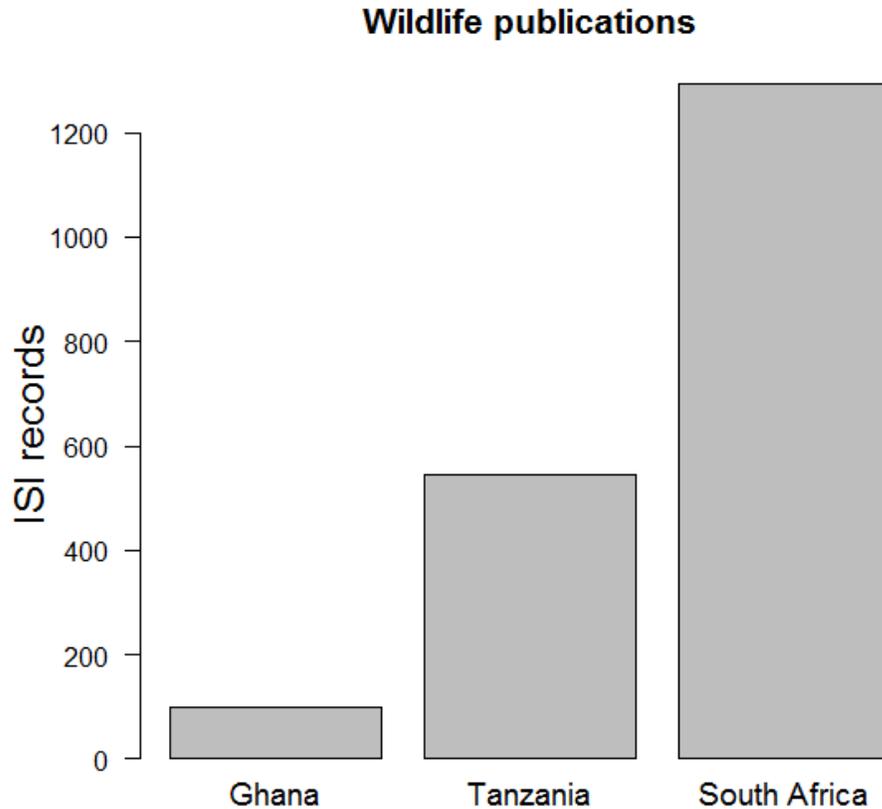
While many mammal species are revered for their economic, traditional, or aesthetic value, they may also be reviled for their negative interactions with people, often causing damage to agricultural and other property or threat to human life (Barnes 1996; Naughton-Treves 1998; White & Lowe 2008). Mammalian carnivores (order Carnivora) are particularly associated with such conflicting human emotions. Large and small predators—such as wolves, lions, leopards, jackals, or mongooses—have been aggressively persecuted throughout their ranges for real or perceived impacts to human livelihoods (Gittleman et al. 2001; Treves & Karanth 2003; Packer et al. 2005; Baker et al. 2008; Inskip & Zimmermann 2009). Conversely, carnivores have become symbols of conservation, inspiring international public support for wildlife protection (Karanth & Chellam 2009). Many carnivore populations have declined in the face of anthropogenic pressure, yet some have shown a remarkable ability to recover when provided with adequate protection (e.g., Smith et al. 2003). Loss and recovery of carnivore populations has highlighted their important functional roles within ecosystems, and focused attention on the significance of carnivore protection or restoration to broader biodiversity conservation (Soulé et al. 2003; Ray et al. 2005b; Sergio et al. 2008; Terborgh & Estes 2010). Reliable information on carnivore populations is needed to inform conservation planning and mitigate human-carnivore conflict, yet this task is made more complex by the rare and elusive nature of most carnivore species (Karanth & Chellam 2009).

### *The West African context*

Conservation conflicts between human and wildlife populations are apparent across much of sub-Saharan Africa (Happold 1995; Balmford et al. 2001; Rondinini et al. 2006). These are compounded by shortfalls in conservation capacity, including funding, governance, and technical training for wildlife research and monitoring (Barrett et al. 2001; Bruner et al. 2004; du Toit et al. 2004; Struhsaker et al. 2005). Within Africa, attention to wildlife conservation has been focused most intensively on well-known parks and biodiversity hotspots in eastern or southern Africa (e.g., Serengeti-Mara, Kruger, Eastern Arc Mountains). While such areas are deserving of attention, disproportionately little effort has been directed toward regions like West Africa, despite the latter's exceptional biodiversity and pressing conservation challenges (Barnes 1999; CEPF 2000; Bakarr et al. 2002; Ray et al. 2005a; Norris et al. 2010). In fact, some conservation biologists have suggested abandoning West Africa, describing it as a “conservation disaster” and arguing that conservation dollars are best spent elsewhere (Terborgh 1999). Indeed, many previous studies present a bleak outlook for wildlife in the region, depicting population declines and extinctions in the face of widespread habitat loss and bushmeat hunting driven by rapidly growing human populations (Barnes 1999, 2002; Oates et al. 2000; Brashares et al. 2001, 2004; Fischer & Linsenmair 2001a; Beier et al. 2002; Oates 2002; Thiollay 2007; Craigie et al. 2010; Norris et al. 2010).

Nevertheless, before abandoning West Africa to conservation triage, it is worth considering the availability of rigorous scientific data for the region. As a cursory means of assessing the knowledge gap, I compared the number of publication records in the ISI Web of Knowledge database (<http://apps.isiknowledge.com>, accessed 27 November 2010) containing the topic keyword “wildlife” paired with either “Ghana”, “Tanzania”, or “South Africa” (and limited to the subject area “Biodiversity & Conservation”). The results are shown in Figure 1 and illustrate the relative paucity of relevant scientific information for this West African country (and for

Africa in general when compared to the nearly 10,000 records returned when the search term “United States” was substituted).



**Figure 1.** The number of publication records in the ISI Web of Knowledge database (accessed 27 November 2010) containing the topic keyword “wildlife” paired with either “Ghana”, “Tanzania”, or “South Africa” (records were limited to the subject area “Biodiversity & Conservation” for simplicity and the specific content of individual records was not evaluated).

Furthermore, some authors have challenged the typical conservation narrative for West Africa of vanishing habitat and wildlife at the hands of exploding human populations. For instance, Fairhead & Leach (1996, 1998) argued that estimates of deforestation in the region have been exaggerated, and that local human populations have in fact promoted forest growth. Similarly, Wardell et al. (2003) highlighted the influence of colonial policies on land use trajectories in West African savannas, and Barnes (1999) noted the role of historical European exploitation in the collapse of regional elephant populations. In Ghana’s Mole National Park—the focal study site for this dissertation—colonial policy had a strong impact on local wildlife. In the 1930s, the British Colonial Administration designated much of what is the current park as a Game Clearance Area in an effort to control tsetse flies, striving to eliminate wildlife and their habitat from the area (GWD 2005). Large numbers of antelope, buffalo and other wildlife were

shot until the policy of game clearance was abandoned in the late 1950s and the area was designated a wildlife reserve. This ironic history of Mole raises the possibility that its wildlife populations were diminished before park establishment, and could even be in a period of recovery. It further highlights the importance of considering local socio-ecological contexts and collecting reliable data before drawing conclusions about conservation effectiveness. Given the uncertainty surrounding present status and past trajectories of many West African wildlife populations, and considering examples of successful recovery of depleted populations in other parts of the world (e.g., wolves in Yellowstone, Smith et al. 2003), calls to abandon conservation efforts in West Africa appear to be unwarranted.

### *Dissertation outline*

Detailed investigation of the many topics introduced in this chapter is beyond the scope of a single dissertation, but the preceding overview provides context for my study of wildlife conservation in a West African protected area. I use Ghana's Mole National Park (hereafter MNP) as a focal site for considering the themes of anthropogenic threat to biodiversity, uncertainty in ecological monitoring, protected area effectiveness, and carnivore conservation, all within a tropical, developing economy context. MNP is Ghana's largest protected area, covering approximately 4600 km<sup>2</sup> of woodland savanna habitat, and it represents a flagship park for the country's wildlife conservation efforts (further details of MNP are provided in subsequent chapters). In this dissertation, I specifically aim to investigate the efficacy of wildlife monitoring in MNP and assess the status of the park's carnivore community.

In Chapter 2, I evaluate a long-term, patrol-based mammal monitoring program that has been operating for four decades in MNP and other Ghanaian parks. The program relies on observations made by local "wildlife guards" during routine law enforcement patrols throughout the park. It has been lauded as a successful example of locally-based monitoring—that is, simple and effective monitoring useful for addressing the shortfall of conservation information in tropical regions (Danielsen et al. 2005a)—and its resulting data have been used to provide evidence of conservation failures in West Africa (e.g., Brashares et al. 2001, 2004; Caro & Scholte 2007; Craigie et al. 2010). However, the program has not previously been compared with more standard methods of wildlife survey, nor have its potential sources of error been evaluated. Given the need for reliable information on wildlife populations and conservation effectiveness in the region, and the increasing availability of analytical techniques for addressing observation error (e.g., Clark & Bjørnstad 2004; MacKenzie et al. 2006; Royle & Dorazio 2008; Cressie et al. 2009), it is an opportune time to critically assess Ghana's wildlife monitoring data.

In Chapter 3, I look more closely at the conservation status of the carnivore community in MNP. Results from Chapter 2 indicated that this guild of mammal species was poorly represented in the patrol-based monitoring data, and that camera-trapping was an effective method for assessing their occurrence and relative abundance. Given the ecological and cultural importance of carnivores, and their propensity to suffer as a result of conflict with local human populations, I strive to ascertain the current status of historically occurring carnivore species in MNP. I also aim to test hypotheses about their relative vulnerability to local extinction. In doing so, I apply a hierarchical multi-species occupancy modeling approach to detection histories derived from a camera-trap survey (conducted from October 2006 to January 2009), and estimate carnivore occurrence probabilities while accounting for imperfect detection. I further consider

evidence from patrol observations, sign and call-in surveys, and village interviews to evaluate the status of the carnivore community and appraise our understanding of intrinsic and extrinsic drivers of carnivore vulnerability in this ecosystem.

In Chapter 4, I extend the hierarchical multi-species occupancy model to more explicitly test hypotheses about extrinsic factors shaping current patterns of carnivore occurrence in MNP. Specifically, I derive spatially explicit GIS layers estimating heterogeneity across the park in illegal hunting pressure, anti-poaching effort, prey biomass, and habitat productivity. I use a Bayesian modeling framework to assess the ability of these indices to explain carnivore occurrence across camera-trap sampling sites. The framework explicitly accounts for the potentially confounding sampling effects of heterogeneous detection probabilities and spatial autocorrelation. I evaluate the strength of support for hypothesized impacts on occurrence for individual species and across the entire community of carnivores.

Finally, in Chapter 5, I summarize the key findings and main conclusions of the dissertation and outline several important directions for future research on wildlife ecology and conservation in MNP and West Africa.

## CHAPTER 2

### An Evaluation of Wildlife Monitoring in a West African Protected Area

#### Introduction

Global declines in biodiversity are increasingly well documented and threaten the welfare and resilience of ecological and human communities (Balmford & Bond 2005; MEA 2005; Sachs et al. 2009; Butchart et al. 2010). Dependable monitoring programs are required to better understand the extent and drivers of these declines, guide management action to slow or stop them, and assess the effectiveness of such conservation interventions (Balmford et al. 2003b, 2005b). Despite international commitments to monitor and protect biodiversity, current ecological monitoring efforts are generally inadequate and biodiversity conservation targets are not being met (Balmford et al. 2005a,b; Dobson 2005, Lindenmayer & Likens 2009; Butchart et al. 2010). The establishment of protected areas has been society's chief response to the biodiversity crisis (Chape et al. 2008), yet the success of these parks and reserves in adequately conserving species and ecosystems is increasingly questioned, and data necessary to evaluate their effectiveness are frequently lacking (Brandon et al. 1998; Terborgh et al. 2002; Chape et al. 2005; Gaston et al. 2008). Similarly, efforts to integrate conservation with development and poverty reduction also often lack appropriate monitoring mechanisms for tracking their progress (Kremen et al. 1994; Salafsky & Margoluis 1999; Wells & McShane 2004).

While recent increases in the establishment of biodiversity monitoring programs represent an encouraging sign, they have been accompanied by debate over appropriate design of monitoring protocols. A prominent argument is that, above all, monitoring programs must have explicit objectives, well-defined targets, and appropriate means of dealing with uncertainty—in the words of Yoccoz et al. (2001) they must adequately address the “Why?”, “What?”, and “How?” of monitoring. Many quantitative ecologists promote a focused and experimental approach to linking monitoring, management and research, such as in adaptive management (Walters & Holling 1990), whereby predictions from *a priori* hypotheses about causal relationships and underlying mechanisms are tested through system manipulations (Yoccoz et al. 2001; Nichols & Williams 2006; Lindenmayer & Likens 2009, 2010b). Proponents of this “strong inference” approach (cf. Platt 1964) also frequently stress the importance of considering common sources of error in monitoring data, particularly errors due to imperfect survey detection and spatial sampling variation (Yoccoz et al. 2001; Pollock et al. 2002; Buckland et al. 2005), but also those related to the use of inappropriate methods and unverifiable data (Karanth et al. 2003; McKelvey et al. 2008).

While concurring with the need for rigorous and unbiased sampling designs, other ecologists have argued that narrowly focused, manipulative monitoring programs are ill-suited to address the cumulative impacts of multiple anthropogenic stressors operating at large spatial and temporal scales, nor are they likely to contend with unanticipated future changes to human and natural systems (Boutin et al. 2009; Haughland et al. 2010). These authors instead propose broader cumulative-effects (or “surveillance”) monitoring programs that integrate data from many taxa and capitalize on existing environmental and anthropogenic gradients to address particular questions within their overarching monitoring objectives (Boutin et al. 2009;

Haughland et al. 2010). Conversely, this style of monitoring has been criticized as “passive” or “omnibus” and an inefficient use of conservation resources by adherents of the adaptive monitoring approach (Nichols & Williams 2006; Lindenmayer & Likens 2009, 2010a,b).

Another element of the monitoring debate stems from pragmatic concerns about the sustainability of monitoring programs and consideration of the geographic and socio-economic context within which they operate. Regions prone to “conservation conflict”, with high biodiversity and rapidly expanding human impacts (i.e., biodiversity “hotspots”, Myers et al. 2000; Balmford et al. 2001), are disproportionately located in tropical and developing countries, where ecological data are typically scarce and monitoring programs most urgently needed (Collen et al. 2008). Unfortunately, these regions also frequently lack the institutions, funding, and technical capacity needed to implement the kind of “professional” scientific monitoring programs designed in wealthier countries (Getz et al 1999; Barrett et al. 2001; Sheil 2001; Balmford & Whitten 2003; Danielsen et al. 2003, 2005a; du Toit et al. 2004). In such areas, reliance on foreign professionals may be neither effective nor desirable in practice, entailing unrealistically high implementation costs and low chances of sustainability, and failing to adequately engage or inform local resource users or managers who ultimately determine conservation outcomes. Alternative models of “locally-based” monitoring have been proposed in response to this apparent “conflict between scientific ideals and practical realities” in developing countries (Danielsen et al. 2000, 2003; Sheil 2001; Sheil & Lawrence 2004; Brashares & Sam 2005). Such locally-based schemes are defined by an emphasis on the participation of local stakeholders but can take many forms, including volunteer surveys, hunter reports, and traditional indigenous systems (Danielsen et al. 2005a, 2009). While there are encouraging signs of the potential effectiveness of local monitoring programs in aiding management decisions, abating conservation threats, and empowering local communities to improve their livelihoods, a key outstanding question centers on their ability to deal with sampling error and thus reliably detect true trends in monitored populations (Rodriguez 2003; Yoccoz et al. 2003; Brashares & Sam 2005; Danielsen et al. 2005a,b, 2009).

Related to such overarching questions of design, biodiversity monitoring programs must also identify appropriate methods for tracking targets of interest. A wide array of survey methodologies have been used to assess species, ecosystems, and anthropogenic impacts, ranging from relatively simple approaches through to those demanding highly technical toolkits. For example, programs to monitor mammal populations have employed many methods, including ground transects for direct sightings or indirect sign, aerial censuses, live- or camera-trapping, genetic methods, telemetry, call playbacks, questionnaires, and indirect habitat assessments (e.g., Wilson et al. 1996; Plumptre 2000; Barea-Azcon et al. 2007; Stoner et al. 2007; Long et al. 2008; Ogutu et al. 2008; Kindberg et al. 2009). Choice of methods should be dictated by focal questions and targets but is also influenced by factors such as cost, logistics, location, and local expertise or capacity. Studies comparing the effectiveness of different survey methods are of considerable use in guiding monitoring programs, yet few have compared simpler methods suited for locally-based initiatives with the often more technical tools of professional programs. Among the exceptions, several studies suggest that local methods are reliable and cost-effective alternatives (e.g., Gaidet-Drapier et al. 2006; Kindberg et al. 2009; Rist et al. 2010), while others indicate that local knowledge does not adequately substitute for professional surveys (e.g., Can & Togan 2009).

In this study, we evaluate a long-term, locally-based wildlife monitoring program in West Africa through a methodological comparison and preliminary examination of potential sources of error. In general, wildlife monitoring and research have received relatively little attention in West Africa when compared to many other parts of Africa and the world, and the resulting scarcity of scientific information hinders conservation planning and management response to the region's widespread hunting and human-wildlife conflicts (Happold 1971; Ntiama-Baidu 1987; Eves & Bakarr 2001; Bakarr et al. 2002; Oates 2002; Ray et al. 2005a). An exception to the paucity of data comes from a long-term monitoring program in the West African nation of Ghana. The Wildlife Division of the Forestry Commission of Ghana (hereafter Ghana Wildlife Division or GWD) has been monitoring illegal hunting and mammal populations in protected areas under its jurisdiction for several decades (Pegg 1969; Asibey 1971; Brashares et al. 2001; Jachmann 2008a,b). The program is based on observations made during regular law-enforcement patrols, representing a form of "surveillance" monitoring (cf. Gray & Kalpers 2005), and has been described as a successful example of locally-based monitoring (Brashares & Sam 2005; Danielsen et al. 2005). Resulting data have been used to infer patterns and drivers of population decline and extinction, study trophic interactions, and assess management effectiveness (Brashares et al. 2001, 2004, 2010; Brashares 2003; Jachmann 2008a,b; Craigie et al. 2010; Burton et al. in press). Nevertheless, the accuracy and precision of this monitoring system have not been formally evaluated.

Here, we present a preliminary assessment of the GWD monitoring program in Ghana's largest protected area, Mole National Park. Specifically, we compared results of recent data from the patrol-based system with those from a concurrent camera-trap survey, representing an alternative "professional" survey method that is increasingly being used to monitor mammal populations (O'Brien et al. 2010; O'Connell et al. 2010). We assessed concordance between the methods with respect to estimates of mammal species richness, diversity, and relative abundance, as well as the incidence of illegal hunting. We further compared spatial variation in estimated patterns as well as their relation to heterogeneity in species attributes, and we explored the potential influence of sampling error on trend estimation from the patrol monitoring data. Our results provide important insight into the strengths and weaknesses of Ghana's long-term mammal monitoring data, and we broadly consider the program's context and implications for the design and implementation of wildlife monitoring efforts elsewhere.

## **Methods**

### *Patrol monitoring data*

The Ghana Wildlife Division's law enforcement monitoring system consists of observations of illegal activity and wildlife made by park staff during regular "anti-poaching" patrols within its wildlife protected areas (Brashares & Sam 2005; GWD 2005; Jachmann 2008a,b). The system began in the late 1960s and continues to the present day, although specific protocols of data collection across the entire period of monitoring are not well documented (recent protocols for some parks were described in GWD & SNV 2004a; see also Jachmann 2008a,b). The general scheme has typically involved daytime foot patrols by teams of 3-5 "Wildlife Guards" (GWD 2005) that record sightings of mammal species and hunters (or hunting sign, i.e., footprints, traps) while patrolling from camps distributed across the parks. A particular target group of

monitored species has not been well defined, but is generally conveyed as “larger” mammals (e.g.,  $\geq 1\text{kg}$ , Brashares et al. 2001, 2004; “similar or larger size than a Maxwell’s duiker (*Cephalophus maxwelli*)”, Jachmann 2008a). While some amount of monitoring data exist for at least nine protected areas in Ghana (Brashares et al. 2001; Jachmann 2008b), we focused on data from Mole National Park (hereafter MNP), Ghana’s largest protected area. MNP encompasses approximately 4600 km<sup>2</sup> of woodland savanna habitat in the country’s Northern Region (Fig. 1) and represents a regionally important protected area within the threatened West Sudanian Savanna Ecoregion (Burgess et al. 2004).

Monitoring data that we assessed for MNP were available in two different formats representing what we termed “historical” and “modern” periods, which together included data from 1968 to 2008 (with the exception of 2002-03, for which no data were available). We focused primarily on a subset of modern data collected between October 2006 and May 2008 for our methodological comparison (described below), but we first provide an overview of the entire dataset. Historical monitoring data spanned the period 1968-2001 and were archived at MNP headquarters within monthly summary reports from patrol camps distributed throughout the park (Fig. 1; Appendix 2.1). We reviewed all available reports and created a standardized database containing the following information: camp name, year and month of report, number of patrols conducted, number of patrol staff at the camp, evidence of illegal activity (including hunters, hunter footprints, traps or snares, empty cartridges, and animal carcasses), and sightings of mammal species (species name, number of detections, and number of individuals counted for the month). We obtained data from a total of 1,965 monthly reports detailing more than 28,000 patrols from 27 patrol camps. Our records were not complete in the sense that reports were not available from all camps in each month of every year, either because they did not exist or had been lost or relocated from the park. We created indices of relative abundance by dividing the number of individuals counted (per species or pooled across species) by the number of patrols conducted as a measure of sampling effort (i.e., a catch-per-unit-effort or CPUE index; Milner-Gulland & Rowcliffe 2007; Jachmann 2008a). For cases where monthly reports included observations but not the number of patrols (~15% of reports), we substituted the mean value across all other reports (14 patrols per month). When pooled across camps and across months within a year, our calculation of sampling effort (number of patrols) was highly correlated with both a coarser measure (number of reports, Pearson  $r = 0.96$ ) and a more detailed measure (number of patrols multiplied by number of patrol staff at camp,  $r = 0.98$ ), but we recognize that it is subject to some degree of error (in terms of missing values and probable variation in patrol length or duration, staff skill or motivation, etc.).

Beginning in late 2004, MNP’s monitoring protocol was adapted to the Management Information System (MIST; Schmitt & Sallee 2002), which incorporates GPS locations to provide spatially explicit data on wildlife sightings, patrol effort and illegal activities in the park. While the basic approach to monitoring did not change, patrol staff were transitioned from the smaller and more widely distributed camps to four larger, centralized “range” camps (GWD 2005). Patrol teams covered routes through their respective ranges, using handheld GPS units to record their positions at periodic intervals and at the locations of observations of mammal species and illegal activities. We assessed data from the MIST program for the “modern” period from October 2004 to May 2008, including observations from over 2,700 patrols extending across much of the park (Fig. 1). For our methodological comparison, we used a subset of the

MIST dataset covering nearly 1,400 patrols (1,612 patrol-days) conducted between October 2006 and May 2008, which overlapped to the greatest extent with the period of the camera trap survey (described below). The representativeness of this subset was assessed by comparing the resulting estimates of species richness and relative abundance with those obtained from the entire monitoring dataset.

### *Camera trap survey*

We compared data from MNP's patrol monitoring system with results of a camera trap survey conducted between October 2006 and January 2009. Camera trapping was chosen as the main method of comparison because of its increasing use and demonstrated effectiveness in mammal survey and monitoring programs (O'Brien et al. 2003, 2010; O'Connell et al. 2006, 2010; Tobler et al. 2008; Rovero & Marshall 2009; Dobson & Nowak 2010; Pettorelli et al. 2010). Furthermore, camera traps generate unambiguous photographic evidence of species occurrence and provide a sharp methodological contrast from patrol observations in other important aspects (e.g., technological complexity, cost, mobility). Our assessment was not designed to evenly match the two methods, but rather to compare results from more typical implementations of each method.

A total of 280 camera stations were set across MNP during the survey period, although data were obtained from only 253 of these (cameras were stolen from nine stations and malfunctioned at another 18). The majority of those stations (227 of 253) consisted of a single passive infra-red DeerCam DC-300 film camera trap unit (Non Typical, Park Falls, WI, USA), with 17 stations consisting of paired DC-300 units (as part of a concurrent photographic capture-recapture study), and nine stations using single units of different camera trap models (1 Leaf River C-1BU, 3 StealthCam MC2-GV, 2 CamTrakker Environmental Unit, 2 Reconyx RC55 and 1 Reconyx Silent Image). Camera stations were deployed in 32 spatially or temporally differentiated groups targeting different portions of the park and different seasons (Fig. 1). Within each group, stations were set systematically at approximately 1-km intervals near landscape features expected to maximize wildlife capture probability, such as dirt roads, wildlife trails, riverine corridors, waterholes, and salt licks. Access and other logistical limitations precluded a random or systematic survey design covering the entire park; our focus was instead on sampling across representative gradients in dominant park features, such as proximity to human settlement (i.e., park edge), availability of water and associated riparian forest habitat, and expected wildlife abundance (on the basis of previous surveys, e.g., Bouché 2006). The northernmost portion of MNP was not sampled because of extremely limited access, reports of infrequent wildlife occurrence (GWD 2005; Bouché 2006), and the existence of few patrol data from the area for comparison (Fig. 1).

At each station, one camera was set on a tree at a height of about 40 cm, facing perpendicular to the expected direction of animal travel and approximately 3 m from the anticipated site of capture. A one-minute delay between subsequent photographs and standard (medium) sensitivity settings were used, and cameras operated continuously until retrieved or the film was fully exposed. Sampling effort was measured in terms of camera trap-days, calculated as the number of days for which a camera was set or until the last photo was taken if the roll was fully exposed before collection. Stations were active for a mean of 21.6 days (SD = 12.8),

yielding a total survey effort of 5,469 trap-days. Sampling effort was highest in central and southeastern portions of the park and during dry season months of November to March, which corresponded with the spatial and temporal intensity of effort in the patrol monitoring system (Fig. 1). Indices of relative abundance for mammal species (or hunters) from the camera-trap data were then calculated as the number of individuals photographed divided by the number of camera-trap days (consecutive photographs captured within a period of 5 minutes and presumed to be of the same individuals were excluded from the dataset) .

### *Comparative analysis*

We used several metrics to compare results of the patrol monitoring system with those from the camera trap survey. We first simply tabulated the total number of mammal species detected by each method and compared these estimates of species richness. We then compared CPUE indices of relative abundance across species for both methods, and we combined richness and relative abundance by calculating two measures of species diversity (Simpson's index and the Shannon-Wiener function; Krebs 1999; Buckland et al. 2005). Given that the period over which we compared the methods was too brief to allow assessment of temporal trends, we substituted space for time and compared spatial patterns in species richness and abundance across the park landscape as discerned by the two methods. MNP had previously been spatially subdivided for management purposes into 24 sectors of roughly similar size (mean size = 188 km<sup>2</sup>; GWD 2005). We used these sectors as management-relevant sampling units for spatial comparison, pooling data from all camera stations or patrol observations falling within a given sector. To create a spatially explicit measure of patrol effort for the CPUE index, we re-created patrol routes from corresponding GPS locations, divided routes into equal 200 m segments (since the distance between consecutive positions varied considerably among patrols), and summed the number of patrol segments within a given sector.

Probabilities of detection can vary substantially across species (Buckland et al. 2005; Zipkin et al. 2010), and we anticipated that the two methods might vary in their abilities to detect certain species. We therefore evaluated the comparative measures in relation to three species traits expected to affect detectability: body mass, daily activity pattern (diurnal vs. nocturnal or crepuscular), and social group size (Table 1). Trait data were obtained from the PanTHERIA database (Jones et al. 2009; supplemented by species-specific sources where necessary, see Chapter 3). Given that abundance indices and trait data were not normally distributed, we used non-parametric statistics to assess correlations and compare means (Spearman rank correlation and Wilcoxon rank-sum test, respectively; Quinn & Keough 2002; Crawley 2007). All statistical analyses were performed in program R version 2.11.1 (R Core Development Team 2010), and analyses of spatial GIS data were done in ArcGIS version 9.3.1 (ESRI, USA).

### *Effect of sampling variation on patrol monitoring trends*

In addition to the methodological comparison between modern patrol data and the camera trap survey, we conducted a cursory assessment of the potential effect of sampling variation (i.e., measurement or observer error) on the interpretation of long-term trends from the historical data. Trend estimation to assess population viability or the importance of environmental drivers (e.g.,

climate, hunting) is a common objective of monitoring programs, but one often made difficult by the confounding of variation due to environmental and population processes with that caused by sampling error (Yoccoz et al. 2001; de Valpine & Hastings 2002; Clark & Bjørnstad 2004; Buckland et al. 2005). Variable observer effort is a common source of sampling bias that affects the detection probability of individuals in a sampled population, and it may be particularly important for monitoring protocols with relatively low levels of standardization, such as GWD's patrol-based system. Previous analyses of GWD monitoring data have used different approaches to dealing with variation in sampling effort, from relying on an assumption of constant effort across space and time (e.g., Brashares 2001, 2004) to applying a strict standardization of effective man-hours on patrol (Jachmann 2008a,b). While the historical dataset does not contain the level of detail required to apply the latter correction, we explored the effect of accounting for sampling effort by comparing trends derived from uncorrected counts with those from our CPUE index of count per patrol.

Even with standardized effort, other unmeasured aspects of sampling can introduce heterogeneity in detection probabilities and thereby influence the relationship between a count and true abundance (Pollock et al. 2002; Williams et al. 2002). Estimating and accounting for detectability can be challenging and there are many potential methods to do so. One approach is to use repeated sampling of a site over a short enough period that it can reasonably be considered "closed" to changes in population status. In this way, differences between replicate samples are assumed to represent sampling error around the true but unknown number of individuals at the site (e.g., Morris & Doak 2002: 158-180). The same approach can be applied to estimates of site occurrence and species richness (Nichols et al. 1998; MacKenzie et al. 2006). Unfortunately, such replicate sampling was not an explicit part of the GWD monitoring program design, making a *post hoc* assessment of detectability difficult. Nevertheless, as a coarse examination of the issue, we applied this approach to a sample of MNP monitoring data. Following Brashares & Sam (2005), we examined a random subset of data for four species with different expected detectabilities: olive baboon (*Papio anubis*) and African buffalo (*Syncerus caffer*) are relatively large, abundant and conspicuous species, whereas oribi (*Ourebia ourebi*) is a small and secretive antelope of intermediate abundance, and leopard (*Panthera pardus*) is a rare and secretive felid with notoriously low detectability. For the historical dataset, we made the simplifying assumption that counts made at one patrol camp in consecutive months within a common season (defining "wet" as June-August and "dry" as December-February to avoid transitional months) should be sampling the same group of species and individuals (i.e., no migration of individuals or changes in species occupancy for that area over that time period). We randomly selected a set of 20 such "replicate" counts for each of the four focal species (from different camps and seasons, with approximately equal patrol effort between matched pairs) and calculated the difference between paired replicate counts as a crude estimate of potential sampling error (noting that this fails to account for sampling variation between patrols within a month—since these finer scaled data are not available for the historical dataset—and thus may underestimate variance). Finer scaled data were available for the modern data from the MIST system, so we estimated the coefficient of variation ( $CV = \text{standard deviation} / \text{mean} \times 100$ ; Quinn & Keough, 2002) for the four focal species from a random sample of counts ( $n = 11-25$ ) from different patrol days within the same month and management sector (i.e., considered to be replicates). We did not consider the problem of "false absence" (i.e., cases where species were not detected at a

site when previous or subsequent surveys suggest they were present), so our preliminary assessment almost certainly underestimates detection bias (see Discussion).

## Results

### *Species richness, diversity and abundance*

Observations of 20 mammal species were recorded by the patrol monitoring system during the period of methodological comparison (Oct. 2006 to May 2008; Table 1, Fig. 2). By contrast, a third more mammal species were detected during the camera trap survey. Three species infrequently recorded by the patrol system were not detected by cameras (Geoffroy's black and white colobus, *Colobus vellerosus*, which is an arboreal species; Bohor reedbuck, *Redunca redunca*; and lion, *Panthera leo*—see Chapter 3 and Burton et al. in press) while 13 photographed species were not included in the patrol data (thus there were 17 species detected by both methods, and both also detected illegal hunting activity; Table 1). Richness estimates were similar for ungulates and primates but differed considerably for carnivores and rodents (Table 1, Fig. 2). Mean body mass across detected species differed significantly between the two methods, with camera traps detecting more smaller-bodied species than patrols (one-sided Wilcoxon rank-sum test,  $W = 199.5$ ,  $P = 0.024$ ; cameras: mean = 185.5 kg, median = 12.8 kg; range = 0.22 – 3825 kg,  $n = 30$ ; patrols: mean = 283.1 kg, median = 47.8 kg, range = 3.7 – 3825 kg,  $n = 20$ ; Fig. 3). Species' daily activity patterns and group sizes also contributed to differences in detectability between the methods. Camera traps detected 11 nocturnal species (of 28 for which activity pattern descriptions were available; Table 1) while patrols only detected 3 (of 20; one-sided binomial proportions test  $\chi^2 = 2.26$ ,  $P = 0.066$ ; Fig. 3), and mean group size was larger across species detected by patrols than for those detected by cameras (patrols: mean = 12.3, median = 10.4; cameras: mean = 8.7, median = 2.0; one-sided Wilcoxon rank-sum test,  $W = 199.5$ ,  $P = 0.062$ ; Fig. 3).

In terms of abundance, total species counts were much higher in the patrol data, reflecting the more continuous spatial and temporal coverage of patrol effort and the narrow field-of-view of stationary cameras relative to mobile patrol teams. The patrol dataset contained 9,649 observations of 60,722 animals (though not distinct individuals given the likelihood of repeated observations over time), equivalent to 6 detections or 38 individuals per day of patrol effort. The camera survey produced 3,430 independent detections of 4,131 individuals, corresponding to 0.63 detections or 0.76 individuals per camera-trap day of sampling effort. Estimates of relative abundance varied widely across species and between the two methods, with methodological discrepancies related to species traits as seen for richness estimates (Fig. 4). There was a significant positive correlation between abundance indices from the two methods (Spearman  $r_s = 0.55$ ,  $P < 0.001$  when all 33 species and humans were included;  $r_s = 0.58$ ,  $P = 0.014$  when including only the 17 species in common; results were nearly identical when using the number of separate observations per unit effort rather than the number of individuals counted per unit effort). However, there was considerable scatter in the relationship, with strong agreement for some species (e.g., kob antelope, *Kobus kob*, and olive baboon, *Papio anubis*) and large disparities for others (e.g., spotted hyena, *Crocuta crocuta*, and bushbuck, *Tragelaphus scriptus*; Table 1, Fig.4). Measures of species diversity combining richness and relative abundance were

higher for the camera trap survey (Shannon-Wiener:  $H_{cameras} = 2.91$ ,  $H_{patrols} = 2.17$ ; Simpson's reciprocal index:  $1/D_{cameras} = 14.6$ ,  $1/D_{patrols} = 6.1$ ).

### *Spatial patterns*

Indices of total mammal abundance for patrol and camera data were significantly correlated across the 17 management sectors sampled by both methods ( $r_s = 0.75$ ,  $P < 0.001$ ; Fig. 4; Appendix 2.2), as were measures of species richness (uncorrected for effort,  $r_s = 0.80$ ,  $P < 0.001$ ). Conversely, indices of species diversity were spatially uncorrelated between the methods (Simpson's D,  $r_s = -0.14$ ,  $P = 0.59$ ), a result driven by the relative dominance of certain common species in the patrol data (e.g., kob, baboon; Table 1). Across-sector correlations in patrol- and camera-derived abundance indices were generally much stronger for larger-bodied, social, and diurnal species (such as many of the larger ungulates) than for smaller, nocturnal and solitary species (like carnivores; Appendix 2.2). The correspondence between indices of hunting activity across sectors was very weak ( $r_s = -0.16$ ), with cameras only sporadically detecting hunters.

### *Representativeness of modern patrol data*

The subset of data used in our methodological comparison appeared to be generally representative of the longer-term MNP patrol monitoring system as a whole. No additional mammal species were included in the MIST monitoring data covering the entire "modern" period (October 2004-May 2008), and the order of species' abundances were virtually identical between this period and the subset used for comparison with the camera-trap data (not shown). The historical dataset (1968-2001) included observations of 35 mammal species (Table 1); however, of the 15 species that did not occur in the MIST subset used for comparison, 9 had less than 10 total observations (including 4 with only 1 record) and only 2 had more than 50 observations over the 33-year period (red river hog, *Potamochoerus porcus*, which likely no longer occurs in the park; and hippopotamus, *Hippopotamus amphibius*, with only a few individuals potentially occurring in the Kulpawn river at northern edge of the park; GWD 2005). Furthermore, few of the 15 species missing from the modern data had recent records in the historical dataset, and there is some taxonomic uncertainty associated with several of them (e.g., mongooses; see Table 1 notes and Chapter 3). The 15 most abundant species were the same for both the historical and modern datasets, and species' rank abundances were very similar (Table 1), although total counts seemed to be low for the historical period relative to the modern sample.

### *Effect of sampling variation*

There was considerable temporal variation in patrol effort in our historical dataset, with a general trend of declining effort over time ( $r_s = -0.38$ ,  $P = 0.026$ ), but more specifically a period of particularly low effort in the mid-1980s (Fig. 5). Correcting for effort had a significant impact on the interpretation of temporal trends, as total annual counts pooled across 33 mammal species (excluding the 1 record each of "rabbit" and "bushbaby", Table 1) largely followed variation in patrol effort, declining strongly in the mid-1980s before increasing more recently (Fig. 5). Accounting for sampling effort (by dividing by the annual number of patrols) changed the

pattern from a generally declining trend ( $r_s = -0.17$ ) to one that tended toward an increase ( $r_s = 0.25$ , though neither correlation was statistically significant,  $P > 0.15$ ; Fig. 5). This pooled abundance index is dominated by the most common species (i.e., those most frequently counted by the patrols), and a better composite index would be the geometric mean of abundance indices (Buckland et al. 2005). However, the general result was similar when looking at individual species (not shown) and our objective was not to conduct a detailed analysis of trends. A confounding influence of sampling effort was also seen in the trend of illegal hunting activity: while uncorrected annual counts of hunting sign and those corrected for patrol effort both showed a general increasing trend over time, the increase in the latter was much stronger ( $r_s = 0.30$ ,  $P = 0.083$  for uncorrected counts,  $r_s = 0.50$ ,  $P = 0.0027$  for the CPUE index; Appendix 2.3). In addition to temporal sampling variation, there was considerable spatial variation in recorded effort levels across the 27 patrol camps from which historical data were available (range = 19 – 2841 patrols per camp, median = 857, mean = 1043, SD = 943), indicating that correcting for effort before interpreting spatial patterns over time would also be very important.

Our preliminary assessment of potential sampling error due to detectability indicated considerable variation in consecutive patrol counts within a sampling unit (which were assumed to be replicate samples of the same local sub-populations; see Methods). The average difference between the number of individual baboons counted in 20 paired replicate samples randomly selected from the historical dataset was 36.7 (SD 49.6), while the overall mean for those 40 counts was 81.6 (SD 81.8), indicating that differences were substantial (equal to, on average, 56% of the magnitude of the mean of paired counts; range = 7-153%). For 20 paired replicate counts of buffalo, the average difference was 35.3 individuals (SD 45.3) compared with an overall mean count of 50.1 (SD 64.8), representing an average difference of 79% relative to pair means (range = 3-198%). The average difference across 20 paired counts of oribi was 7.1 individuals (SD 5.4), the mean count was 15.5, and the average magnitude of the paired difference relative to mean was 67% (range 0-124%). There were only 10 paired monthly counts of leopard at the same patrol camp, and the majority were of a single individual (mean = 1.5, SD = 1), so differences were smaller (mean = 0.8, SD = 1.3) and represented an average magnitude of 37% relative to paired means (0-133%). Results were similarly variable in our sample of modern “replicate” counts (2004-2008 MIST dataset), with coefficients of variation for baboon ( $n = 25$  counts), buffalo ( $n = 11$ ), and oribi ( $n = 14$ ) equal to 49, 74 and 54, respectively. The modern dataset contained only 17 records of leopard, of which only 7 were sightings and few were close in space or time, confirming that detectability was likely very low for this species (see also Chapters 3 and 4).

## Discussion

We believe that our results send a cautionary signal regarding use of wildlife data generated from MNP’s locally-based law enforcement monitoring program. While reinforcing previous assertions that the program generates a large amount of otherwise unavailable information for this regionally important protected area (e.g., Brashares & Sam 2005), we found the data subject to biases that warrant careful analysis and interpretation. MNP patrol observations tended to systematically underestimate the presence and abundance of certain important members of the mammalian community, such as most predators, and even counts of well-detected species

seemed affected by substantial sampling error. Although these problems do not invalidate the use of MNP's monitoring data, they do suggest that conclusions about resulting patterns of species richness or population dynamics risk being misguided without due consideration of potential biases. Nevertheless, our results also highlight certain strengths of GWD's monitoring system and provide broader lessons for the design and interpretation of wildlife monitoring programs in developing regions where they are urgently needed.

### *Program strengths and study limitations*

When subjecting wildlife monitoring data to scrutiny, it is important to keep sight of the monitoring program's broader context. The primary aim of GWD's patrol system is the deterrence of illegal hunting within protected areas (i.e., law enforcement), and our comparative results suggest it is effective at detecting signs of hunting activity (at least relative to our camera trap sampling but more assessment is warranted, e.g., Gavin et al. 2010). The system also seemed to perform relatively well at monitoring large, diurnal mammals (such as many ungulates and primates), which represent high-value targets of bushmeat hunting and a traditional focus of "game" management (Mason 1993; Ntiama-Baidu 1998; Eves & Ruggiero 2002; Loibooki et al. 2002; Jachmann 2008a,b). Furthermore, it is not particularly surprising that patrols did not reliably detect more elusive species like carnivores, and other comparative studies have noted that detectability—and hence correspondence between different methods—tends to increase with body size (e.g., Silveira et al. 2003). It is also important to recognize that true temporal and spatial patterns of mammalian richness and abundance in MNP remain unknown, and that, like all survey methods, our camera trapping effort also sampled the park's populations with error. Perfect correspondence between methods should therefore not be expected, and our camera data may not be the best representation of "truth" against which to compare the patrol data (the question of what constitutes a "good" level of agreement between different methods warrants further attention). Moreover, some of our assumptions require further testing (e.g., consistency of CPUE index, validity of consecutive patrol counts as replicate samples), and more detailed work is needed to assess consequences of the observed sampling error for interpretation of trends from the patrol monitoring data.

### *Reliability of the patrol-based wildlife monitoring data*

Despite recognizing strengths of the GWD system and caveats of our comparison, it is important to consider potential implications of our results for the appropriate use of MNP's wildlife monitoring data. Firstly, it seems worthwhile to state that if a program's primary objective is law enforcement and sufficient resources are not available to devote to wildlife monitoring methods, then the program should not be expected to produce reliable wildlife data. If wildlife monitoring is indeed an important objective, then adequate attention should be devoted to developing appropriate protocols. The clear and explicit framing of monitoring objectives is therefore critical (Yoccoz et al. 2001). If only certain "game" species are to be monitored (e.g., larger ungulates), data collection and analysis should be restricted to these specific targets (although such a narrow focus may be less appropriate given the significance of diverse taxa to both ecosystem functioning and local livelihoods; Asibey 1974; Sinclair & Byrom 2006, Sinclair et al. 2007). Furthermore, potential sources of error should be acknowledged, addressed within the

monitoring design as much as possible, and propagated through subsequent analyses using the resulting data (Yoccoz et al. 2001, Pollock et al. 2002). Recent GWD monitoring protocols appear to have emphasized the careful accounting of patrol effort (Jachmann 2008a,b), but other common biases like detectability have not been well addressed. Our results highlight the importance of imperfect detection, both in the sense of undetected species within the community and undetected individuals at a sampling site. Likewise, a previous analysis of another record of long-term patrol sightings in MNP for one species (red-flanked duiker, *Cephalophus rufilatus*) applied the occupancy modeling approach of MacKenzie et al. (2003) and suggested that detectability was significantly less than one and declined over time (C. Burton, unpublished manuscript, Appendix 2.4). Indeed, the assumption of equal detectability over time and space is likely to be violated in practice (Williams et al. 2002; MacKenzie et al. 2006, Royle & Dorazio 2008), potentially confounding interpretation of population trends. The strength of inference from monitoring programs such as GWD's could thus likely be significantly improved by additional attention to methodological detail (e.g., Pollock et al. 2002, MacKenzie & Royle 2005; see recommendations below).

### *Consideration of other program features*

Irrespective of the GWD monitoring program's current capability to account for sources of sampling error and accurately track wildlife populations, the program produces other important benefits. These include basic tangibles like providing employment in a region with considerable poverty, as well as specific management tools such as an ability to track staff performance and increase motivation (Jachmann 2008b). In fact, proponents of "locally-based" monitoring systems stress that a predominant emphasis on the generation of robust wildlife data is unrealistic and inappropriate for many monitoring programs in developing nations (Sheil 2001; Danielsen et al. 2003, 2005a). They highlight other important (and interrelated) features of successful locally-based programs—such as long-term sustainability, cost-effectiveness, involvement of local stakeholders, and ease of incorporation into management decisions—and we briefly consider each of these for the case of the GWD monitoring system.

With regard to sustainability, the persistence of the GWD monitoring program for over four decades in a developing region where wildlife management has not generally been a priority is quite unique and remarkable. Nevertheless, further scrutiny raises potential warning flags about the program's performance over time. For instance, the historical dataset available at MNP shows great variation in the number of monthly reports filed over time, with a period of particularly poor reporting in the 1980s. While it is possible that this reflects the loss or displacement of completed reports rather than true variation in patrol monitoring effort, the period corresponds to a time of broader economic decline in Ghana when, according to the MNP management plan, "the park experienced considerable problems [...] infrastructure was neglected and poaching was virtually uncontrolled" (GWD 2005: 18). Other sources also point toward poor management capacity and low staff morale at that time (Jamieson 1987; B. Jamieson pers. comm. Nov. 2007). Periods with greater recorded effort correspond to the initial momentum of the program (Pegg 1969; Asibey 1971; B. Jamieson pers. comm. Nov. 2007) and more recent support from donor-funded projects (GWD 2005). These correlations signal that, unsurprisingly, the program's effectiveness likely vacillates with the broader economic context

within which park management is situated. This highlights the fact that locally-based monitoring programs are not immune to the effects of international economic influences like changing donor priorities, and that securing sustainable sources of funding remains a common priority (Rodriguez 2003).

On the topic of funding, the low cost of many locally-based programs has been highlighted as a key feature (Danielsen et al. 2003, 2005). We have not conducted a detailed cost assessment for the MNP monitoring program, but Brashares & Sam (2005) and Jachmann (2008a) indicate a relatively low cost on the order of US\$1-15/km<sup>2</sup>/year. While this would appear to be a positive feature of the program, it is worth asking if this level of funding is sufficient. Notwithstanding the recommendation to better address sampling error (and the associated argument that data quality influences the cost-effectiveness of monitoring; Nichols & Williams 2006), there are signs that more operational funding is required. For example, we witnessed program deficiencies in areas such as basic equipment for field staff (e.g., hiking boots, camping gear), transportation costs (e.g., fuel, vehicle repairs), and capacity for effective data management (e.g., decaying historical reports, incomplete and error-prone databases; C. Burton personal observations; Appendix 2.1). Such problems are certainly not unique to the GWD program and we use them only to highlight the widespread need for greater financial and technical support of tropical biodiversity monitoring efforts like this one (Rodriguez 2003; Balmford et al. 2003a; Balmford & Whitten 2003). As noted above, the impact of international donor-funded projects can be substantial yet often unsustainable. Another relevant example from MNP pertains to a system of financial incentives (e.g., bonuses for hunters arrested, long distances walked) that reportedly improved patrol staff performance during a recent donor-funded project (Buedi & Addae-Wireko 2005; GWD 2005), but had the unintended negative consequence of reducing staff morale and performance when the project ended and incentives ceased. Such examples underscore the importance of careful planning for sustained improvements in program effectiveness.

Evidence for the success of the GWD monitoring program in closely involving local stakeholders and leading to rapid management decisions could also be seen as equivocal. While GWD officers and wildlife guards are certainly intimately involved as local stakeholders in the conservation of park resources, the formal involvement of broader stakeholders from communities around MNP (and other parks) has in the past been minimal or, in fact, adversarial in the sense of conflict between patrol staff and local hunters or park wildlife and nearby farmers (Mason 1993; Danso et al. 1994). This has led to more recent promotion of collaborative management between GWD-managed parks and neighboring communities, including new initiatives for participatory monitoring of wildlife in community reserves (GWD 2000; GWD & SNV 2004b; Sheppard et al. 2010).

Within GWD, management of law enforcement monitoring has typically been “top down” (i.e., the responsibility of a senior officer) and significantly influenced by foreign consultants (as in, for example, recent program restructuring to range-based and MIST systems; GWD 2005). Much of the analysis and interpretation of results has also been performed by outside experts (e.g., Brashares et al. 2004; Jachmann 2008a,b; this study; but see Buedi & Addae-Wireko 2005 and note that this observation could be influenced by publication bias). The program does likely facilitate rapid management response, particularly with respect to anti-poaching efforts (e.g., patrol deployments to areas of recent hunting activity), though this is difficult to track with available data. Jachmann (2008b) suggests that feedback from the monitoring system has

recently resulted in improvements in patrol staff performance and corresponding reductions in illegal hunting. Nevertheless, an explicit role for feedback from the monitoring program does not appear to be institutionalized, particularly with respect to the wildlife data, as evidenced by its near lack of mention in a recent MNP management plan (GWD 2005) and expressions of skepticism about data reliability made by consultants involved in management planning (P. Marshall and P. Howard, pers. comm. July 2005). In sum, these reflections suggest that, despite the noted strengths of the GWD program, it may in many ways not represent an ideal model of effective locally-based monitoring. In fact, a simple dichotomy between locally-based and professional (or “conventional”) scientific monitoring systems may not be useful in practice since many programs (like this one) combine elements of both and should be assessed based on their distinct features and the specific context in which they operate (Danielsen et al. 2009).

### *Recommendations for more effective monitoring*

Given the challenges identified for the reliable monitoring of wildlife in Ghana, can we suggest recommendations for improving this or other comparable programs? As noted above, we concur with Yoccoz et al. (2001) and others in stressing the importance of defining explicit objectives and ensuring that chosen methodologies are capable of meeting them. For instance, it may be more tractable for the GWD program to focus only on certain carefully chosen indicator species linked to particular management questions, rather than on the entire “larger” mammal community (e.g., Gray & Kalpers 2005). Regardless of target species, incorporating an assessment of sampling error into the protocol would be beneficial. Perhaps a small proportion of patrol routes could be designated as “replicate” samples to monitor sampling variation, or covariates known to affect detectability could also be monitored (analogous to current tracking of patrol effort; Jachmann 2008a,b). Such adjustments need not be complex or require a program overhaul. While simplicity is key to successful patrol-based monitoring, collaboration with a statistician could produce significant improvements in the strength of inference at minimal additional cost. An emphasis on identifying and linking local technical support to management, and on building local capacity in requisite skills, could be of great benefit to monitoring effectiveness (for example, the Wildlife Biology program at Ghana’s Kwame Nkrumah University of Science and Technology is a local resource with faculty and graduate students familiar with sampling design). Following the arguments of Nichols & Williams (2006) and Lindenmayer & Likens (2009, 2010b), inference from the data would also be strengthened by linking monitoring to specific management questions defined by conceptual models and *a priori* hypotheses. A recent MNP management plan briefly promotes the concept of adaptive management (GWD 2005: 87) but does not identify particular questions or models to be tested by the monitoring data, even though such models are implicit in the plan (e.g., effect on mammal populations of hunting pressure, water availability, and fire frequency). Specific monitoring of key predictor variables, including both environmental and socioeconomic factors (Bawa & Menon 1997), would also help improve understanding of the greater park ecosystem, as would the facilitation of focused research programs to complement monitoring (i.e., test hypotheses identified by surveillance using a more experimental approach). *Post hoc* inference from unfocused surveillance monitoring has a poor ability to identify causal relationships (Nichols & Williams 2006) and may often be disassociated from particular program features if they are poorly documented (e.g., targets, methodological protocols, sampling errors). In general, greater

emphasis on making monitoring data more transparent and readily available (including metadata and means of error propagation) to both local stakeholders and the broader conservation community would be a great benefit.

Another important improvement to the GWD monitoring program might be the periodic use of complementary methods for testing or “calibrating” the relationship between patrol observations and more robust measurements of species abundance or richness (e.g., Pollock et al. 2002). Our results demonstrate the usefulness of camera trapping, particularly for monitoring more elusive species (i.e., smaller or nocturnal species, carnivores). To our knowledge, this is the first large-scale application of camera trapping in a West African savanna environment, and we hope it stimulates further use and testing of this method. Camera trapping provides additional benefits, particularly by producing unequivocal photographic evidence of animal occurrence that can be archived, assessed by outside experts, and used to increase awareness and enthusiasm for monitored wildlife (e.g., photographic presentations to tourists, donors, senior government officials). Resulting data can also be readily used for other studies on, for example, animal morphology or activity patterns, and they are well-suited to robust analytical frameworks like mark-recapture and occupancy modeling (O’Connell et al. 2010; see also Chapters 3 and 4). Of course, camera trapping is not a panacea; it requires large initial investments in equipment and training and can be subject to various problems, including technical malfunctions or inconsistent performance, theft or animal damage, and detection biases (this study; Swann et al. 2004; Larrucea et al. 2007; Kelly 2008; Treves et al. 2010). Other methods have been used to survey wildlife in MNP, such as aerial censuses (GWD 2005; Bouché 2006) and sighting transects (Jamieson 1972; Wilson & Kpelle 1993), but they have not been related to the patrol monitoring data and are also subject to significant biases (e.g., aerial surveys are only appropriate for the largest mammals and sighting transects are made difficult by low visibility in dense vegetation; e.g., Jachmann 2002). As part of our study, we also piloted sighting transects using the Distance method (Buckland et al. 2001) and implemented sign transects and interviews of villagers and staff as alternative survey methods (more details in Chapter 3). However, we found the usefulness of these methods to be limited by problems such as infrequent sightings, poor tracking substrate, and questionable reliability (particularly for interviews; Chapter 3; Burton 2009). While further methodological comparison is warranted, we suggest that camera trapping is a useful and reliable method that meets high standards of evidence (McKelvey et al. 2008).

#### *Broader relevance and future work*

Our study represents a cursory evaluation of one particular monitoring program, but we think it has broad relevance to monitoring efforts elsewhere. The GWD system is implemented in many other parks in Ghana, and preliminary results from a similar study in one of them (Ankasa Conservation Area in southwestern Ghana; C. Burton, unpublished data) indicate that many of the issues raised are equally relevant. Community-based monitoring programs are also increasingly being implemented or proposed in Ghana in response to policy changes promoting community-based wildlife management (e.g., Sheppard et al. 2010). Such programs are likely to face similar challenges to the GWD monitoring, particularly in terms of limited funding and technical capacity, low animal detectabilities, and restricted resources to support data management and analysis. Patrol-based (also known as ranger-based) and community-based

monitoring programs are also widespread and increasing across Africa and other parts of the world (Gaidet et al. 2003; Danielsen et al. 2005a, 2009; Gray & Kalpers 2005; Berkes et al. 2007), and are sorely needed to inform conservation initiatives and promote sustainable livelihoods. Preliminary analyses from comparative assessments of several programs in different countries suggest that the issues raised in our study are not unique to Ghana (Danielsen et al. in prep.). If these monitoring programs are to succeed in adequately tracking wildlife and other biological resources, it is a critical time for concerted focus and international support in the pursuit of reliable and practical methods for adaptive monitoring and management (Danielsen et al. 2009; Lindenmayer & Likens 2010b).

In conclusion, we recognize the importance and value of monitoring components of biological diversity, such as Ghana's larger mammal communities, and we particularly stress the need for locally relevant and reliable monitoring programs in species-rich regions that have thus far received inadequate attention. It is necessary to capitalize on and strengthen existing efforts, like the Ghana Wildlife Division's mammal monitoring program, while also supporting creative new initiatives that increase local participation and relevance. However, it is equally important to emphasize that programs charged with the responsibility of informing society about the status of biodiversity must be capable of producing reliable data. Some may feel that a strong focus on methodological detail adds unnecessary complexity to monitoring, and that broad patterns produced by locally-based programs are likely to reflect underlying biodiversity trends. This could be true, and certainly more work is specifically needed to ascertain the true wildlife dynamics reflected in the GWD monitoring data. However, we suggest that without adequate testing this assertion would lie outside the realm of scientific monitoring. As noted by Nichols & Williams (2006), the identification of monitoring objectives and management actions should be based on the value judgments of a community of relevant stakeholders, but the remaining components of effective monitoring for conservation are largely the purview of ecological scientists and technical experts, who must receive adequate training and support, and work closely with stakeholders to provide the reliable information they need.

**Table 1.** Mammal species detected in Mole National Park, Ghana, by the patrol monitoring system and camera trap survey, with species traits that affected detectability by the two methods (average trait values from Jones et al. 2009 when available).

Common name	Scientific name <sup>e</sup>	Body mass (kg)	Activity period	Group size	Relative abundance (count per unit effort) <sup>a</sup>		
					Cameras	Patrols (2006-08)	Patrols (1968-2001)
Kob	<i>Kobus kob</i>	80.0	diurnal	40	10.11	12.21	1.50
Olive baboon	<i>Papio anubis</i>	17.7	diurnal	40	8.54	5.95	4.21
Spotted hyena	<i>Crocuta crocuta</i>	63.4	nocturnal	8	6.71	0.02	0.0003
Bushbuck	<i>Tragelaphus scriptus</i>	43.3	mixed/crepuscular	1	6.31	1.28	0.67
Warthog	<i>Phacochoerus africanus</i>	82.5	diurnal	5	5.08	2.93	1.29
Hartebeest	<i>Alcelaphus buselaphus</i>	160.9	diurnal	20	4.63	3.44	2.22
Elephant	<i>Loxodonta africana</i>	3824.5	diurnal	19.5	4.44	0.95	0.24
White-tailed mongoose	<i>Ichneumia albicauda</i>	3.6	nocturnal	1	3.14	0	0 <sup>b</sup>
Green monkey	<i>Chlorocebus sabaues</i>	3.7	diurnal	12	3.13	2.22	1.21
Leopard	<i>Panthera pardus</i>	52.4	mixed/crepuscular	1	2.96	0.01	0.004
Large-spotted genet	<i>Genetta pardina</i>	2.0	nocturnal	1	2.85	0	0.003 <sup>c</sup>
Waterbuck	<i>Kobus ellipsiprymnus</i>	204.4	mixed/crepuscular	12	2.63	3.82	1.58
Crested porcupine	<i>Hystrix cristata</i>	13.4	nocturnal	1	2.47	0	0.001 <sup>c</sup>
African buffalo	<i>Syncerus caffer</i>	592.7	mixed/crepuscular	12	1.81	1.05	1.48
Aardvark	<i>Orycteropus afer</i>	56.2	nocturnal	1	1.57	0.00	0.0003
Human <sup>d</sup>	<i>Homo sapiens</i>	-	-	-	1.46	0.76	0.03
Roan antelope	<i>Hippotragus equinus</i>	264.2	diurnal	12	1.33	0.97	0.77
Patas monkey	<i>Erythrocebus patas</i>	8.0	diurnal	28	1.21	1.47	0.76
Red-flanked duiker	<i>Cephalophus rufilatus</i>	12.1	diurnal	1	1.17	0.13	0.30
Scrub hare	<i>Lepus saxatilis</i>	2.6	nocturnal	-	0.95	0	< 0.0001 <sup>c</sup>
Grey duiker	<i>Sylvicapra grimmia</i>	15.6	mixed/crepuscular	1	0.82	0.22	0.29
African civet	<i>Civettictis civetta</i>	12.1	nocturnal	1	0.59	0	0.001

**Table 1.** Continued

Marsh cane rat (grasscutter)	<i>Thryonomys swinderianus</i>	3.8	nocturnal	1	0.42	0	0.002
Marsh mongoose	<i>Atilax paludinosus</i>	3.6	mixed/crepuscular	1	0.37	0	0.03
Caracal	<i>Caracal caracal</i>	12.0	nocturnal	1	0.37	0	< 0.0001
Gambian mongoose	<i>Mungos gambianus</i>	1.6	diurnal	6.7	0.13	0	0 <sup>b</sup>
Striped ground squirrel	<i>Xerus erythropus</i>	0.6	-	-	0.11	0	0
Side-striped jackal	<i>Canis adustus</i>	10.4	nocturnal	2	0.07	0.004	< 0.0001
Oribi	<i>Ourebia ourebi</i>	17.2	diurnal	2	0.05	0.17	0.78
Senegal galago	<i>Galago senegalensis</i>	0.2	nocturnal	3.5	0.05	0	< 0.0001 <sup>c</sup>
Giant pouched rat	<i>Cricetomys gambianus</i>	1.3	-	-	0.04	0	0
Geoffroy's black and white colobus	<i>Colobus vellerosus</i>	7.7	diurnal	16	0	0.04	0.13
Lion	<i>Panthera leo</i>	158.6	nocturnal	8.7	0	0.01	0.01
Bohor reedbuck	<i>Redunca redunca</i>	43.3	mixed/crepuscular	4	0	0.0006	0.04
Red river hog	<i>Potamochoerus porcus</i>	70.0	mixed/crepuscular	10.6	0	0	0.06 <sup>c</sup>
Hippopotamus	<i>Hippopotamus amphibius</i>	1536.3	mixed/crepuscular	-	0	0	0.004
Yellow-backed duiker	<i>Cephalophus silvicultor</i>	62.0	mixed/crepuscular	1	0.00	0.00	0.002
Wild dog	<i>Lycan pictus</i>	22.0	nocturnal	9.3	0.00	0.00	0.0007
"Long nose mongoose" <sup>b</sup>							0.02 <sup>b</sup>
"Dwarf mongoose" <sup>b</sup>							0.001 <sup>b</sup>

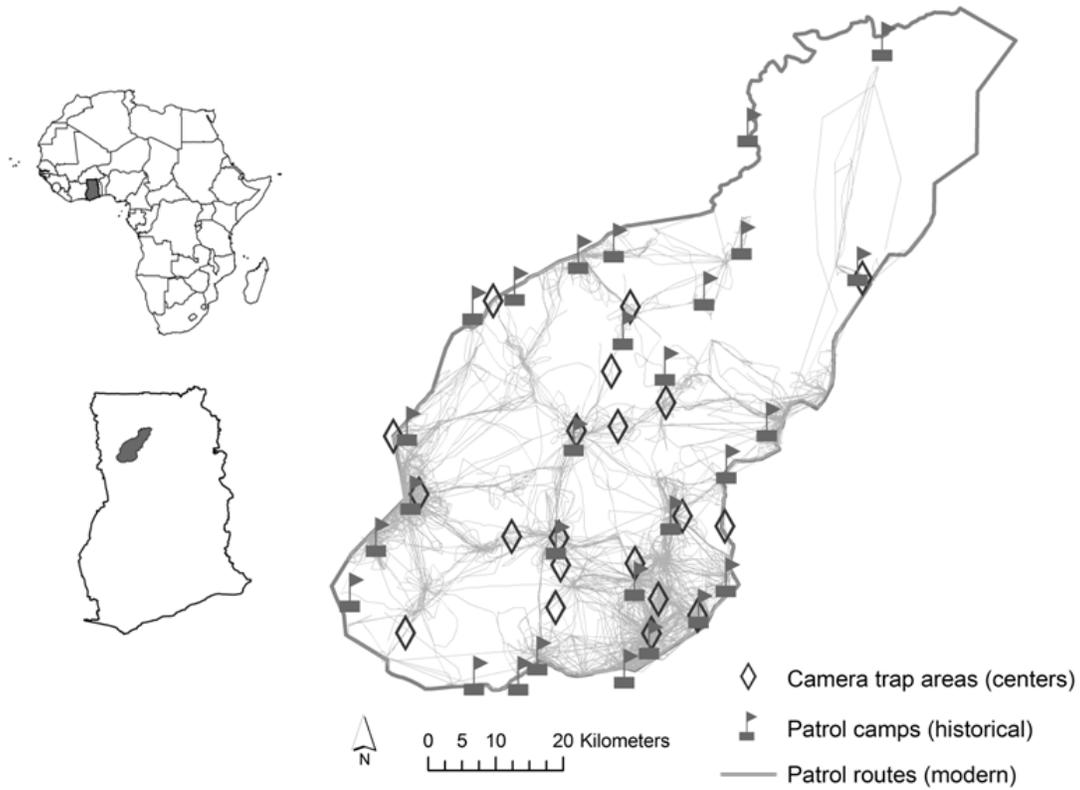
<sup>a</sup> Indices of relative abundance calculated as number of individuals counted per unit of effort, which was set at 100 camera-trap days for the camera survey (5,469 total effort) and 1 patrol-day for the patrol counts (1612 total for the modern dataset and 28,225 for the historical).

<sup>b</sup> Mongoose species were not clearly or correctly identified in the historical patrol data as long nose and dwarf mongoose do not occur in Ghana (see Chapter 3).

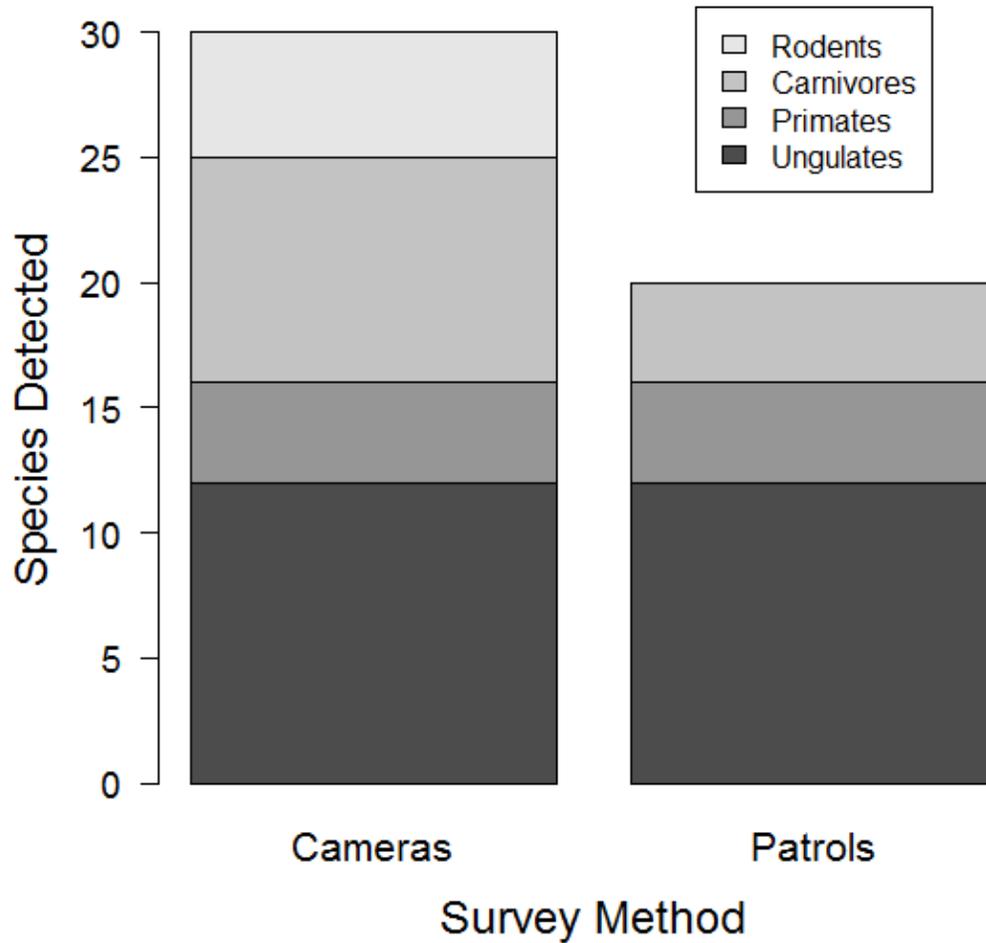
<sup>c</sup> Large-spotted genet was assumed for records of “genet” in the historical dataset, crested porcupine for records of “porcupine”, senegal galago for 1 record of “bushbaby”, and scrub hare for 1 record of “rabbit”. “Bush pig” was also assumed to be the same as “red river hog”.

<sup>d</sup> Observations of humans included signs of illegal hunting activity for the patrol data (e.g., footprints, poaching camps, traps).

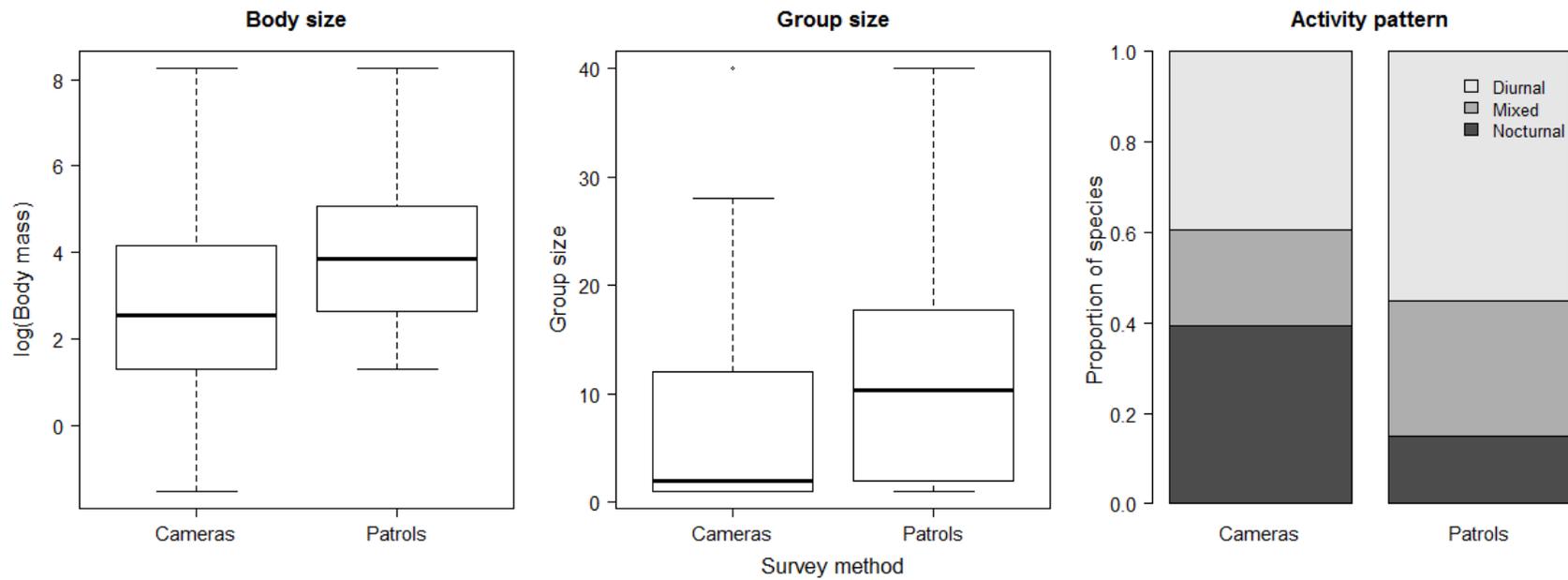
<sup>e</sup> Species nomenclature follows IUCN red list 2010, Wilson & Reeder (2005). See also Grubb (1998).



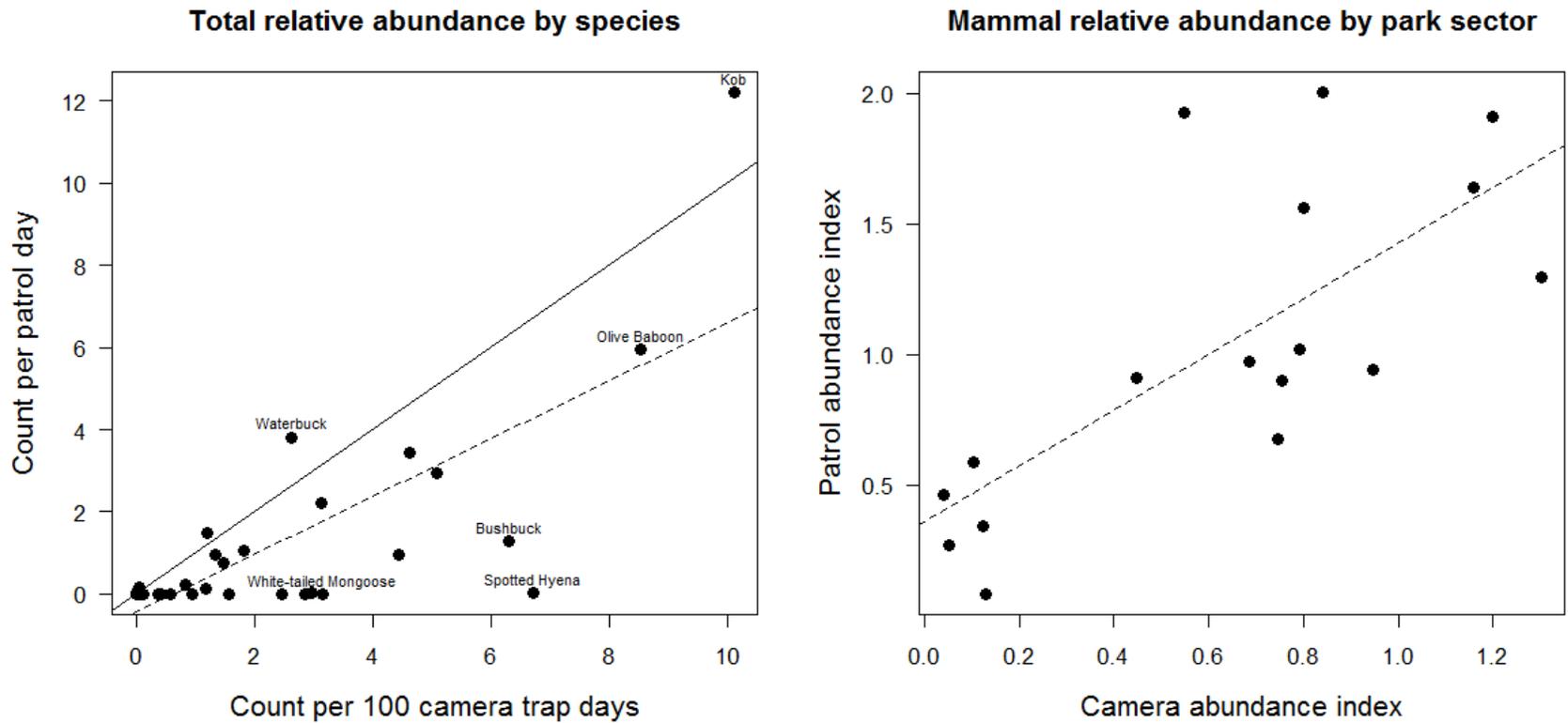
**Figure 1.** Study area and sampling map, showing location of Ghana in Africa (top left), Mole National Park in northern Ghana (bottom left), and the distribution within the park of camera-trap sampling areas, approximate patrol paths for the period of methodological comparison (2006-2008), and patrol camps from which monthly summary reports were created for the historical dataset (1968-2001).



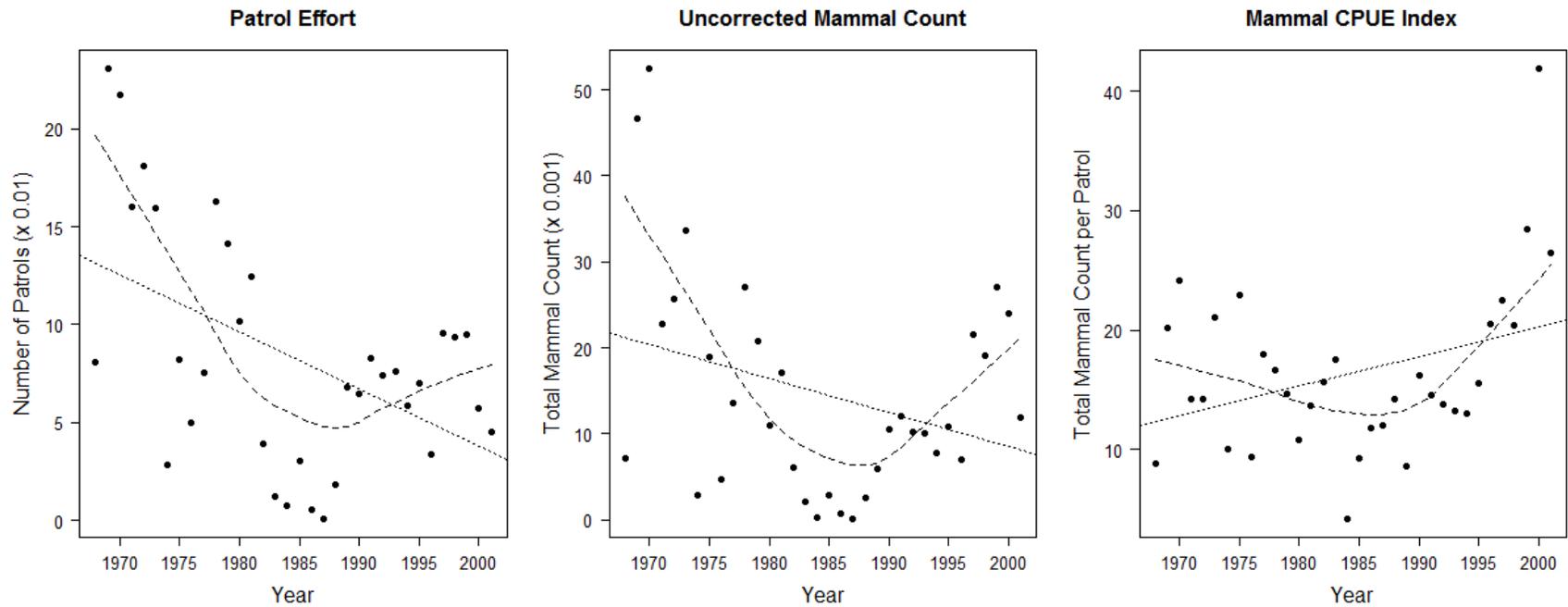
**Figure 2.** Comparison of species richness estimates for Mole National Park from the camera trap survey and patrol monitoring observations (for the 2006-2008 comparison period). For simplicity elephant and aardvark are included under “Ungulates” and scrub hare under “Rodents”.



**Figure 3.** Summary of trait values across species detected in Mole National Park by the camera-trap survey and patrol monitoring observations (for the 2006-2008 comparison period).



**Figure 4.** Relative abundance indices generated from patrol and camera-trap data in Mole National Park (over 2006-2008 period of comparison). Left panel shows total abundances (per unit effort) across all 34 species detected (including humans, with select species highlighted to illustrate strong or weak concordance). Right panel shows abundance indices across all mammal species for 17 park management sectors within which both methods detected at least one species. Dashed lines give linear fits ( $R^2 = 0.58$  for left panel,  $R^2 = 0.54$  for right panel) and solid line on left panel shows the 1:1 relationship (though note different scales of effort).



**Figure 5.** Trends in annual patrol effort (left), total mammal counts (middle), and counts corrected for effort (CPUE index, right) across 33 mammal species (pooled counts) in Mole National Park over the historical monitoring period (1968-2001). Differing interpretations of overall trend in mammal abundance are highlighted by linear fits (dotted lines), while the effect of a decline in patrol effort during the middle of the monitoring period is emphasized in the smoothed lowest fits (dashed lines).

## **Supporting Information for Chapter 2**

**Appendix 2.1:** Photos of historical patrol monitoring data stored at Mole National Park.

**Appendix 2.2:** Further detail on comparison of species relative abundance estimates from patrol and camera-trap data across management sectors in Mole National Park.

**Appendix 2.3:** Temporal trend comparison for observations of illegal hunting activity in Mole National Park.

**Appendix 2.4:** Title and abstract of unpublished manuscript on a detectability analysis using long-term patrol monitoring data from Mole National Park.

**Appendix 2.1:** Photographs of historical monthly reports from the Ghana Wildlife Division's patrol-based monitoring system in Mole National Park, Ghana, that were reviewed and entered into a database for this project. Note the deteriorating condition of the archived reports. (Photos by C. Burton at MNP Headquarters, November 2006.)





**RANGER POST MONTHLY REPORT**

STATION: - JANPARA CAMP  
 REPORTER: - LAWRENCE MEMSAH  
 DATE: - 26<sup>th</sup> JUNE 1972.

1. POACHING AND PATROLLING

a. POACHERS: - NIL.  
 b. TRAPS, SNARES, ETC.: - NIL.  
 c. DEAD ANIMALS: - NIL.  
 d. OVERNIGHT PATROLS: - We attended twenty full night patrols and ten for day patrols.

2. VEGETATION, SALT LICKS, WATERHOLES, WEATHER.

VEGETATION: - Pityrespum parker, for this month, it is very useful to human life as well as animals such as baboon, bush buck and Red flanked duiker.  
 SALT LICKS: - We visited seven saltlicks five of them to good for animals for this month. Such as, Roan antelope and Buffalo visited it regularly.

15

16

**WATERHOLES:** - Only six water holes were visited this month. They were little of use and sometimes little cold.

**WEATHER:** - Clear and sometimes little cold.

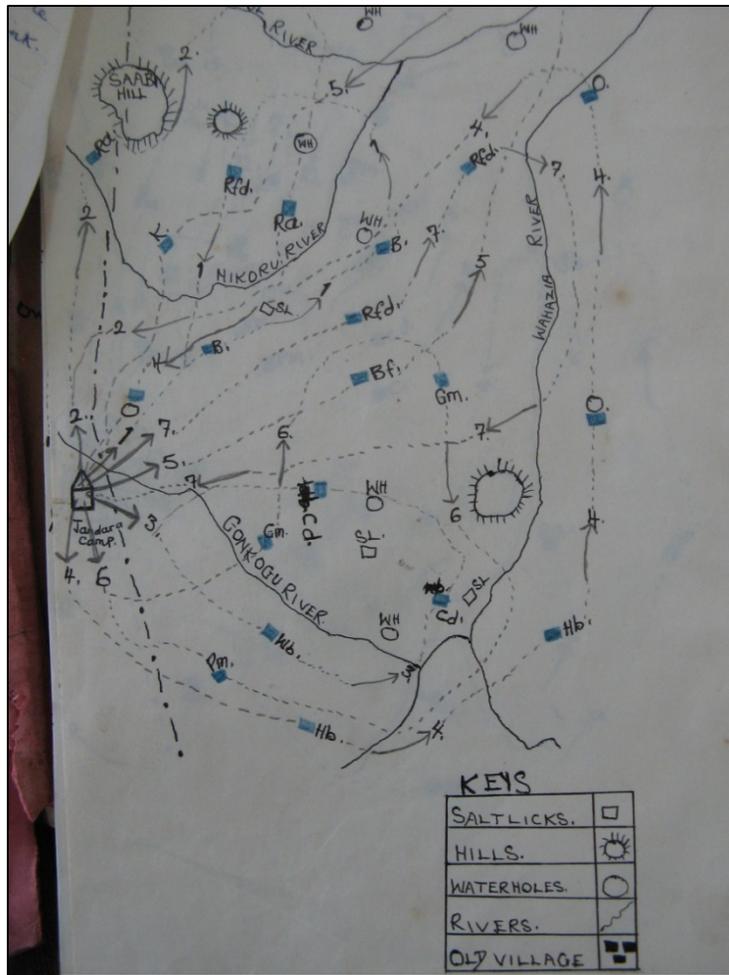
**LIGHTRAIN:** - According to my own knowledge as for this month, there was two light rain and one heavy rain.

3. OBSERVATION OF ANIMALS.

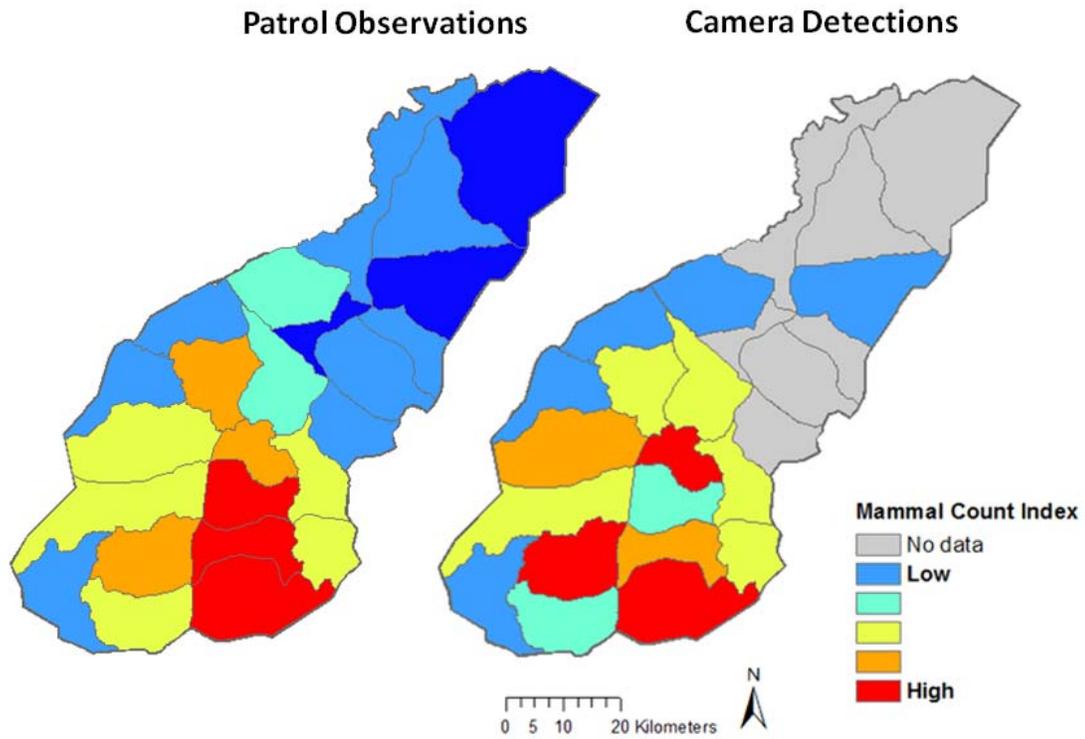
Oribi = 22.	Kob = 16.
Waterbuck = 31.	Red flanked duiker = 10.
Hartebeest = 13.	Buffalo = 14.
Crowned duiker = 15.	Red buck = 6.
Wart hog = 34.	Adark = 2.
Colombus monkey = 1.	Civet cat = 2.
Baboon = 10.	Bush buck = 20.
Totals: 156.	

4. STAFF ON DUTY.

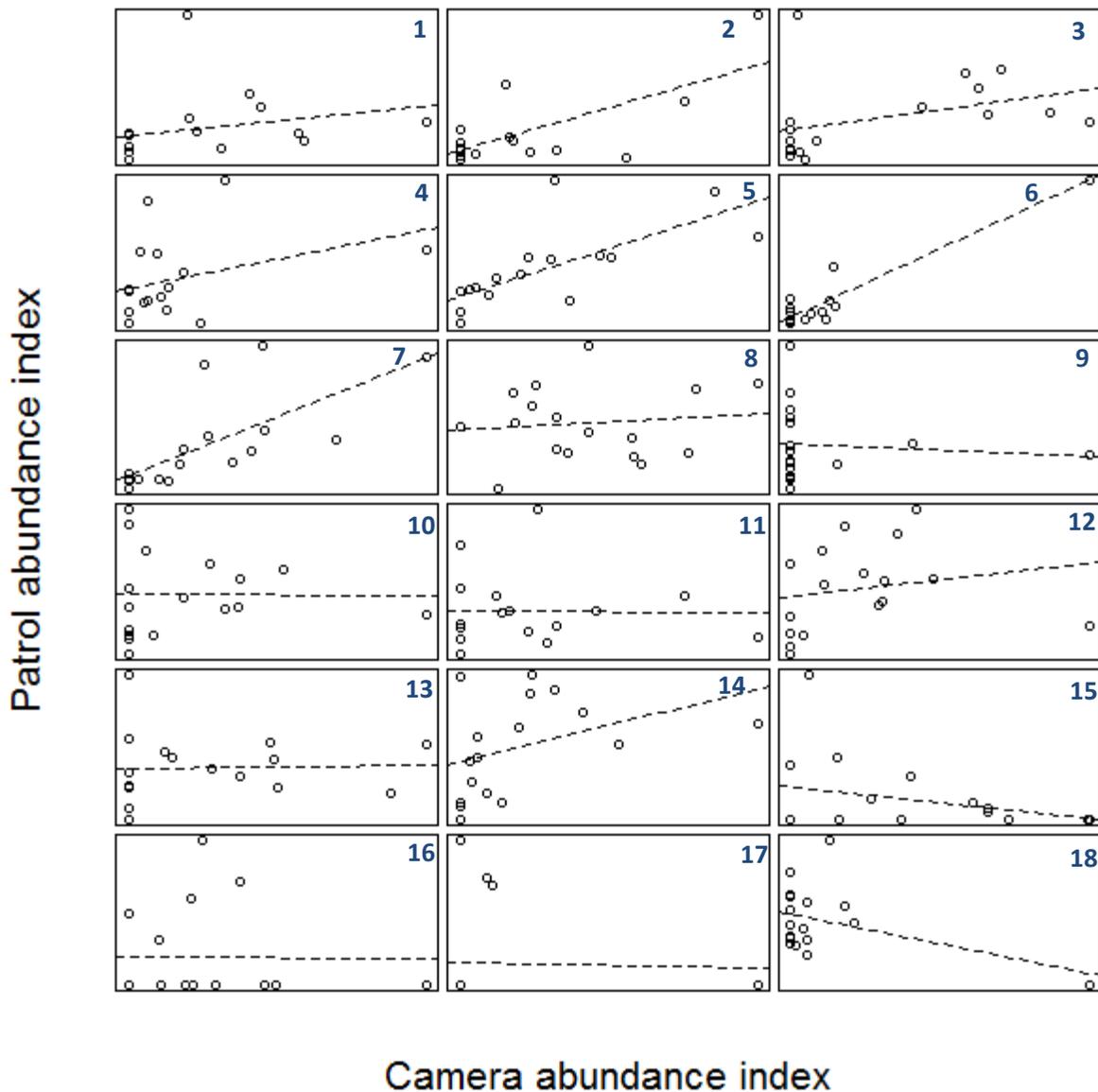
Bole Grushie: Gls  
 Adama Tapumeh: Porter.  
 Lawrence Mensah: G.A.



**Appendix 2.2:** Further detail on comparison of species relative abundance estimates from patrol and camera-trap data across management sectors in Mole National Park.

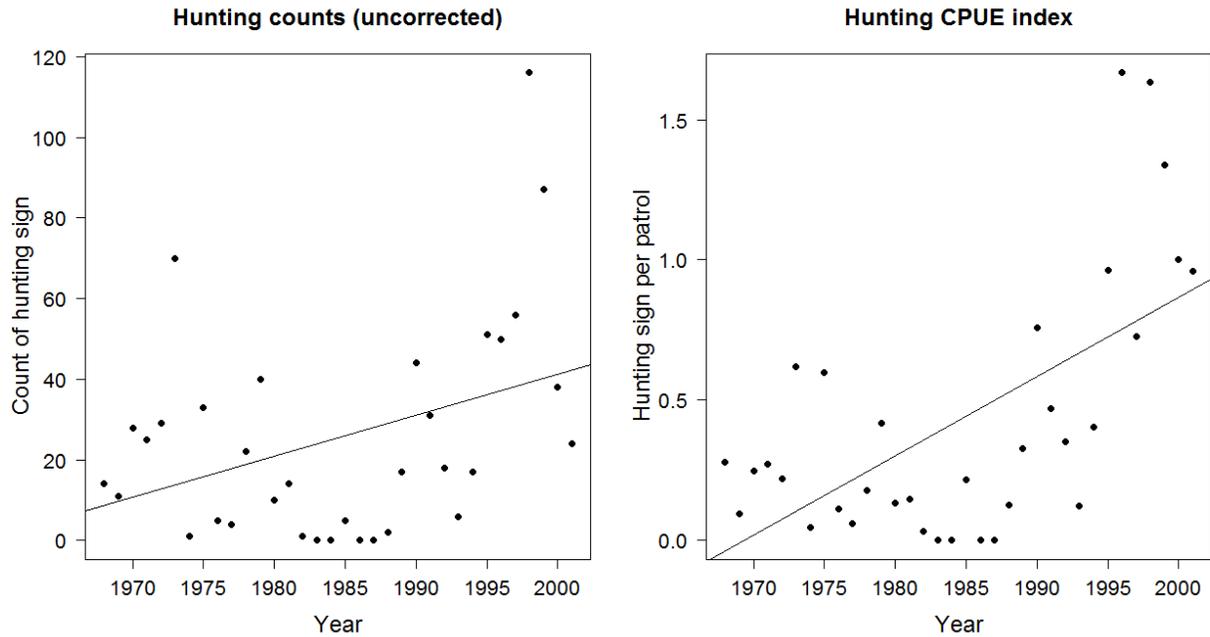


Relative abundance of all mammal species detected by patrols (left) and camera traps (right) across 24 management sectors in Mole National Park, 2006-2008.



Relationship between species-specific abundance indices for patrols and cameras across 17 management sectors in Mole National Park. Plot numbers correspond to the following species (with Spearman correlation coefficient,  $r_s$ . Scientific names in Table 1): 1. Elephant (0.51); 2. Buffalo (0.28); 3. Hartebeest (0.55); 4. Roan antelope (0.44); 5. Waterbuck (0.81); 6. Kob (0.60); 7. Warthog (0.84); 8. Bushbuck (-0.01); 9. Oribi (0.01); 10. Grey duiker (0.15); 11. Red-flanked duiker (0.13); 12. Olive baboon (0.45); 13. Patas monkey (0.11); 14. Green monkey (0.56); 15. Spotted hyena (-0.08); 16. Leopard (0.10); 17. Side-striped jackal (0.49); 18. Human Hunter (-0.16). Dashed lines show linear fit (which are in many cases influenced by outliers and do not always reflect the non-parametric correlation coefficient). The strength of species' correlations (i.e., value of  $r_s$  for plot) was positively related to mean body mass, group size, and diurnal activity.

**Appendix 2.3:** Temporal trend comparison for observations of illegal hunting activity in Mole National Park.



Comparison of trends in detections of illegal hunting activity by the patrol monitoring system in Mole National Park, Ghana, from 1968-2001: uncorrected counts on the left and counts corrected by patrol effort on the right (catch-per-unit-effort or CPUE index).

**Appendix 2.4:** Title and abstract of unpublished manuscript on a detectability analysis using long-term patrol monitoring data from Mole National Park. (Manuscript available from author.)

**The Effect of Imperfect Detectability on Mammal Monitoring Trends  
in Ghana's Nature Reserves**

Cole Burton

May 11, 2005

**Abstract.** Imperfect detection is a potential source of error that is frequently overlooked in wildlife monitoring programs designed to assess changes in occupancy. Recent methods have been developed to explicitly account for detection probability in estimating site occupancy, colonization and local extinction, but they have not yet been widely tested. I applied the method of MacKenzie et al. (2003) to data from a 30-year monitoring program in Mole National Park, Ghana, using the red-flanked duiker (*Cephalophus rufilatus*) as a test species. Model results suggest that the probability of detecting a duiker at a site where it was present was significantly less than 1 and declined over time with abundance. Low detectability can explain the discrepancy between 'naïve' estimates of occupancy, which declined from a mean of 0.72 for 1969-79 to 0.43 for 1990-98, and model estimates in which occupancy remained very close to 1 throughout the monitoring period. Implications for wildlife monitoring programs and directions for further work are discussed.

## CHAPTER 3

### Unpredicted Patterns of Persistence in an Endangered Carnivore Community

#### Abstract

Mammalian carnivores play key ecological roles and are of great cultural significance, yet many are increasingly threatened and inadequately studied. Carnivore extinctions frequently have cascading impacts through an ecosystem, so effective management of ecological communities requires an understanding of carnivore vulnerability. We conducted the first detailed assessment of the carnivore community in Ghana's Mole National Park, a poorly studied West African savanna ecosystem expected to support carnivore populations of regional importance. Only 9 of 16 historically occurring carnivore species were detected in a camera-trap survey covering 253 stations deployed for 5,469 trap days between October 2006 and January 2009. A hierarchical multi-species occupancy model applied to the camera-trap data indicated low overall likelihoods of false absence despite low per-survey probabilities of detection. Results from concurrent sign, call-in, and village surveys, as well as long-term law enforcement patrol records, provided more equivocal evidence of carnivore occurrence but supported the conclusion that many carnivores have declined and are likely functionally or fully extirpated from the park, including the top predator, lion (*Panthera leo*). Contrary to expectation, variation in carnivore persistence was not explained by ecological or life-history traits such as body size, home range size or fecundity, thus raising doubt as to the predictability of carnivore community disassembly. Village interviews and park records indicate that hunting for traditional purposes and in retaliation for livestock depredation may affect some carnivores. While further work is needed to elucidate the causes and consequences of carnivore declines in Mole, our results imply an urgent need for new conservation initiatives to better protect and ultimately restore the region's embattled carnivore populations. We also suggest a need for more empirical study of the response of entire carnivore communities to anthropogenic impact in order to improve understanding of carnivore extinction risk.

#### Introduction

Despite their recognized ecological and cultural significance, mammalian predators in the Order Carnivora are increasingly and disproportionately impacted by anthropogenic activities (Gittleman et al. 2001; Karanth & Chellam 2009). More than one-quarter of mammalian carnivore species (hereafter "carnivores") are currently considered threatened by extinction, with many more undergoing significant population declines (Schipper et al. 2008). As strongly interacting species, carnivores can exert broad influence on ecological processes, and changes in their populations frequently lead to cascading impacts throughout an ecosystem (Ray et al. 2005b; Beschta & Ripple 2009; Prugh et al. 2009; Roemer et al. 2009). Documenting and predicting carnivore responses to anthropogenic impacts are thus critical components of effective wildlife conservation and management.

Recent studies highlight the influence of intrinsic biological traits on extinction risk in carnivores and other mammals (Purvis et al. 2000; Cardillo et al. 2004, 2005; Karanth et al. 2010). Large body size, in particular, is frequently associated with greater vulnerability, and many large carnivores are among the most threatened taxa. However, the value of body size as a

predictor of vulnerability is primarily due to its correlation with other characteristics of species that are more directly tied to persistence (e.g., home range size, fecundity, conflict with humans). In fact, it is increasingly apparent that species persistence is affected by complex interactions among intrinsic traits and extrinsic threats, with the relative importance of body size and other biological attributes being dependent on local context (Beissinger 2000; Isaac & Cowlshaw 2004; Cardillo et al. 2008; Davidson et al 2009; Fritz et al 2009).

Most studies of carnivore extinction risk have focused either at a broad, macroecological scale (e.g., Cardillo et al. 2004), or on the viability of a single species or population (e.g., Kelly & Durant 2000; Linkie et al. 2006). Few studies have investigated persistence across an entire carnivore community, within which a range of life-history traits exist in a common environmental context on a scale at which conservation interventions are implemented (Cowlshaw et al 2009; Karanth and Chellam 2009). Moreover, carnivore research and conservation in Africa has focused on East and southern Africa and few data exist for populations in West Africa (Bauer et al. 2003b; Ray et al. 2005a), despite the acute threats to wildlife entailed by the region's high human densities and widespread hunting for bushmeat (Brashares et al. 2001; Fischer & Linsenmair 2001a). What little data exist are not encouraging for carnivores in the region; for instance, the lion (*Panthera leo*) has been classified as regionally Endangered (Bauer & Nowell 2004) and the African wild dog (*Lycaon pictus*) is thought to have been largely eradicated (Woodroffe et al. in Sillero-Zubiri et al. 2004). A more detailed understanding of variation in extinction vulnerability within carnivore communities facing such high levels of threat is not only important for regional conservation efforts, but also to inform conservation planning in less impacted areas at risk of future increases in anthropogenic pressure (Cardillo et al. 2004, 2006).

In this study, we assessed patterns of persistence across the carnivore community in Ghana's Mole National Park (MNP), a regionally important protected savanna ecosystem. Specifically, we combined results of camera trapping, sign and call-in surveys, village interviews, and patrol records, and used an analytical approach accounting for imperfect detection to estimate the likelihood of local extirpation for 16 carnivore species that differ greatly in their ecological and life-history traits and vary in body size by more than two orders of magnitude. We compared patterns of persistence against 17 characteristics of species, including body size, home range size and fecundity (Table 1), to test for common predictors of vulnerability. We also considered the broader causes and consequences of carnivore community collapse in this West African ecosystem.

## Methods

### *Study Area*

Mole National Park (MNP) is the largest of Ghana's protected areas and covers approximately 4600 km<sup>2</sup> of woodland savanna habitat in the country's Northern Region (roughly between 09°11' – 10°06' N and 01°22' – 02° 16' W; Fig. 1). It lies within the threatened West Sudanian Savanna Ecoregion (Burgess et al. 2004) and was first established as a game reserve in 1958 and a national park in 1971. Elevation in MNP ranges from approximately 120-490m above sea level, and soils are mainly low fertility plinthic ferralsols and rhodic nitisols (Wilson & Kpelle 1993; GWD 2005). Open savanna woodland is the dominant habitat type, with tree cover

averaging ~30% and grasses reaching 2-3m in height during the wet season (Schmitt & Adu-Nsiah 1993 in GWD 2005). Mean annual rainfall is ~1100 mm, with >90% falling during the April-to-October wet season, and mean annual temperature is ~28°C, with highs above 40°C in the hottest months of March and April (GWD 2005). Most of the park's rivers are seasonal and drain into the White Volta River; water is a limiting factor during the dry season when wildlife concentrate near sources of permanent water along the Mole River and its tributaries (GWD 2005). Widespread burning during the dry season is the most significant direct human impact to park habitats.

There have been few published wildlife studies conducted in MNP, and none focused on carnivores, but the recent park management plan speculates that 42 larger mammal species (>200g and excluding bats) exist in the park (GWD 2005). Previous surveys indicate the presence of regionally significant populations of savanna ungulate and primate species (Wilson & Kpelle 1993; GWD 2005; Bouché 2006), although the current status of mammal populations within the park is uncertain. Based on law enforcement patrol monitoring records, Brashares et al. (2001) estimated that six large mammal species had been extirpated from MNP since 1968, and population declines have been suggested for several additional species (Brashares & Sam 2005; GWD 2005; East 2006). Bouché (2006) recently estimated that large mammal densities in MNP are lower than in several protected areas in neighboring countries, but some sources have questioned claims of local extinction (Dowsett unpublished manuscript; East 2006) and implied that many resident wildlife populations may be stable or even increasing (Wilson & Kpelle 1993; Grubb et al. 1998; East 1999; Jachmann 2008b). Regardless of the precise status of wildlife populations in MNP, pressure from surrounding human communities is significant—approximately 30,000 people live in 29 villages located within 10 km of the park boundary—and widespread hunting both inside and outside the park remains a significant challenge for park management (Wilson & Kpelle 1993; Mason 1993; GWD 2005; Jachmann 2008a).

### *Survey Methods*

Our primary means of assessing the status of carnivores in MNP was through the use of camera traps, a technique that generates reliable evidence of occurrence (McKelvey et al. 2008) and has proven useful in surveying other populations of cryptic carnivores (Karanth & Nichols 1998; Carbone et al. 2001; Balme et al. 2009a; Pettorelli et al. 2010). We supplemented camera-trap data with those obtained from sign, call-in and spotlight surveys, park law enforcement patrol observations, and interviews with local villagers.

#### *(a) Camera trapping*

We obtained data on carnivore occurrence from 253 camera stations established within MNP between October 2006 and January 2009 (Fig. 1). A total of 280 stations were set, but cameras were stolen from nine stations and malfunctioned at another 18. The majority of stations (227 of 253) consisted of a single passive infra-red DeerCam DC-300 film camera trap unit (Non Typical, Park Falls, WI, USA), with 17 stations consisting of paired DC-300 units (as part of a concurrent photographic capture-recapture study), and nine stations using single units of different camera trap models (1 Leaf River C-1BU, 3 StealthCam MC2-GV, 2 CamTrakker Environmental Unit, 2 Reconyx RC55 and 1 Reconyx Silent Image).

Camera stations were set with two primary sampling objectives: (i) to target areas where carnivores were expected to occur, based on existing knowledge of prey distributions, habitat characteristics and MNP patrol staff observations; and (ii) to sample across gradients of three factors expected to influence carnivore occurrence, namely proximity to human settlement (i.e., park boundary), potential prey abundance, and availability of water and associated riparian forest habitat. Access limitations precluded a random or systematic survey design covering the entire park, but sampling across these gradients provided a representative sample of dominant park features (Fig. 1). The northernmost portion of MNP was not sampled because of extremely limited access and reports of low prey densities in that area (GWD 2005; Bouché 2006). Camera stations were deployed in 20 spatially and temporally differentiated groups targeting different portions of the park and different seasons (Fig. 1). Within each group, stations were set systematically at ~1-km intervals at features expected to maximize carnivore capture probability, such as dirt roads, wildlife trails, riverine corridors, waterholes, and salt licks. The location of each station was recorded with a handheld GPS unit, and site habitat features were noted (e.g. tree cover, grass height, water availability). Cameras were set on trees at a height of approximately 40 cm, facing perpendicular to the expected direction of animal travel and about 3 m from the anticipated site of capture. A one-minute delay between subsequent photographs and standard (medium) sensitivity settings were used, and cameras operated continuously until retrieved or the film was fully exposed. Each photograph was automatically stamped with the date and time of the capture event.

Sampling effort was measured in terms of camera trap-days, calculated as the number of days for which a camera was set or until the last photo was taken if the roll was fully exposed before collection. Stations were active for a mean of 21.6 days (SD = 12.8), yielding a total survey effort of 5,469 trap-days. Sampling effort was highest in the central and southeastern portions of the park (Fig. 1), where prey abundance and water availability were expected to be highest (GWD 2005; Bouché 2006), and during the dry season months of November to March, when access was greatest and water sources most limiting (and thus attractive) for wildlife.

#### *(b) Other Methods*

Given the limitations in spatial and temporal extent of our camera survey, and to provide complementary means of assessing occurrence, we collected data using other methods having different degrees of spatial and temporal resolution, namely: sign, call-in and spotlight surveys, park law enforcement patrol records, and interviews with local villagers.

##### *(i) Sign, call-in and spotlight surveys*

Observations of carnivore tracks and scat (i.e., natural sign or spoor) were recorded both systematically and opportunistically during foot and vehicle travel around and between the camera sampling sites (Fig. 1). GPS location and characteristics such as size, tracking substrate, or scat content were recorded for each sign observed, and each was assigned a probable species identification (or higher taxonomic grouping if species could not be resolved). Identifications were aided by Stuart & Stuart's (2000) reference guide and a MNP patrol staff member with extensive local wildlife tracking experience (E. Bani), with final determinations made by one observer (A.C.B.) for consistency. Variable length transects totaling approximately 330 km (mean transect length = 6 km, SD = 4 km) were surveyed by foot, and routes totaling about 1400 km were surveyed by vehicle (mean route length = 33 km, SD = 21 km; vehicle was driven at

~10-20 km/h). Most routes were repeated within and between seasons over the period of camera-trap sampling (Oct. 2006 – Jan. 2009).

In addition to camera and spoor sampling, five call-in station surveys were conducted between 2 March and 5 April 2007 in areas of high prey density, using a protocol adapted from Ogutu & Dublin (1998), Mills et al. (2001) and Bauer (2007). Surveys lasted approximately 1 hour, with four conducted between 1900-2230 hours and one from 0530-0630. Each survey consisted of two cycles of the following broadcast sequence: 3 minutes of warthog distress squeals, 5 minutes of silence, 3 minutes of buffalo distress bleats, 6 minutes of spotted hyena vocalizations (i.e., whooping, squabbling at a kill), and 10 minutes of silence. Sounds were broadcast using an mp3 player (Creative Zen Nano), car amplifier (Dual XPA 2100 Mosfet), and two 45W, 8-ohm, 285mm horn speakers (Elan UHC-30) mounted at 180° on top of a truck. A 2-million candlepower spotlight was used to scan for animals responding to calls. We also completed three nighttime spotlight transects of approximately 10 km along sections of road in the southeastern portion of the park. The vehicle was driven at 10-15 km/h while two observers shone spotlights and scanned for animals on either side. The number of call-in and spotlight surveys was limited because their feasibility was restricted by dense vegetation (i.e. poor visibility) and the difficulties of traveling within the park by vehicle at night (hazardous or non-existent roads).

#### (ii) Patrol records

Mole National Park management has implemented large mammal monitoring based on observations made by field staff during regular law enforcement patrols (Brashares & Sam 2005; GWD 2005; Jachmann 2008b; see Chapter 2). Spatially explicit patrol monitoring records covering the period October 2004 to May 2008 and including data from about 2,800 patrols spread across much of the park were examined for reported sightings of carnivore species. To estimate longer-term trends in carnivore populations, we also extracted carnivore sighting records from nearly 2,000 monthly patrol summary reports stored at MNP headquarters and containing data from an estimated 28,000+ patrols distributed across the park over the period 1968-2001 (Fig. 1). Counts from modern and historical patrols were combined and a simple annual index of relative abundance was calculated as the number of individuals observed in a year standardized by a unit of effort set at 100 patrols (i.e., essentially a catch-per-unit-effort index, cf. Jachmann 2008a,b).

#### (iii) Interviews

As part of a concurrent study on local ecological knowledge and human-wildlife relationships, we conducted 68 semi-structured interviews based on a standardized questionnaire with key informants (individuals or small groups) living in 27 villages adjacent to MNP (mean = 2.5 interviews per village, range = 1-8; Fig. 1; Appendix 3.3). Respondents were asked to name all of the wildlife species they knew to occur locally, and were specifically asked about nine medium and large carnivore species after being shown a photograph of each.

### *Historical Carnivore Occurrence and Traits*

To assess temporal changes in MNP's carnivore community, we established an historical baseline by constructing a list of potential carnivore species based primarily on the detailed

occurrence records assembled and assessed by Grubb et al. (1998). We also examined a checklist of mammal species included in the most recent MNP Management Plan (GWD 2005), historical patrol monitoring records archived at the park headquarters (described above), and distribution maps available from the 2008 IUCN Red List of Threatened Species (IUCN 2008; Schipper et al. 2008). For the latter, we downloaded shapefiles describing the extent of occurrence for each species and determined which ranges overlapped the boundary of Mole National Park (using ArcGIS 9.3.1, ESRI, Redlands, CA, USA). Our final list included 16 species representing the recent historical or “intact” carnivore community for MNP (i.e., from the time of park establishment circa 1960; Table 2; Appendix 3.1).

After identifying the baseline carnivore community in MNP, we collated data for a set of 17 species-level traits reflecting intrinsic and extrinsic factors expected to influence extinction risk within this carnivore community (Table 1). Our primary data sources were the PanTHERIA database (Jones et al. 2009) and species accounts from the IUCN Red List of Threatened Species (IUCN 2008), but we also used other sources for certain variables and species (Table 2; Appendix 3.2). Large body size (represented here as adult body mass) is frequently associated with higher extinction risk and often correlates with other extinction-promoting traits, including slow life-history and rarity (McKinney 1997; Purvis et al. 2000). To describe carnivore life-history variation independently of body size, we chose gestation length and weaning age to represent reproductive output and timing, respectively (Cardillo et al. 2004; Bielby et al. 2007; Fritz et al. 2009). Rarity was characterized in terms of population density and geographic range size; the former was averaged across locations for which estimates were available, and the latter was estimated for both the West African region (Cameroon through Mauritania; calculated from the IUCN shapefiles described above) and Ghana (using the historical extent of known occurrence described by Grubb et al. 1998). We included several ecological and behavioral indicators thought to influence carnivore extinction vulnerability, namely home range size, group size, diurnal activity, habitat specialization, and diet breadth (Woodroffe & Ginsberg 1998; Purvis et al. 2000; Cardillo et al. 2004; Ray et al. 2005a; Table 1). To examine potential variation in exposure to extrinsic pressures, we calculated an index of threat for each species based on the number of known threats identified in IUCN 2008 Red List accounts (using the IUCN Threats Classification Scheme v3.0), and a derived binary indicator of threat due to human conflict (i.e., IUCN threat categories 2.1, 2.3, or 5.1, related to crops, livestock, and hunting, respectively). We also derived a similar binary indicator of “adaptability” to human habitats based on whether a species was listed as occurring in the “Artificial-Terrestrial” habitat category of the IUCN Habitats Classification Theme v3.0. Our village interviews provided data on local perception, frequency of consumptive use (for bushmeat or other traditional practices) and livestock conflict for 9 of the 16 carnivore species (Table 1; Appendix 3.3)

### *Estimating Carnivore Occurrence, Relative Abundance, and Richness*

To estimate the occurrence and abundance of carnivores in MNP, we tabulated the number of species detected across all 253 camera stations and calculated two indices of relative abundance for each species: (i) the proportion of stations at which the species was detected (i.e., “naïve” occupancy, MacKenzie et al. 2006), and (ii) the number of independent detections of the species per 100 trap days. For a given station, photographs were considered to be independent detections for this purpose if they satisfied the following criteria: (i) consecutive photographs of different

individuals of the same or different species, (ii) consecutive photographs of individuals of the same species taken more than 5 minutes apart, and (iii) nonconsecutive photos of individuals of the same species (cf. O'Brien et al. 2003). We also considered evidence of carnivore occurrence from other methods (see above), although resulting data were generally less verifiable and not as well-suited to our analytical framework (see Discussion).

A significant challenge to surveying rare and elusive species and documenting local extinctions is the problem of imperfect detection (MacKenzie et al. 2006; Roberts & Kitchener 2006; Kéry et al. 2006; Tingley & Beissinger 2009). Specifically, it can be difficult to determine whether an unobserved species is truly absent from a site (or collection of sites), as opposed to being present but undetected. In addition to considering evidence from multiple survey methods with different detection biases, we applied a multi-species site-occupancy modeling framework (Royle & Dorazio 2008) to explicitly account for imperfect detection in our camera trap survey. We treated consecutive trap days as repeat surveys at a given camera station and used this temporal replication to estimate the probability that a species not detected at a sampling location was truly absent (i.e.,  $1 - (\text{probability of "false absence"})$ ). We consider the occurrence of a species at a camera station to be equivalent to its use of the habitat at that site (MacKenzie et al. 2006). Briefly, the multi-species model involves a three-level hierarchical framework in which the observation data, representing detections of different species at the different stations (= sites), are conditional upon a latent binary variable describing the true occurrence status of those particular species and sites, which in turn is conditional upon another latent variable indicating whether a species was actually present in the sampled community. This third level uses the data augmentation framework of Royle et al. (2007a) and depends on the specification of a hypothetical "supercommunity" expected to contain the real community, and it is key to the robust estimation of community attributes like species richness while accounting for the probability of undetected species. Further details of the modeling framework are given in Appendix 3.4 and Royle & Dorazio (2008:379-389; see also Dorazio et al. 2006; Kéry & Royle 2008; Zipkin et al. 2010).

A subset of 224 camera stations was used for the occupancy analysis, as data from the remaining 29 stations were unsuitable for the repeated sampling framework (due to technical problems including inconsistent operation and date-stamp malfunction). We added 11 "all-zero" species to our carnivore occurrence dataset, giving a "supercommunity" of 20 carnivore species from which our detections were sampled, which represents a liberal hypothesis of the number of potentially undetected species (Royle et al. 2007a; Royle & Dorazio 2008). We fit the model to our data using a Bayesian approach to parameter estimation implemented in software programs R 2.10.1 (R Development Core Team 2009) and WinBUGS 1.4.3 (Lunn et al. 2000), modifying code provided in Royle & Dorazio (2008). Non-informative priors were used and posterior probabilities for the parameters were generated with Markov Chain Monte Carlo sampling (MCMC, Link et al. 2002; Appendix 3.4).

### *Testing Predictors of Persistence*

We tested the relationship between carnivore persistence and the ecological and life-history traits using decision-tree models and two different indices of persistence (i.e., response variables) generated from the camera trap survey: (i) a binary variable indicating species presence/absence (i.e., detected or undetected), and (ii) a continuous variable corresponding to the estimated

probability of occurrence ( $\psi_i$ ) for each carnivore from the multi-species occupancy model (with a value of 0 for species that were not detected). While occurrence probability does not equate directly to persistence in this case (i.e., species could persist at different frequencies of occurrence across sites), it better reflects the possibility of imperfect detection since species that are detected rarely would have a low value of  $\psi_i$  similar to any species that might actually have been present but undetected (for which  $\psi_i = 0$ ).

Decision-tree models have been proposed as effective tools for assessing extinction risk and have several advantages over traditional parametric approaches, since they can avoid assumptions of distributional form or data independence, identify context-dependent associations among multiple correlated predictor variables, and improve predictive power (De'ath & Fabricius 2000; Davidson et al. 2009; Bielby et al. 2010). We used classification and regression trees (for the binary and continuous response variables, respectively) implemented in the R package *tree* (Ripley 2009) to assess the ability of species traits to explain variation in estimated persistence among carnivores. This procedure grows a tree by binary recursive partitioning, choosing splits in explanatory variables that maximize homogeneity within groups with respect to the response variable (De'ath & Fabricius 2000). Because decision-tree models can be sensitive to uncertainty in the underlying data, we also used the random forest approach to combine predictions of many independent trees into a more robust composite model (Prasad et al. 2006; Cutler et al. 2007; Davidson et al. 2009). Using the R package *randomForest* (Liaw & Wiener 2002), we assessed variable importance and classification error rate (for presence/absence) or proportion of variance explained (for  $\psi_i$ ) based on 5000 random trees from bootstrap samples of the 16 carnivore species and 13 predictor variables (those with values for all species). The importance of a variable is evaluated in random forests based on how much worse the prediction would be if the values for that predictor variable were permuted randomly (Prasad et al. 2006; Cutler et al. 2007). The bivariate relationships between all 17 predictors (including population density and three variables derived from interview data—the four variables that did not have values for all 16 species; Table 1) and the two response variables were assessed with: (i) Fisher's exact test for categorical predictors and binary response (presence/absence), (ii) Spearman's rank correlation test for continuous predictors and continuous response ( $\psi_i$ ), or (iii) Wilcoxon rank-sum test comparing values of a continuous variable (e.g., body mass) grouped by a binary variable (e.g., presence/absence).

Given that decision-tree models do not rely on the assumption of independence between data points, we did not explicitly correct for phylogenetic relationships in our sample of carnivore species (Davidson et al. 2009; Bielby et al. 2010). All statistical tests were implemented in program R version 2.10.1 (R Development Core Team 2009).

## Results

### *Carnivore detections, relative abundance, and trend*

Of the 16 carnivore species known to have occurred historically in Mole National Park, we obtained unequivocal evidence for the persistence of only nine (Table 2). Spotted hyena (*Crocuta crocuta*) was the most frequently detected carnivore in the camera trap survey, followed by white-tailed mongoose (*Ichneumia albicauda*), leopard (*Panthera pardus*) and large-spotted genet (*Genetta pardina*), while side-striped jackal (*Canis adustus*) and Gambian

mongoose (*Mungos gambianus*) were rarest among photographed carnivores (Table 2). The remaining seven “historical” carnivore species, including lion (*Panthera leo*) and wild dog (*Lycaon pictus*), were not detected by the camera trap survey, nor could their presence be confirmed by the sign, call-in or spotlight surveys (Table 2). We also did not observe any colonizations of previously unreported carnivore species.

Recent patrol records (2004-2008) contained only 32 observations of four carnivore species (Table 2), including three instances of reported lion sightings (the last from April 2007). The historical patrol reports (1968-2001) included 268 records of 11 carnivore species (Table 2), although there was ambiguity in the identification of mongoose and genet species and most species had very few observations (median = 8, range = 1-99, mean = 24.1). The number of individuals counted (per unit patrol effort) across all carnivore species declined over the 40-year period of monitoring (1968-2008; Spearman’s rank correlation  $r_s = -0.33$ ,  $P = 0.04$ ), although counts of smaller carnivores were erratic and less reliable for trend estimation. Among large carnivores, lion and leopard were both most frequently reported and their indices of relative abundance declined significantly over time (lion:  $r_s = -0.47$ ,  $P < 0.01$ ; leopard  $r_s = -0.50$ ,  $P < 0.01$ ; Fig. 2). There were only five records of wild dog, with the last sighting reported in 1995, and only 17 of spotted hyena, with the majority reported in recent years (13 from 2004-2008).

Village interview responses had the greatest associated uncertainty, with ambiguity in the timing and reliability of reported observations making it more difficult to assess persistence. Nine carnivore species were identified by interview respondents (Table 2), with lion and leopard being the two most commonly recognized species (75% and 70% of respondents, respectively), and honey badger (*Mellivora capensis*) and serval (*Leptailurus serval*) being the least well known (14% and 34%; smaller carnivores were only reported by three respondents and ambiguously as “genet” or “mongoose”). There were few reports of recent sightings (i.e., within the previous 5 years) for the four species undetected by the camera-trap survey: serval (17% of respondents), wild dog (12%), lion (11%), and honey badger (3%). Species most frequently described as either no longer occurring or having decreased in abundance were lion (34%), leopard (30%), and wild dog (17%). The percentage of respondents reporting traditional consumptive uses of carnivore species (for ceremonial, medicinal or nutritional purposes) ranged from a low of 5% for honey badger to a high of 55% for lion. Lion (45%) and spotted hyena (25%) were most frequently cited as causes of livestock depredation, and several instances of retaliatory killing were reported.

### *Probabilities of occurrence and detection*

Estimates of probabilities of carnivore occurrence, detection, and richness were generated from the hierarchical multi-species occupancy model using camera trap data. The posterior median probability of carnivore species richness,  $N$ , was 9 (mean = 9.9, sd = 1.5, Fig. 3), suggesting that the camera trap survey detected all, or nearly all, of the carnivore species present in the sampled community. The possibility that species went undetected in our surveys could not be dismissed entirely, as the 95% credible interval for  $N$  included up to 13 species. However, the estimated probability of > 10 species occurring was < 0.2 (Fig. 3).

The posterior mean probability of occurrence at a site (i.e., camera station) across the carnivore community was estimated to be 0.21 (sd = 0.10), which can also be interpreted as the

estimated proportion of sampled sites used on average by carnivores in MNP. The mean probability of detection given occurrence was only 0.058 per site per day (sd = 0.030), but across all sites and trap-days, this translated into a probability of false absence of essentially 0 (Appendix 3.4). Accounting for imperfect detection significantly increased estimates of occurrence probability over “naïve” estimates for all nine observed carnivore species (Table 2). Posterior mean probabilities of occurrence were highly correlated with the index of relative abundance (photos per 100 trap-days, Spearman  $r_s = 0.97$ ,  $P < 0.001$ ), and ranged from ~0.07 for side-striped jackal and Gambian mongoose up to 0.54 for spotted hyena (Table 2). Side-striped jackal and Gambian mongoose also had the lowest estimated detectabilities (0.02), while large-spotted genet had the highest (0.12; Table 2). Occurrence and detection probabilities were positively correlated ( $r_s$  for means = 0.97,  $P = 0.043$ ; posterior mean of covariance parameter  $\rho = 0.53$ ), suggesting both were likely related to underlying patterns of species abundance (Royle & Dorazio 2008). Occurrence probability generally increased with body mass ( $r_s = 0.65$ ,  $P = 0.067$ ; Table 2) and home range size ( $r_s = 0.63$ ,  $P = 0.076$ ) for the nine carnivores detected, but detection probability was not correlated significantly with either variable (body mass  $r_s = -0.017$ ,  $P = 0.98$ ; home range size  $r_s = 0.22$ ,  $P = 0.58$ ), indicating that larger and wider-ranging species occurred at (or used) a greater proportion of sites but were not more likely to be detected at a given site where they occurred (Table 2).

### *Correlates of persistence*

Contrary to expectation, carnivore persistence in MNP was not significantly related to any of the 17 intrinsic or extrinsic factors examined in our analysis (Table 1, Fig. 4, Appendix 3.2). Activity period was the only variable selected in a tree classifying presence vs. absence, suggesting nocturnal species were more likely to persist, but the model produced a high misclassification error rate (5 of 16 species misclassified = 31%, which is not significantly different from random = 50%, binomial test  $P = 0.21$ ). The regression tree model suggested that a greater probability of carnivore occurrence was associated with a larger known species distribution in Ghana and, among those with more restricted distributions, a smaller average group size (Appendix 3.2); however, the model fit was also poor, explaining only 31% of the variation in species occurrence (null deviance = 0.461, residual deviance = 0.318). The random forest models confirmed that results of the classification and regression trees were not robust and that the variables we used were poor predictors of recorded patterns in carnivore persistence (classification error rate on presence/absence = 81%; variance in occurrence probability explained = 31%; Appendix 3.2). Similarly, tests of association between presence/absence or occurrence probability and each of the 17 variables did not provide any evidence of significant bivariate relationships (Fisher’s exact tests,  $P > 0.35$ ; Spearman’s  $|r_s| < 0.52$ ,  $P > 0.15$ ; Wilcoxon rank sum  $P > 0.22$ ; Fig. 4).

## **Discussion**

Our survey of Mole National Park’s carnivore community suggested nearly half (7 of 16) of the formerly occurring carnivore species may now be functionally or virtually extinct in the park. In addition, low estimated probabilities of occurrence and evidence from patrol records and village interviews indicate populations of many species observed to persist in the park have declined significantly over the last four decades. Contrary to ecological theory and our predictions, there

were no obvious life-history or other correlates of carnivore persistence in MNP. Our inability to identify a clear set of predictors of species persistence could stem from weaknesses or bias in our survey approach, but, we argue, it more likely reflects the complex and interactive drivers of wildlife decline in this ecosystem.

### *Survey strengths and limitations*

Camera traps proved to be an effective tool for detecting elusive carnivores within MNP, consistent with recent studies from other areas (e.g., Moruzzi et al. 2002; Pettorelli et al. 2010). The camera-trap survey generated important data on these poorly studied populations, including verifiable evidence for the persistence of “unconfirmed” species such as caracal (GWD 2005). Camera-trap data also are well-suited to the analytical framework of occupancy modeling that requires repeated surveys over short time frames to estimate detection probabilities (Mackenzie et al. 2002, 2006), and our multi-species model supported the conclusion that there were few or no undetected carnivores within the sampled area. Nevertheless, further assessment of modeling assumptions is warranted (Appendix 3.4), as is consideration of the spatial and temporal scope of sampling. Our survey effort was highest in the central and southeastern portions of the park and during the dry season, so species avoiding these areas or times could have had reduced detectability. While further effort in areas poorly covered by our surveys is needed (particularly the far north of MNP, Fig. 1), we consider it unlikely that these areas support additional carnivore species given evidence of low prey densities, higher human impacts, and limited dry-season water sources (GWD 2005; Bouché 2006). The supplementary survey methods yielded additional insight and broader spatial and temporal coverage, although photographic data provided the highest evidentiary standard for assessing persistence (McKelvey et al. 2008; Roberts et al. 2010). Recent patrol sightings suggest MNP’s top predator, the lion, may still occur in the park at a very low density, and village interviews also indicated that lion as well as serval, honey badger and even wild dog could persist. However, patrol records and interviews are more difficult to substantiate and the weight of evidence suggests that species undetected in camera surveys are at best very rare in the park and likely functionally (if not entirely) extirpated from the ecosystem.

### *Carnivore extinction vulnerability*

The apparent patterns of persistence across the MNP carnivore community were not explained by hypothesized predictors of extinction vulnerability. We were particularly surprised that body size was a poor predictor of persistence, a result unlikely to be driven by detection bias since a species’ estimated detection probability in the camera-trap survey was uncorrelated with body mass (or with other traits). There is thus little evidence from MNP to support the premise that large carnivores consistently are more vulnerable to extinction and smaller carnivores correspondingly increase via trophic release (Prugh et al. 2009; Ritchie & Johnson 2009). The fact that carnivore species apparently lost from MNP include both the largest in body size (lion) and the largest in home range and lowest in density (wild dog) supports observations of carnivore declines elsewhere in Africa (Woodroffe & Ginsberg 1998; Bauer & Van Der Merwe 2004; Ray et al. 2005a). Nevertheless, most of the carnivore species lost from MNP do not represent extremes in their ecological or life-history traits or in their interaction with humans

(e.g., serval, large grey mongoose). Empirical models of extinction vulnerability are, by necessity, dependent on data from relatively well-studied species, and may therefore be limited in their predictive ability across typical ecological communities containing many data-deficient species. Relative to large carnivores, smaller carnivores have generally been much less extensively studied, and our results raise the question of whether they may be more vulnerable than expected or previously appreciated. It is also worth noting the uncertainty underlying values of species traits used in our analysis (and others), particularly for poorly studied West African populations that may differ importantly from conspecifics or congeners in East or southern Africa (e.g., Bauer et al. 2003a; Gaubert et al. 2004; Appendix 3.1).

The broad variation in species persistence observed in our study suggests that carnivore community disassembly may not easily be predicted at a local scale. This is consistent with recent studies showing extinction vulnerability to be highly variable and determined by complex interactions between intrinsic traits and extrinsic pressures (Cardillo et al. 2008; Davidson et al. 2009; Fritz et al. 2009). Human population density has been proposed as an important predictor of extinction risk in Ghana and elsewhere (Woodroffe 2000; Brashares et al. 2001), and Cardillo et al. (2004) suggested that the influence of biological traits on carnivore extinction risk may be less pronounced at human densities lower than 10 people/km<sup>2</sup>, which roughly corresponds to densities in the area surrounding MNP (Jachman 2008a; C. Burton, unpublished data). This raises the possibility that ecological and life-history traits could become more important predictors of carnivore persistence as human populations grow around the park (such as for other protected areas in Ghana, Brashares 2003). Nevertheless, human density is a proxy for direct impacts such as hunting, which are already significant in MNP (GWD 2005; Jachman 2008a; Fig. 5; Chapter 4), and there was no apparent correlation between carnivore persistence and variation in local anthropogenic threats estimated from interview data (e.g., traditional hunting, livestock conflict). Elucidating rules of community disassembly is key to accurate prediction of anthropogenic effects on ecosystem functioning (Woodroffe & Ginsberg 2005; Zavaleta et al. 2009), thus a lack of discernible pattern presents a challenge for conservation planning and calls for the accumulation and synthesis of more locally-specific data on carnivore community responses to human impact.

#### *Extrinsic drivers of decline*

Given the evidence of decline and probable extirpation within MNP's historical carnivore community, there is a need to identify driving factors upon which management intervention could be focused. Prey depletion is a suspected threat to carnivore populations in West Africa given the widespread hunting of ungulates and primates for bushmeat (Eves & Bakarr 2001; Brashares et al. 2004). Illegal hunting is widespread in and around MNP, as evidenced by frequent signs of hunting activity recorded by the law enforcement patrol monitoring system (Jachman 2008a; Fig. 5; Chapter 4). Nevertheless, many medium- and larger-sized prey appear to be relatively abundant within portions of the park (Bouché 2006; Chapter 4), so it is not clear that larger carnivores are limited by an inadequate prey base. Very little is known about the availability of small prey for smaller carnivores, thus a detailed assessment of prey biomass in MNP is needed to better understand predator carrying capacity (Karanth et al. 2004; Hayward 2007; Treves et al. 2009).

Direct persecution is a known threat for many carnivores, particularly large, wide-ranging predators like lions and leopards (Inskip & Zimmermann 2009). Our interviews and additional market surveys provided insight into human-carnivore conflict around MNP, suggesting that local use of carnivore products (i.e., skins, organs) is relatively widespread, and that retaliatory killing for livestock depredation also occurs (Fig. 5). Instances of illegal hunting of carnivores within MNP have been recorded by the law enforcement program and additional deaths likely result from the widespread use of “gin” (leg-hold) traps on farms adjacent to the park boundary and within the park (Fig. 5). While traditional or subsistence hunting of carnivores has been noted previously in West Africa (Colyn et al. 2004; Brugiere et al. 2005; Djagoun et al. 2009), it has received relatively little attention in the bushmeat literature (Eves & Bakarr 2001).

MNP’s savanna woodlands appear to be relatively intact, which suggests habitat degradation in the park has not likely been a major factor underlying carnivore declines, although the potential effects of extensive dry-season burning warrant further study (Klop & Prins 2008). Conversely, habitat surrounding the park is variably altered or degraded by human settlement, farming and livestock grazing, which has undoubtedly increased park isolation and edge effects and thereby constrained the effective size of carnivore populations. Small, isolated populations could be subject to various problems, including inbreeding depression and Allee effects (Courchamp et al. 2002; Bjorkland 2003), but we lack the data to evaluate their importance for Mole’s carnivores. Similarly, disease has been shown to be an important driver of decline in other carnivore populations (Cleaveland et al. 2007), but very little is known about wildlife disease dynamics in MNP. Finally, interspecific competition (particularly intraguild predation) is a recognized threat for many African carnivores (Palomares & Caro 1999; Caro & Stoner 2003). Our data suggest a potential increase in MNP’s spotted hyena population, which may have resulted from, and perhaps contributed to, the decline of lions and other carnivores with which hyenas compete (Ray et al. 2005a; Watts & Holekamp 2009).

### *Consequences and conservation prospects*

The loss of carnivores could have important consequences for the MNP ecosystem. Trophic cascades triggered by the removal of top predators have been implicated in compromised ecological functioning across a range of systems (Terborgh & Estes 2010). Based on patrol monitoring records in several of Ghana’s protected areas, Brashares et al. (2010) inferred a “mesopredator release” of olive baboons following large carnivore declines, raising the possibility of significant ecological and social damage from an overabundant pest (e.g., Hill 2000). Other mesocarnivores also play important ecological roles that could be altered by their loss or release (Roemer et al. 2009). Conversely, functional redundancy across predator guilds could buffer against major ecological shifts when carnivores are lost, provided remaining species can compensate (Ives & Cardinale 2004; Woodroffe & Ginsberg 2005; Gonzalez & Loreau 2009). Our results raise the possibility that predator diversity promotes resilience in the MNP ecosystem, since carnivores of various sizes and functions have persisted and a “release” of prey populations has not been observed (Bouché 2006; C. Burton, unpublished data). Nevertheless, functional roles and trophic dynamics require further study in the MNP ecosystem, and it is possible that anthropogenic impacts such as hunting are overwhelming natural top-down and bottom-up forces.

Ecological consequences aside, the loss of carnivores from MNP has important conservation and socio-cultural implications. Protected areas represent the last refuge for many carnivores (Ray et al. 2005a), yet even these refuges may not provide effective protection. Lion declines have recently been reported in other West and Central African parks (Bauer et al. 2003b; Henschel et al. 2010; Tumenta et al. 2010), suggesting this apex predator is in the midst of a regional extinction crisis. Little is known about most other carnivore populations in the region, but it is evident that their viability is far from secure. The disappearance of local populations not only underlies the global extinction crisis (Ceballos & Ehrlich 2002) but also undermines local customs and beliefs (Mason 1993; CI-Ghana 2002) and limits potential economic gains from tourism linked to charismatic carnivores (Lindsey et al. 2005).

There is an urgent need to better understand the dynamics of carnivore conservation in West Africa, including status, threats, ecological implications, and socio-cultural dimensions. Remaining populations must be better protected by increasing support for underfunded enforcement and monitoring programs (e.g., Jachmann 2008a,b) while enhancing emerging efforts to improve park-community relations and alleviate conflicts between conservation and livelihoods (e.g., GWD 2000; Murphree 2002). Ultimately, a long-term vision for regional-scale conservation is needed to restore these carnivore populations and their embattled ecosystems.

**Table 1.** Species-level traits tested as predictors of carnivore persistence in Mole National Park, Ghana, with the predicted direction of effect and range of values observed across 16 carnivore species (see Methods and Appendix 3.1 for details).

Variable	Predicted direction of greater extinction vulnerability	Range of values
Adult body mass	Larger mass	544 – 158,624 g
Activity period	Diurnal activity	Diurnal, Nocturnal, Mixed
Home range size	Larger home range	0.8 – 817 km <sup>2</sup>
Gestation length	Longer gestation	56.8 – 112.3 days
Weaning age	Older age	20.9 – 371.4 days
Population density <sup>a</sup>	Lower density	0.01 – 3.7 individuals/km <sup>2</sup>
Group size	Larger groups	1 – 9.3
Diet breadth <sup>b</sup>	Narrower diet range	1 – 3 diet categories
Habitat breadth <sup>c</sup>	Fewer habitat types	2 – 20 IUCN habitat categories
Distribution in Ghana <sup>d</sup>	Restricted distribution	3 – 55 occurrence grid cells
West African range <sup>e</sup>	Smaller range	36,509 – 6,196,580 km <sup>2</sup>
Threats <sup>f</sup>	More threat factors	0 – 19 IUCN threat factors
Human conflict <sup>f</sup>	Prone to conflict	Yes or No
Adaptability <sup>c</sup>	Not adaptable to human habitats	Yes or No
Local use <sup>g</sup>	Greater local use	6 – 73% reported use
Livestock conflict <sup>g</sup>	More livestock conflict	0 – 45% reported livestock conflict
Local perception <sup>g</sup>	Less positive perception	8 – 36% reported positive perception

<sup>a</sup> No population density value was available for *Genetta thierryi*.

<sup>b</sup> Four possible diet categories: plant, invertebrate, small vertebrate, large vertebrate.

<sup>c</sup> Inferred from use of the “Artificial-Terrestrial” habitat category of the IUCN Habitats Classification Scheme v3.0.

<sup>d</sup> Based on Grubb et al. (1998) where known occurrences were mapped in grid cells of 15 minutes of latitude by 15 minutes of longitude.

<sup>e</sup> Calculated in ArcGIS 9.3.1 from the IUCN 2008 extent of occurrences (see Methods).

<sup>f</sup> Inferred from reported threat categories of Agriculture, Livestock, and Hunting/Persecution in the IUCN Threat Classification Scheme v3.0.

<sup>g</sup> Based on responses from village interviews for the subset of nine larger carnivores (see Appendix 3.3).

**Table 2.** Evidence for the occurrence of carnivore species in Mole National Park based on six types of survey data (collected during 2006-2009 unless otherwise noted) arranged in decreasing order of verifiability or reliability: C = camera trap, D = direct sighting or call, S = sign (track or scat), MP = modern patrol observations (2004-2008), HP = historical patrol records (1968-2001), V = village interviews. Historical occurrence was ascertained from evidence compiled in Grubb et al. (1998; see Methods). Indices of relative abundance (detection frequency and proportion of sites) and model-estimated probabilities of site occurrence and per-survey detection are based on camera trap results (see Methods). Evidence for the persistence of the seven species listed below the mid-line is weak and they are presumed to now be extremely rare or extirpated from the park (see text).

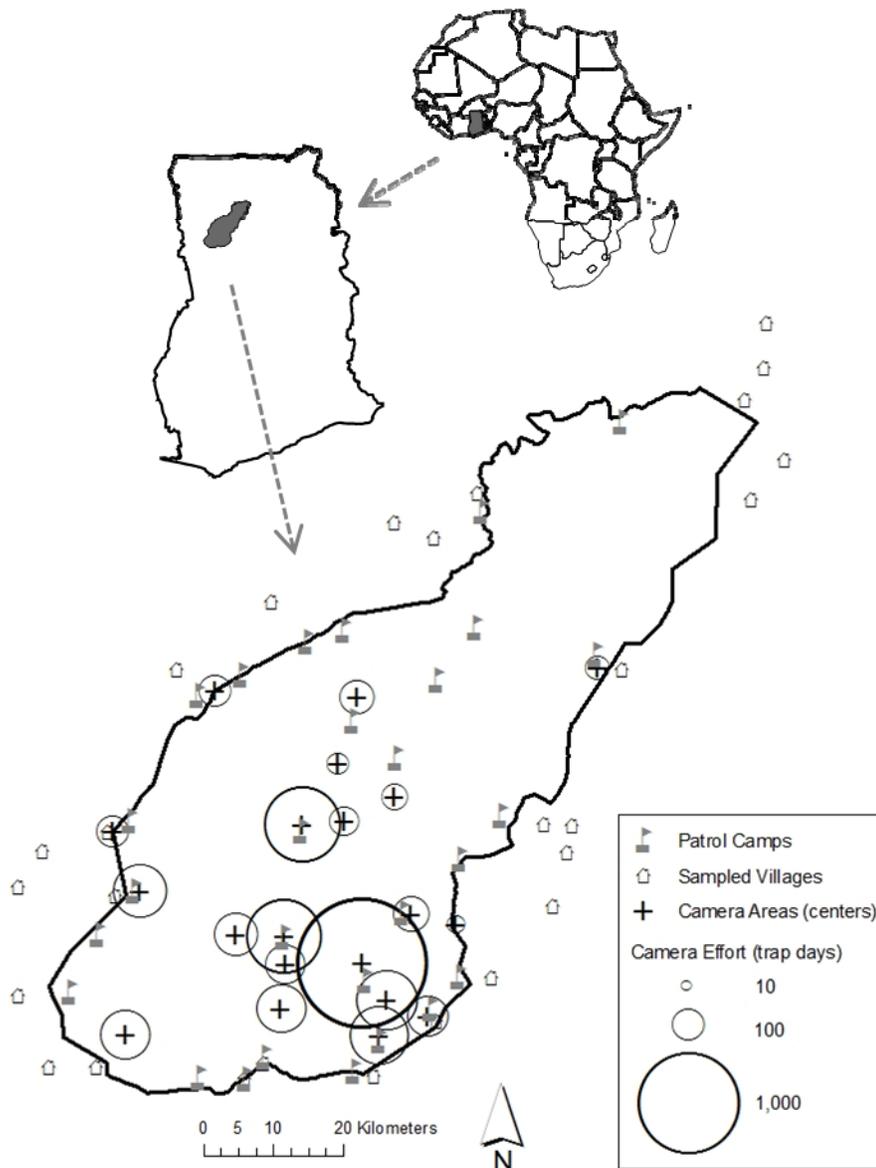
Scientific name	Common name	Body mass (kg)	Evidence <sup>a</sup>	Detection frequency <sup>b</sup>	Prop. sites	Pr(occurrence) <sup>c</sup> mean (sd)	Pr(detection) <sup>c</sup> mean (sd)
<i>Crocuta crocuta</i>	Spotted Hyena	63.4	C, D, S, MP, HP, V	6.53	0.42	0.54 (0.04)	0.101 (0.006)
<i>Ichneumia albicauda</i>	White-tailed Mongoose	3.6	C, S	3.11	0.26	0.30 (0.03)	0.110 (0.010)
<i>Panthera pardus</i>	Leopard	52.4	C, S, MP, HP, V	2.91	0.29	0.46 (0.05)	0.056 (0.006)
<i>Genetta pardina</i>	Large-spotted Genet	2.0	C, D, S	2.85	0.22	0.28 (0.03)	0.123 (0.011)
<i>Civettictis civetta</i>	African Civet	12.1	C, S, HP, V	0.59	0.09	0.21 (0.06)	0.032 (0.009)
<i>Caracal caracal</i>	Caracal	12.0	C, S, HP, V	0.37	0.05	0.13 (0.05)	0.031 (0.010)
<i>Atilax paludinosus</i>	Marsh Mongoose	3.6	C, D, S, HP	0.35	0.04	0.08 (0.03)	0.061 (0.019)
<i>Mungos gambianus</i>	Gambian Mongoose	1.6	C	0.09	0.02	0.07 (0.07)	0.022 (0.013)
<i>Canis adustus</i>	Side-striped Jackal	10.4	C, D, MP, HP, V	0.05	0.01	0.07 (0.10)	0.020 (0.015)
<i>Panthera leo</i>	Lion	158.6	MP, HP, V	0	0	-	-
<i>Lycaon pictus</i>	Wild Dog	22.0	HP, V	0	0	-	-
<i>Mellivora capensis</i>	Honey Badger	9.0	V	0	0	-	-
<i>Leptailurus serval</i>	Serval	12.0	V	0	0	-	-
<i>Herpestes ichneumon</i>	Large Grey Mongoose	3.0	- <sup>a</sup>	0	0	-	-
<i>Herpestes sanguineus</i> <sup>d</sup>	Slender Mongoose	0.5	- <sup>a</sup>	0	0	-	-
<i>Genetta thierryi</i>	Hausa Genet	1.4	- <sup>a</sup>	0	0	-	-

<sup>a</sup> Equivocal evidence that could not be confidently identified to species is excluded. This includes: ambiguous tracks or scat of small or meso-carnivores; historical patrol records of “genet”, “long nose mongoose” and “dwarf mongoose”; interview responses mentioning “genet” or “mongoose”.

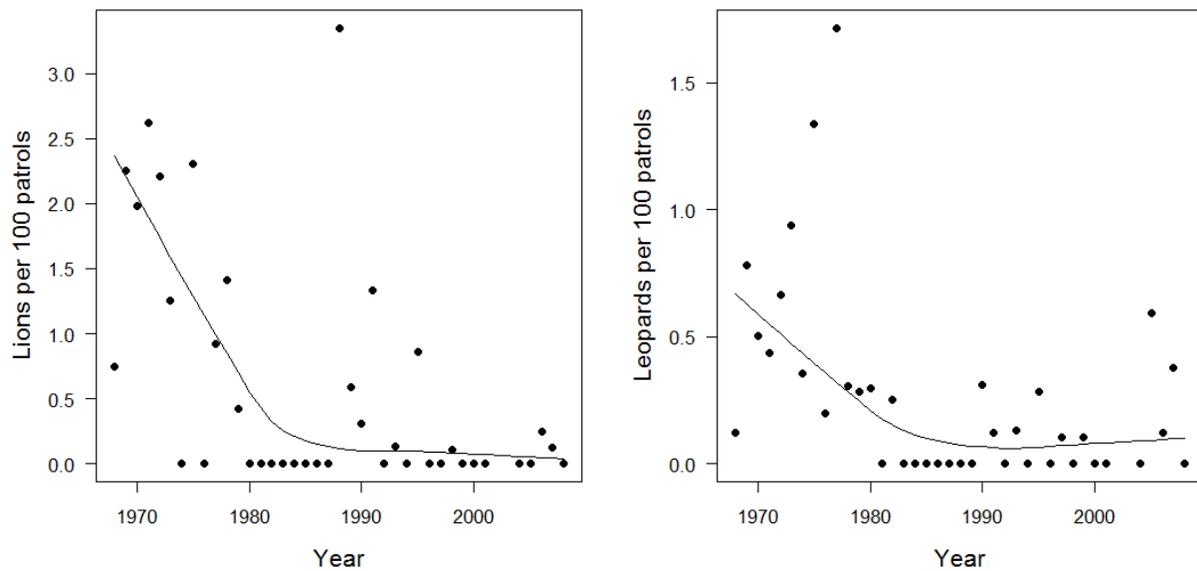
<sup>b</sup> RAI = Relative Abundance Index, calculated as independent detections per 100 trap days across all 253 camera stations.

<sup>c</sup> Probabilities of site occurrence and per-survey detection estimated from the multi-species occupancy model based on detections across 224 stations. Means and standard deviations from 5000 samples of posterior probability distribution (see Methods).

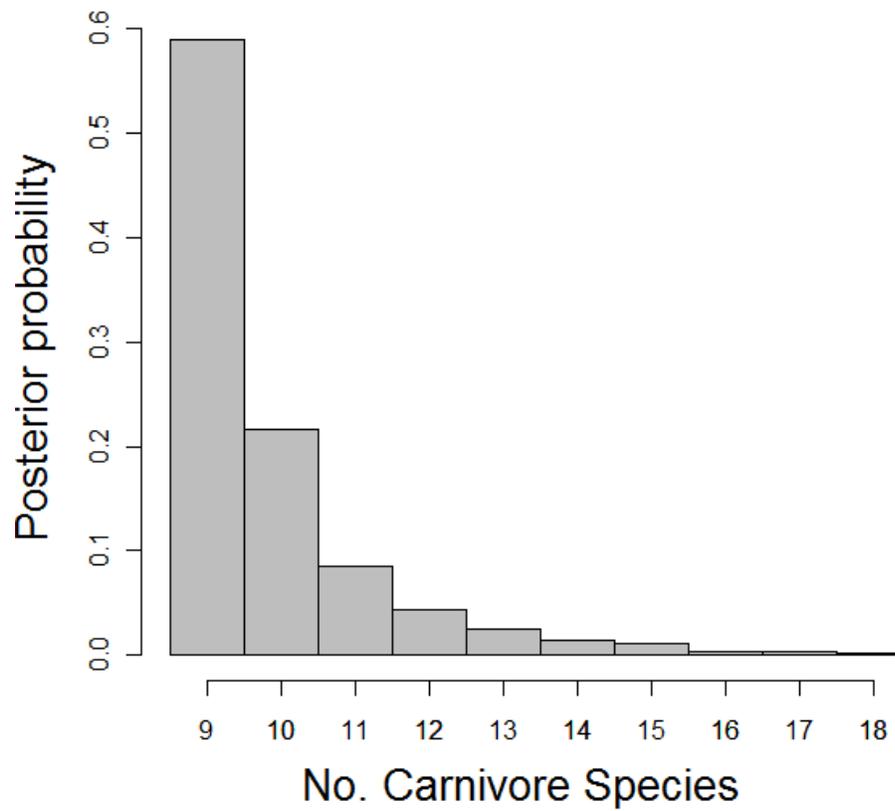
<sup>d</sup> Slender mongoose is also frequently known as *Galerella sanguinea*.



**Figure 1.** Map of Mole National Park, showing its location and the spatial distribution of camera-trap sampling, village interviews, and law enforcement patrol camps (from which long-term records were available). Camera-trap sampling is represented by the centroid of cameras within a spatio-temporal group and a circle proportional to the total number of trap-days for that group (the 253 individual camera stations are not directly shown). Sign surveys and call-in sampling were conducted primarily within the circles depicting camera sampling effort.

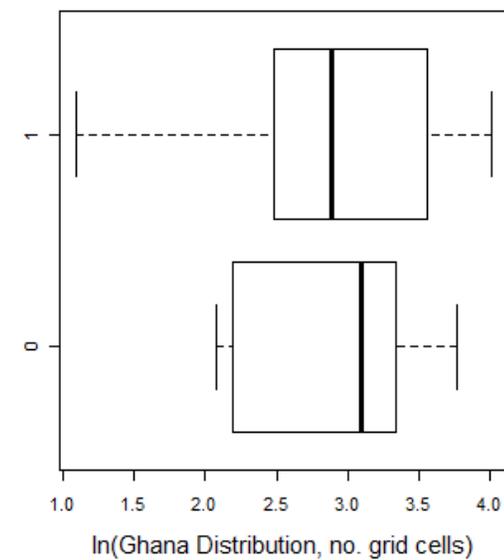
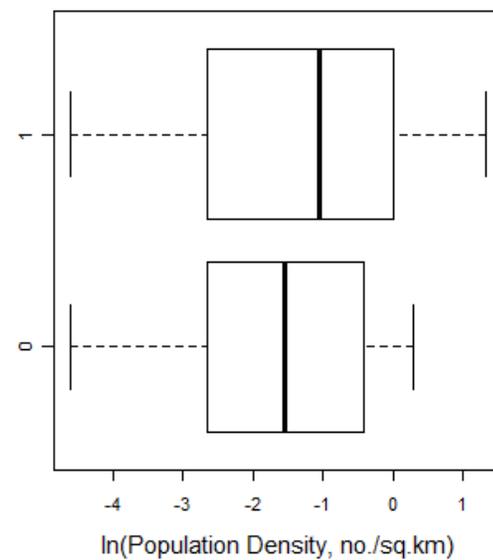
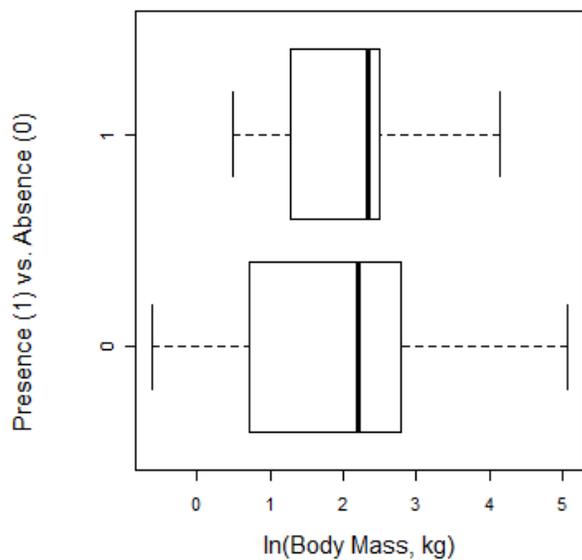
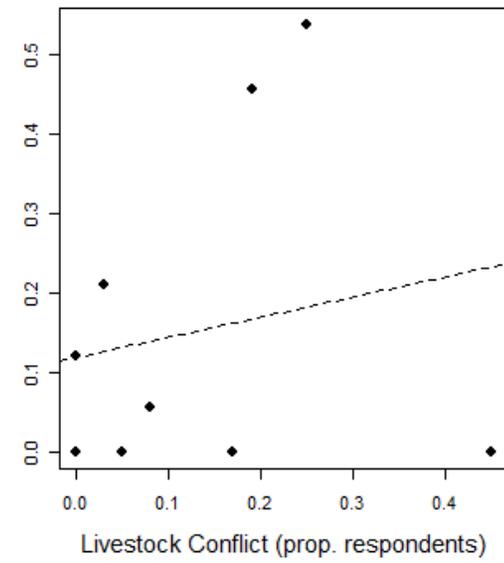
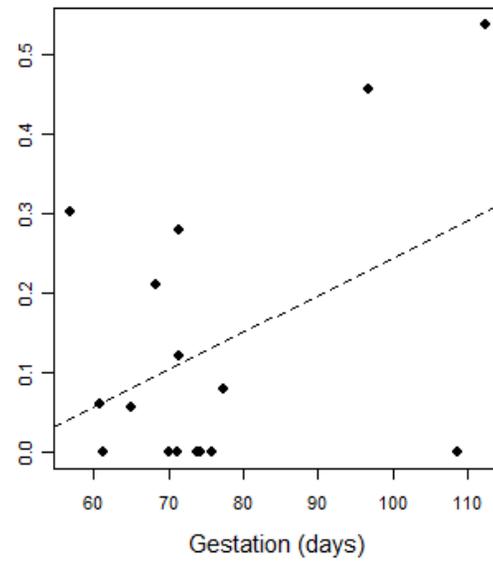
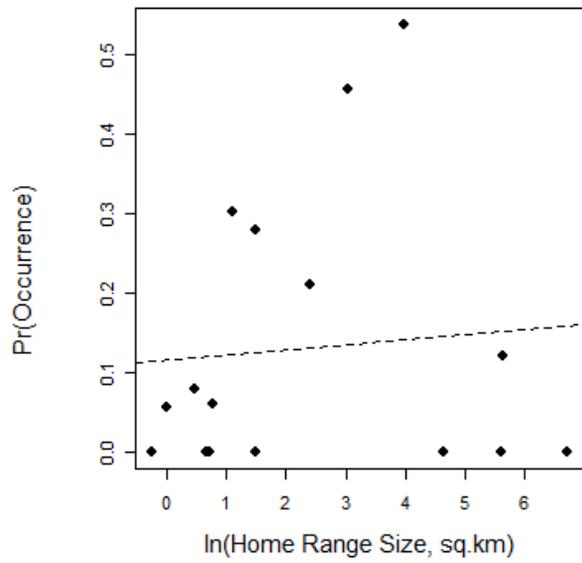


**Figure 2.** Relative abundance (individuals counted per 100 patrols) of lions (left) and leopards (right) observed during law enforcement patrols conducted in Mole National Park over the period 1968-2008. Trends (solid lines) were fit with a locally-weighted polynomial regression (*lowess* function in program R version 2.10.1).



**Figure 3.** Posterior probability distribution for the number of carnivore species occurring in the Mole National Park wildlife community, estimated from a hierarchical multi-species occupancy model applied to camera-trap survey data.

**Figure 4.** (next page) Bivariate relationships between estimated persistence of carnivore species in Mole National Park and, by example, 6 of 17 species traits tested. The top row shows carnivore probability of occurrence (estimated from the multi-species occupancy model based on camera trap detections) plotted against (from left to right): home range size, gestation length, and proportion of interview respondents indicating livestock conflict. The bottom row compares values of (from left to right) body mass, population density, and extent of known occurrence in Ghana, against carnivore presence or absence (based on the camera trap survey). None of the 17 variables were significantly associated with either measure of persistence (see main text).





**Figure 5.** Photographic evidence of illegal hunting in and around Mole National Park, clockwise from top left: lion killed by local hunters in August 2004 (photo credit: Wildlife Division of Ghana); patrol staff recording details of an illegal hunting camp; “gin” trap set in the park; leopard skin for sale in a tourist market near the park.

## **Supporting Information for Chapter 3**

**Appendix 3.1:** Determining historical occurrence of carnivore species in Mole National Park.

**Appendix 3.2:** Further details on determining species ecological and life-history traits and testing correlations with persistence.

**Appendix 3.3:** Additional detail on questions administered and results of interviews conducted in villages around Mole National Park.

**Appendix 3.4:** Details of the hierarchical multi-species occupancy model and probability of false absence.

### **Appendix 3.1:** Determining historical occurrence of carnivore species in Mole National Park.

Our primary source for determining the historical presence of carnivores in Mole National Park (MNP), Ghana, was the detailed summary of occurrence records compiled from museum specimens and the literature by P. Grubb in Grubb et al. (1998), who presented evidence for the occurrence of the 16 carnivore species used in our study. Evidence for the historical presence of wild dog (*Lycaon pictus*) and honey badger (*Mellivora capensis*) was considered reliable but limited, being based on Robertson's (1977) checklist of mammals derived from an Aberdeen University expedition to MNP. With the exception of the large grey mongoose (*Herpestes ichneumon*), all 16 carnivore species were included in a checklist of mammal species presented in the most recent MNP management plan (GWD 2005: Appendix 3), although genets were listed only to genus (*Genetta sp*) and evidence for the continued presence of several species was considered uncertain or unreliable (serval, *Leptailurus serval*; caracal, *Caracal caracal*; lion, *Panthera leo*; honey badger, wild dog). The occurrence of *H. ichneumon* in MNP noted by Grubb et al. (1998) was not based on recent evidence, perhaps explaining the omission of this species in the recent park checklist. Historical patrol monitoring records archived at MNP headquarters included reported sightings of 11 carnivore species, although identification of smaller carnivores is problematic as the records include the ambiguous names “genet”, “long nose mongoose” and “dwarf mongoose” (in addition to the less equivocal “marsh mongoose”). The former could refer to either or both of the genet species noted by Grubb et al. (1998) for MNP (*Genetta pardina* and *G. thierryi*). The dwarf mongoose (*Helogale parvula*) is a very small mongoose found in East and southern Africa (Kingdon 1997) and the MNP observations were likely of slender (*Herpestes sanguineus*) or Gambian (*Mungos gambianus*) mongoose. Similarly, the long-snouted mongoose (*Herpestes naso*) is a larger species found in Central Africa (Kingdon 1997), and thus the patrol records likely refer to *H. ichneumon* or the white-tailed mongoose (*Ichneumia albicauda*).

As an additional source of information on carnivore species potentially occurring in MNP, we examined digital species distributions produced for the Global Mammal Assessment (Schipper et al. 2008) and downloaded as shapefiles from IUCN (2008). The estimated ranges (extents of occurrence) of 22 carnivore species overlapped the MNP boundary, including 15 of the species indicated by Grubb et al. (1998)—the estimated range of wild dog did not include MNP, reflecting the fact that it is now considered extirpated from the area (McNutt et al. 2008). We conservatively chose to exclude the seven additional species [African clawless otter (*Aonyx capensis*), wild cat (*Felis silvestris*), banded mongoose (*Mungos mungo*), common genet (*Genetta genetta*), zorilla (*Ictonyx striatus*), spot-necked otter (*Lutra maculicolis*), and striped hyena (*Hyaena hyaena*)] as we could find no other evidence of their historical occurrence in MNP (or even Ghana in some cases) and the estimated extents of occurrence likely include areas where the species may not actually occur (given that they are essentially minimum convex polygons encompassing known occurrence sites, IUCN 2008). Nevertheless, a less conservative analysis allowing greater uncertainty might further consider the possible historical occurrence in MNP of wild cat, common genet and African clawless otter (all three of which occurred elsewhere in Ghana according to evidence presented in Grubb et al. 1998).

### **Appendix 3.2:** Species ecological and life-history traits and their relationship with persistence.

We identified a set of 17 species-level traits reflecting intrinsic and extrinsic factors expected to influence extinction risk within the MNP carnivore community (Tables 1, S1). These traits were selected based on theoretical expectations and empirical evidence suggesting their potential influence on a species vulnerability to extinction (McKinney 1997; Purvis et al. 2000; Brashares 2003; Cardillo et al. 2004). Our primary data source for assigning values to eight of these traits was the PanTHERIA database compiled by Jones et al. (2009), which comprised values for 30 ecological and life-history variables extracted or derived from over 3,000 literature sources. We used other sources for specific variables, including IUCN Red List species descriptions (IUCN 2009), Grubb et al. (1998), and our interview data (as described in the Methods section). We limited our set of candidate variables for detailed analysis to those we hypothesized to be of greatest relevance to carnivore extinction risk, but other potential variables were also considered. In particular, Bielby et al. (2007) identified potentially important indicator variables for reproductive output and timing in carnivores in addition to the two we used (gestation length and weaning age); however, including litter size, age at sexual maturity or interbirth interval in our analyses did not significantly change results (not shown).

Many among the 16 carnivore species that we considered for MNP are poorly studied in general, and data specific to West Africa are often lacking. In several instances the PanTHERIA database did not contain values for the species and variables of interest, chiefly for the smaller carnivores (genets and mongooses). For this reason we also searched the primary literature and reviewed other secondary sources (Estes 1991; Kingdon 1997; Grubb et al. 1998; Ernest 2003; Cardillo et al. 2004; Ray et al. 2005a; IUCN 2008) for data on specific variables and species (Table S2). Where no data could be found for a given variable and species, we substituted a value from a closely related species (or group of species) that was not included in our analysis (following recently published phylogenies, e.g., Gaubert & Begg 2007; Patou et al. 2009), provided the substituted value did not represent a significant outlier relative to the range of values for other species (Table S2).

It is widely recognized that species may not represent independent sampling units due to phylogenetic relatedness, and consequently many studies of extinction vulnerability explicitly account for relatedness through methods such as phylogenetically independent contrasts or phylogenetic GLMs (Cardillo et al. 2004; Fritz et al. 2009; Bielby et al. 2010). However, the use of phylogenetic comparative methods to account for non-independence remains controversial, and such methods may also introduce error, such as that related to phylogenetic uncertainty or “over-correction” (see Bielby et al. 2010 for a recent review). Furthermore, decision-tree models do not rely on the assumption of independence between data points (Sullivan et al. 2006; Davidson et al. 2009). We therefore chose not to explicitly correct for phylogenetic relationships in our sample of carnivore species.

**Table S1.** Values for 17 ecological and life-history traits used to describe carnivore species in Mole National Park, Ghana. Primary data sources were Jones et al. (2009) and IUCN (2008), but other sources are noted in Table S2. See Table 1 and text for details.

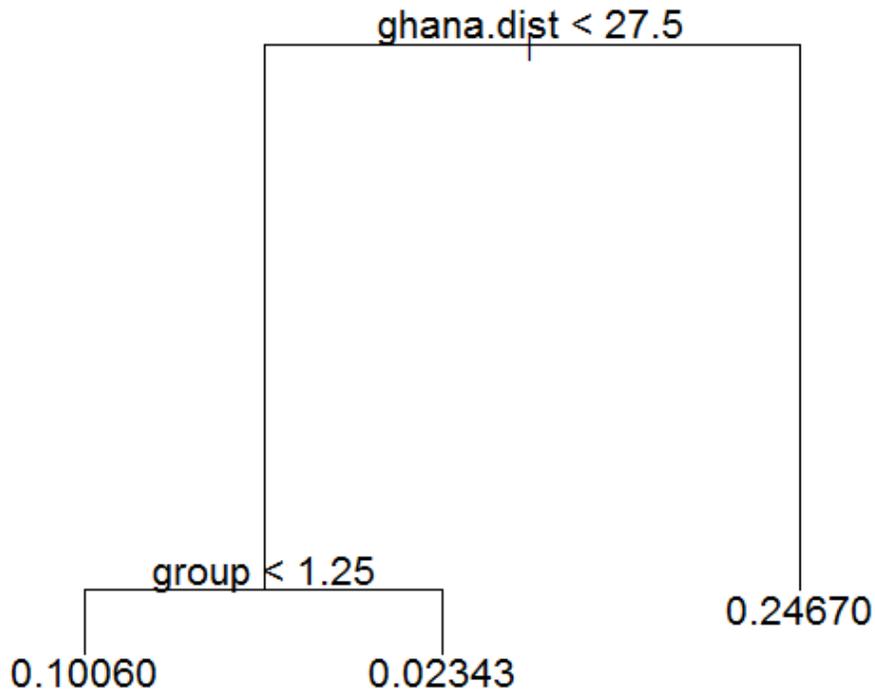
Species	Body mass (kg)	Activity period	Home range size (km <sup>2</sup> )	Gestation length (days)	Weaning age (days)	Population density (ind./km <sup>2</sup> )	Group size	Ghana range	West African range (100,000 km <sup>2</sup> )
<i>Canis adustus</i>	10.4	1	1.0	65.0	52.9	0.74	2	3	23.87
<i>Lycaon pictus</i>	22.0	3	816.7	71.2	27.3	0.01	9.3	9	0.37
<i>Caracal caracal</i>	12.0	1	275.8	71.5	120.4	0.35	1	4	19.54
<i>Leptailurus serval</i>	12.0	2	2.0	73.7	104.7	0.42	1	22	25.70
<i>Panthera leo</i>	158.6	1	103.9	108.7	197.9	0.11	8.7	36	3.64
<i>Panthera pardus</i>	52.4	2	21.1	96.7	123.5	0.07	1	55	15.94
<i>Atilax paludinosus</i>	3.6	2	1.6	77.3	35.9	1.80	1	17	32.33
<i>Galerella sanguinea</i>	0.5	3	0.8	61.3	54.4	1.32	1	43	33.51
<i>Herpestes ichneumon</i>	3.0	2	2.1	75.9	58.1	0.65	1.5	8	33.07
<i>Ichneumia albicauda</i>	3.6	1	3.0	56.8	41.8	3.70	1	12	29.67
<i>Mungos gambianus</i>	1.6	3	2.2	60.9	20.9	0.01	6.7	18	17.08
<i>Crocuta crocuta</i>	63.4	1	53.8	112.3	371.4	0.12	8	33	31.37
<i>Mellivora capensis</i>	9.0	2	272.7	70.0	60.0	0.07	1.7	9	61.97
<i>Civettictis civetta</i>	12.1	1	11.0	68.4	82.9	1.00	1	35	37.61
<i>Genetta pardina</i>	2.0	1	4.5	71.5	87.8	0.07	1	36	13.34
<i>Genetta thierryi</i>	1.4	1	4.5	74.2	71.8	NA	1	22	25.52

**Table S1 (cont'd).**

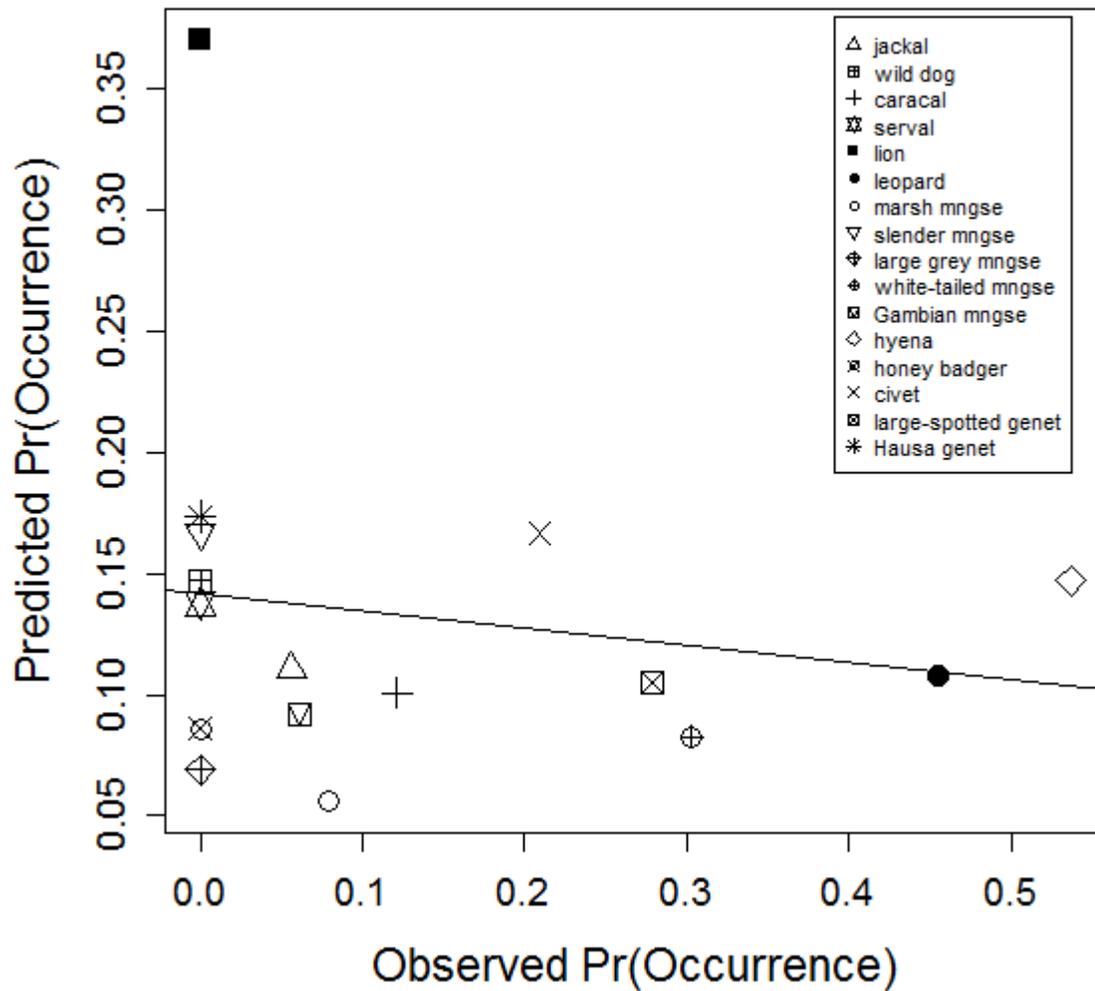
Species	Habitat types	Threats	Conflict	Adaptability	Diet categories	Local use	Livestock conflict	Local perception
<i>C. adustus</i>	7	1	1	1	3	0.28	0.08	0.30
<i>L. pictus</i>	5	6	1	0	1	0.22	0.17	0.25
<i>C. caracal</i>	7	6	1	0	2	0.33	0	0.17
<i>L. serval</i>	7	11	1	1	2	0.25	0.05	0.17
<i>P. leo</i>	7	12	1	0	1	0.73	0.45	0.34
<i>P. pardus</i>	20	19	1	0	2	0.70	0.19	0.36
<i>A. paludinosus</i>	8	0	0	0	3	NA	NA	NA
<i>H. sanguineus</i>	6	0	0	1	3	NA	NA	NA
<i>H. ichneumon</i>	8	0	0	0	3	NA	NA	NA
<i>I. albicauda</i>	5	0	0	1	3	NA	NA	NA
<i>M. gambianus</i>	2	0	0	0	3	NA	NA	NA
<i>C. crocuta</i>	4	2	1	1	1	0.36	0.25	0.17
<i>M. capensis</i>	6	3	1	0	3	0.06	0	0.08
<i>C. civetta</i>	4	0	0	1	3	0.41	0.03	0.23
<i>G. pardina</i>	5	0	0	1	3	NA	NA	NA
<i>G. thierryi</i>	3	0	0	0	3	NA	NA	NA

**Table S2.** Additional notes on particular data sources and substitute values used to describe the ecological and life-history traits of carnivore species in Mole National Park, Ghana.

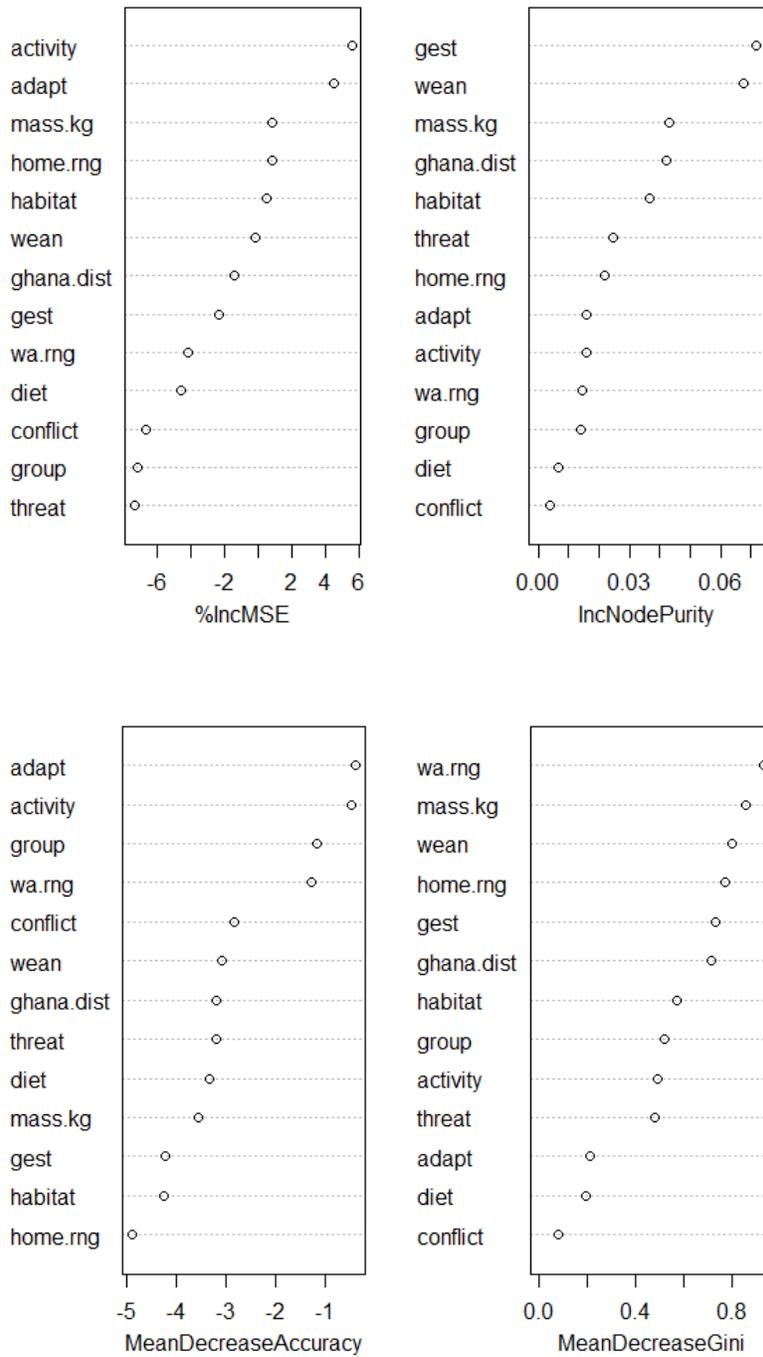
Species	Variables	Substitutions	Sources
<i>Genetta pardina</i>	Body Mass, Activity Period, Gestation Length, Weaning Age, Home Range Size	Values from <i>G. maculata</i> (primarily), <i>G. tigrina</i> or <i>G. genetta</i>	Jones et al. 2009; Admasu et al. 2004a; Estes 1991.
<i>Genetta thierryi</i>	Activity Period, Gestation Length, Weaning Age, Home Range Size	Values from <i>G. genetta</i>	Jones et al. 2009; Admasu et al. 2004a; Estes 1991.
<i>Civettictis civetta</i>	Home Range Size		Admasu et al. 2004a; Ray et al. 2005a
<i>Mellivora capensis</i>	Home Range Size, Gestation Length, Weaning Age		Begg et al. 2005a,b; Ray et al. 2005a
<i>Mungos gambianus</i>	Group Size, Home Range Size	Home range value from <i>M. mungo</i>	Jones et al. 2009; Sillero-Zubiri & Bassignagni 2001, Wilson & Kpelle 1993
<i>Ichneumia albicauda</i>	Gestation Length, Weaning Age, Home Range Size	Values for gestation and weaning from <i>Cunictis penicillata</i>	Jones et al. 2009; Admasu et al. 2004b; Estes 1991.
<i>Lycaon pictus</i>	Group size		Woodroffe et al. 1997



**Figure S1.** Regression tree model estimating the relationship between probability of occurrence for 16 carnivore species in Mole National Park (estimated from the multi-species occupancy model based on camera-trap detections) and 13 predictor variables describing species ecological and life-history traits (see Table 1 and main text). The model indicated species with known distributions in Ghana (“ghana.dist”) comprising 28 or more 15’x15’ grid cells had greater occurrence probabilities (top node), and of those with smaller distributions, species with group sizes less than 1.25 were more likely to occur (lower node). Values at branch ends are mean occurrence probabilities for species contained in that branch. However, the model explained only 31% of the variation in carnivore species occurrence (see main text).



**Figure S2.** Predicted vs. observed probabilities of occurrence for the 16 historically known carnivore species in Mole National Park. Predicted values were generated from the random forest regression tree model (averaged over predictions of the “out-of-bag” response variables from trees fit to 5,000 bootstrap samples) using 13 ecological and life-history variables (see Methods). Observed values are estimates from the multi-species occupancy model based on camera trap data. (Full species names given in Table 2.)



**Figure S3.** Variable importance plots for 13 ecological and life-history traits used as predictor variables in random forest (RF) models to explain variation in persistence across 16 carnivore species in Mole National Park (full variable names and details in Table 1). Values represent different measures of the importance of each variable in terms of its contribution to the model's predictive power, calculated by comparing predictions from model permutations that include the

variable with those that do not (higher values signify greater importance). The top two plots are for the RF regression model on probability of species occurrence (estimated from the multi-species occupancy model based on camera trap detections), showing the mean increase in mean squared error (“%IncMSE”, top left) and node purity (“IncNodePurity”, top right, measured by residual sum of squares) due to exclusion of the variable. The bottom two plots are for the RF classification model on presence or absence of carnivore species (determined from the camera trap survey) and show the mean decrease in accuracy (“MeanDecreaseAccuracy”, bottom left) and in the Gini Index (“MeanDecreaseGini”, bottom right). Values of variable importance were low and inconsistent across the two models and four measures, illustrating the poor accuracy of the models (see main text).

**Appendix 3.3:** Additional detail on questions administered and results of interviews conducted in villages around Mole National Park.

The questions in Table S3 were administered in 68 interviews conducted with individuals or small groups in the following 27 villages adjacent to Mole National Park, Ghana (Fig. 1; the number of interviews for each village is indicated in parentheses): Bawena (4), Belepong (1), Chasia (1), Dabori (1), Ducie (2), Gbantala (1), Goriba (1), Grubagu (1), Grupe (4), Holomuni (1), Jang (4), Jelinkon (1), Jinfronu (4), Kabampe (2), Kananto (4), Kong (1), Kparia (2), Kpulumbo (4), Larabanga (4), Mognori (4), Murugu (8), Sagya (2), Seiyiri (4), Soma (1), Yagbon (1), Yazori (4), Zanwara (1). Respondents were of various ages and chosen in consultation with the village chief and/or elders based on being knowledgeable of local wildlife.

**Table S3.** Questions administered to individual or small-group key informants during semi-structured interviews in villages around Mole National Park.

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1. Please name all the wild animals you can think of that live in this area.
  2. Which of the animals are the most abundant?
  3. Do any animals that used to occur here no longer occur now?
  4. Are there any other animals that you now see less often than you used to? <sup>a</sup>
  5. Are there any animals that you now see more often than you used to? <sup>a</sup>
  6. Are any animals important to you or the community? Please give reasons.
  7. Do any animals cause problems for you or the community? Please describe.
  8. For each of the following animal photos, please indicate:
    - a. Do you know this animal?
    - b. Have you seen this animal?
    - c. When was the last time you saw it?
    - d. Do you see this animal more or less often now than you used to? <sup>a</sup>
    - e. Do you like or dislike this animal? Please explain.
    - f. Is this animal important to you and the community? If yes, why?
    - g. Does this animal cause problems? If yes, in what way? When was the last time?
    - h. If this animal causes problems, how do you deal with it?
      - i. Have you ever had to kill this animal?
      - ii. Have you ever asked for assistance from Wildlife Division (MNP)? Did you receive assistance?
- 

<sup>a</sup> Respondents were asked to choose a reference time period for these questions from among three locally important and well-known events dating to 1957, 1983 or 2000.

### Appendix 3.4: Details of the hierarchical multi-species occupancy model and probability of false absence

We applied the multi-species occupancy model developed by Royle & Dorazio (2008) to explicitly account for imperfect detection and in our camera trap survey. The structure of the model is described by:

$$y_{ik}|J_k, p_i, z_{ik} \sim \text{Bin}(J_k, p_i, z_{ik})$$

$$z_{ik}|\psi_i, w_i \sim \text{Bern}(\psi_i, w_i)$$

$$w_i|\Omega \sim \text{Bern}(\Omega)$$

where:

$y_{ik}$  is the observed detection or nondetection of species  $i$  at site  $k$

$J_k$  is the number of repeat surveys at site  $k$

$p_i$  is the probability of detection at a site for species  $i$  (given its presence)

$z_{ik}$  is the true unobserved presence or absence of species  $i$  at site  $k$

$\psi_i$  is the probability of occurrence at a site for species  $i$

$w_i$  indicates the presence or absence of species  $i$  in the community of species sampled

$\Omega$  is the probability that a species in the hypothetical “supercommunity” is vulnerable to sampling, and

Bin and Bern represent binomial and Bernoulli probability distributions, respectively.

Rather than modeling species-specific probabilities of occurrence and detection, heterogeneity in these probabilities among species is modeled using a bivariate normal distribution on the logit scale (Royle & Dorazio 2008). In applying this model, we made the simplifying assumptions that (i) the overall carnivore community was closed to extinction or colonization during our survey period; (ii) camera stations were independent sampling units representative of the broader habitats being used by carnivores; (iii) repeat observations at a given camera station were independent; (iv) probabilities of occurrence and detection were constant across sites and independent among species (i.e., no interactions); and (v) heterogeneity in species occurrence and detection is adequately described by a normal distribution (on the logit scale). Some or all of these assumptions may be violated to some extent but we feel that they are reasonable approximations for the camera trap dataset (cf. Kéry & Royle 2008, 2009). The modeling framework allows these assumptions to be relaxed and future work will test their relative importance to inference for this dataset.

We fit the model to our data using a Bayesian approach to parameter estimation implemented in software programs R 2.10.1 (R Development Core Team 2009) and WinBUGS 1.4.3 (Lunn et al. 2000), with the R package *R2WinBUGS* (Sturtz et al. 2005). We adapted model code provided in Royle & Dorazio (2008) to allow the number of repeat surveys,  $J_k$ , to vary across sites  $k$  (original code is available at [www.mbr-pwrc.usgs.gov/HMbook](http://www.mbr-pwrc.usgs.gov/HMbook)). Non-informative

priors were used and posterior probabilities for parameters were generated with Markov Chain Monte Carlo sampling (MCMC, Link et al. 2002), for which we used 5 chains of 55,000 iterations, with the first 5,000 iterations discarded as “burn in” and a thin value of 50, giving a total of 5,000 samples. Model convergence was assessed from visual inspection of the MCMC chains and using the Gelman-Rubin statistic (“Rhat” in *R2WinBUGS*), for which values near 1 indicate likely convergence (Gelman et al. 2004; Gelman and Hill 2007).

### *Estimating the probability of false absence*

The per-survey probability of detection estimated for each species from the model can be used to estimate the probability of detecting a particular species at a particular site given the survey effort at that site (i.e., the number of camera-trap days). This value, denoted  $p^*$ , is equivalent to the power of the survey for species  $i$  at site  $k$ , and is calculated as:

$$p^*_{ik} = 1 - (1 - p_i)^J$$

where  $J$  is the number of repeat surveys at site  $k$  (Royle & Dorazio 2008, see also Moritz et al. 2008).

The probability of false absence,  $p^{fa}$ , for that species at that site can then be calculated as:

$$p^{fa}_{ik} = 1 - p^*_{ik}$$

and the probability of not detecting species  $i$  in the entire survey (i.e., getting a false absence across all  $K$  sampled sites) is given by:

$$p^{fa}_i = \prod_K (1 - p^{fa}_{ik}) .$$

Applying these equations to our camera trap survey with a per-survey detection probability of 0.02, equivalent to the lowest estimated detection probability (for side-striped jackal, Table 2), we obtained an estimated probability of false absence of essentially 0 ( $p^{fa}_i = 3 \times 10^{-116}$ ), indicating that our power to detect a rare and elusive carnivore across all of the camera stations was essentially 1.

## CHAPTER 4

### **A Hierarchical Multi-Species Modeling Approach to Assessing Carnivore Responses to Hunting, Habitat and Prey Heterogeneity within a Savanna Protected Area**

#### **Introduction**

Protected areas are a cornerstone of global conservation efforts to shield wildlife from anthropogenic impacts such as hunting and habitat loss (Ceballos et al. 2005; Chape et al. 2005; Naughton-Treves et al. 2005). The number and extent of protected areas (hereafter PAs or parks) have grown exponentially over recent decades, yet their ecological effectiveness is increasingly in question since many are too small and isolated, lack adequate capacity for law enforcement, and are beset by illegal hunting and resource collection (Soulé et al 1979; Newmark 1987, 2008; Caro & Schulte 2007; Dobson & Lines 2008; Gaston et al. 2008). Moreover, rapid human population growth around PAs and the attractiveness of a park's otherwise scarce resources may result in elevated impacts at PA edges and cause increased isolation and edge effects (DeFries et al. 2005; Wittemyer et al. 2008). Such detrimental effects may be particularly severe for large, wide-ranging species prone to conflict with humans, most notably mammalian carnivores (Woodroffe & Ginsberg 1998; Revilla et al. 2001; Inskip & Zimmermann 2009; Balme et al. 2010). PA networks are key to the long-term viability of many carnivore species (Carroll et al. 2004), so an understanding of carnivore responses to human-induced and natural changes in and around PAs is critical not only to the conservation of threatened carnivore populations, but also to the effective protection of ecosystems in which they play important functional roles (Terborgh et al. 2001; Soulé et al. 2003).

Anthropogenic activities can impact carnivore populations both directly and indirectly. Direct persecution is often a major threat as carnivores are hunted as trophies (Packer et al. 2009), for traditional uses (e.g., ceremonial, medicinal, nutritional; Chapter 3), and in retaliation for real or perceived threats to livestock or human life (Ogada et al. 2003; Treves & Karanth 2003). Furthermore, many carnivore species are wary by nature and avoid areas of elevated human activity, such that even non-lethal activities (e.g. pastoralism, tourism) can influence their occurrence and viability (Hebblewhite & Merrill 2008; Reed & Merenlender 2008; Van Meter et al. 2009). Besides these direct anthropogenic influences, hunting of prey populations can be an important indirect human impact on carnivore viability, given that the availability of suitable prey is a key determinant of carnivore occurrence and abundance (Karanth et al. 2004). Finally, habitat destruction can influence carnivores both directly and indirectly and is predicted to affect some species more than others (e.g., Riley et al. 2003). Effects of habitat change on carnivores may be mediated through the response of their prey, or other factors such as associated changes in disease dynamics (Cleaveland et al. 2007).

Management efforts attempt to address the threats faced by carnivores in and around PAs through more effective enforcement of anti-poaching laws (Linkie et al. 2003; Hilborn et al. 2006), creation of partially protected buffer zones (Linnell et al. 2005; Balme et al. 2010), restoration of habitat and prey (i.e., increasing predator carrying capacity; Hayward et al. 2007), and resolution of human-carnivore conflict (Shivik 2006; Woodroffe et al. 2007; Balme et al. 2009b; Maclennan et al 2009). However, in practice, these interventions are exceedingly difficult to implement for political, economic and social reasons. Given limited resources, PA managers

must identify approaches that will provide the greatest conservation return on their investment, but designing and implementing these optimal strategies requires an understanding of carnivore responses to specific stressors. Furthermore, management actions targeted to address responses of entire carnivore communities may be more ecologically and cost effective than single-species approaches.

A significant challenge to assessing carnivore populations and their responses to anthropogenic impact is the often infrequent and imperfect nature of survey detections (Long et al. 2008). Accurate modeling of species' distributions and habitat suitability typically requires large samples of observations and implicitly assumes that species are absent from surveyed locations where they are not detected (Guisan & Zimmerman 2000). However, the rare and elusive nature of many carnivore species frequently translates into small sample sizes and low detection probabilities, and hence biased population estimates (Thompson et al. 2004). Fortunately, recent advances in survey and statistical techniques can be applied to address this challenge. Camera trapping has proven an effective technique for detecting cryptic carnivores (Moruzzi et al. 2002; Pettorelli et al. 2010), particularly for mark-capture estimation of abundance for individually identifiable species (Karanth & Nichols 1998; Balme et al 2009a). The nature of camera-trap surveys—with camera stations sampling repeatedly over time at specific sites—is well-suited to an occupancy modeling analytical framework that explicitly accounts for imperfect detection (O'Brien et al. 2010). The use of occupancy as a surrogate for abundance has been widely adopted (MacKenzie et al. 2006) and is appropriate for widespread, low-density carnivore populations (Royle et al. 2008). Furthermore, recently developed hierarchical multi-species occupancy models capitalize on the information content of multiple detection histories across an entire community to improve inference for rare species with few detections (Zipkin et al. 2009, 2010). Hierarchical models also provide a flexible modeling framework capable of addressing other important assumptions, including spatial independence among sampling sites (Royle & Dorazio 2008; Cressie et al. 2009). Models explicitly accounting for spatial autocorrelation are increasingly being applied to the estimation of animal occurrence patterns (Augustin et al. 1996; Lichstein et al. 2002; Dormann et al. 2007), and have in many cases been shown to improve inference (Wintle & Bardos 2006; Carroll et al. 2010).

In this study, we used a Bayesian hierarchical multi-species occupancy model accounting for spatial autocorrelation to assess patterns of carnivore occurrence in relation to key landscape features in Mole National Park, Ghana (hereafter MNP). MNP is among the largest protected areas in West Africa and, as with most of this region, its carnivore populations are poorly studied yet subjected to considerable pressure from the region's high human densities and widespread hunting for bushmeat (Brashares et al. 2001; Bauer et al. 2003b). Illegal hunting is a central management concern in MNP, and previous work indicates that the park's carnivore community has been heavily impacted, with evidence of human-caused mortality and the decline and likely extirpation of several species (Chapter 3; Burton et al. in press). Nevertheless, the direct and indirect effects of hunting on MNP's carnivore populations are unknown. We used law enforcement patrol records to develop a spatially explicit index of hunting pressure and test the hypothesis that hunting is a major determinant of carnivore occurrence patterns in MNP. Using a Bayesian model selection framework, we further tested the importance of other anthropogenic and natural factors on carnivore occurrence, including prey biomass, habitat type, and law enforcement protection. Our approach not only informs the conservation of MNP's regionally

important carnivore populations, but is also broadly applicable to the robust assessment of rare and elusive species subject to environmental change.

## **Methods**

### *Study area*

MNP is the largest of Ghana's protected areas and covers approximately 4600 km<sup>2</sup> of woodland savanna habitat in the country's Northern Region (~ 09°11' – 10°06' N and 01°22' – 02° 16' W). Elevation ranges from 120-490 m and open savanna woodland is the dominant habitat type, with tree cover averaging about 30% and grasses reaching 2-3m in height during the April-to-October wet season (GWD 2005). Mean annual rainfall is approximately 1100 mm and most of the park's rivers are seasonal, draining into the White Volta River.

### *Camera trap survey*

We conducted a camera trap survey between October 2006 and January 2009 to estimate carnivore occurrence patterns in MNP (more details of the survey are given in Chapter 3). For this study, we used data from 224 camera stations deployed along gradients in three factors expected to influence carnivore occurrence, namely proximity to human settlement (i.e., park boundary), potential prey abundance, and availability of water and associated riparian forest habitat (Fig. 1). Most stations consisted of a single passive infra-red DeerCam DC-300 film camera trap unit (Non Typical, Park Falls, WI, USA) set on a tree at a height of about 40cm, facing perpendicular to the expected direction of animal travel and approximately 3m from the anticipated site of capture. Stations were set in spatially and temporally differentiated sampling groups, within which they were spaced systematically at about 1-km intervals near specific features expected to maximize carnivore capture probability, such as dirt roads, wildlife trails, waterholes, and salt licks. Sampling effort at a station was calculated as the number of days for which a camera was set (or until the last photo was taken if the roll was fully exposed before collection) and total effort across the 224 stations was 4,867 trap-days (mean = 21.7, SD = 13.0). Effort was highest in the central and southeastern portions of the park (Fig. 1) and during the dry season months of November to March. Detection or non-detection of carnivore species was recorded at each station for each trap day, yielding a response variable representing an uncorrected or "naïve" estimate of carnivore occurrence across the sampling sites (Mackenzie et al. 2006).

### *Hypothesized predictors of carnivore occurrence*

We hypothesized that spatial patterns of carnivore occurrence in MNP would be influenced by variation in hunting pressure and human disturbance, anti-poaching patrol effort, prey biomass and habitat type (Table 1). To test our hypotheses we created spatially explicit indices representing each of these factors and extracted values for each sampling location (i.e., camera station) from the camera trap survey. Analyses were conducted using ArcMap 9.3.1 (ESRI, CA, USA) in the UTM30N projection (WGS1984 datum) and density surfaces (described below)

were created using a kernel density estimator in the Spatial Analyst ArcMap extension (with a 2 km search radius and output resolution of 500 x 500m).

*(i) Hunting pressure and human disturbance*

Carnivore species are often killed in Ghana and elsewhere as a perceived threat to livestock and human life or for traditional purposes (Chapter 3; Burton 2009). We therefore hypothesized that carnivores would be less likely to occur in portions of MNP experiencing heavy hunting pressure. We used spatially explicit observations of illegal hunting activity in the park made during law enforcement patrols (Jachmann 2008a,b; Chapter 2) to construct an index of variation in hunting pressure. Evidence of illegal hunting—ranging from direct sightings and arrests to indirect signs such as hunting camps, traps or hunter footprints—were recorded by teams of 3-6 staff during regular foot patrols across much of the park (Fig. 1), with specific locations determined using handheld GPS units. We used data from nearly 1,400 patrols conducted between October 2006 and May 2008 and comprising 688 observations of illegal hunting to create a density surface of hunting activity across the park. We then divided this by a similar density surface describing patrol effort (see below) to derive a spatial index of relative hunting pressure across the park (equivalent to a catch-per-unit-effort or CPUE index; cf. Jachmann 2008a). As an alternative measure of human disturbance in MNP, we calculated the Euclidean distance from each sampling location to the nearest boundary of the park. This simple index represents potential edge effect and is often used as a proxy for hunting pressure (and it was highly correlated with the distance to the nearest village, Pearson  $r = 0.91$ ).

*(ii) Law enforcement protection*

Law enforcement (“anti-poaching”) patrols are intended to deter illegal hunting activity and thereby provide protection to park wildlife (Hilborn et al. 2006; Jachmann 2008a,b). We hypothesized that carnivores would be more likely to occur in areas within MNP that were more effectively protected by a greater level of patrol effort. We anticipated that this effect might be distinct from that associated with the amount of hunting activity detected per unit patrol effort (above), given that hunters could have been avoiding more heavily patrolled areas and that patrol routes were influenced by many factors (e.g., access, wildlife, management zones). Patrol teams recorded their locations with handheld GPS units at regular intervals along patrol routes, and we used these locations to construct a density surface of patrol effort across the park.

*(iii) Prey*

The availability of suitable prey species is a key determinant of the distribution and abundance of carnivore populations (e.g., Karanth et al. 2004). Prey availability may represent a natural influence on carnivores but could also reflect an indirect anthropogenic effect if prey are depleted by exploitation. We used two data sources to create indices characterizing spatial patterns of prey biomass in MNP. First, we used spatially referenced sightings of potential mammalian prey species recorded during the October 2006—May 2008 law enforcement patrols to create a kernel density surface representing the longer term (i.e., multi-season) distribution of

prey biomass. This dataset included approximately 8,600 sightings of nearly 58,000 individuals of 14 ungulate or primate species (Appendix 4.1; see also Chapter 2). Prey counts were converted to biomass estimates by multiplying the number of individuals of a particular species counted by the body mass of that species, using values of estimated average adult body mass from the PanTHERIA database (Jones et al. 2009). The prey biomass surface was then divided by the patrol effort surface (as for hunting above) to create a spatial CPUE index of prey biomass. Since most of the carnivore species detected in MNP were of medium or small size (i.e., < 15 kg; see Results and Appendix 4.1), we also calculated an index of small prey biomass including only those species weighing less than 18 kg.

Our second prey index was derived from the camera trap survey and represented an estimate of prey biomass at each camera site for the specific period over which it was sampled (i.e., short term, seasonally specific). The number of detections of a particular prey species at a given camera station (excluding multiple photos of ostensibly the same individual obtained < 5 minutes apart) was multiplied by that species' average adult body mass (obtained from Jones et al. (2009) for mammals and Dunning (2008) for birds) and standardized by sampling effort into a CPUE index of kg of prey biomass per 100 camera trap days. Twenty-eight potential prey species were detected during the camera survey, including 21 mammal and 7 bird species (Appendix 4.1), and, as for the patrol sightings, separate biomass indices were calculated for all prey species combined and for only smaller prey weighing less than 18 kg. Camera trap detections included many more small prey species than patrol observations, and thus likely translated into more relevant indices for smaller carnivore species, although all of our prey indices omit or underrepresent the smallest prey items (e.g., small rodents, insects) and are therefore less suitable for the smallest carnivores (e.g., mongooses, genet).

### *(iii) Habitat*

MNP's habitat is dominated by relatively intact open woodland savanna and we hypothesized that habitat heterogeneity would have a less pronounced effect on carnivore occurrence patterns than variation in hunting pressure or prey biomass. Nevertheless, the park experiences pronounced seasonal variation in vegetative cover—with dense grasses growing 2-3 m high in the wet season and frequently burned in the dry season—and narrow bands of riverine forest represent distinctive habitat features associated with important water sources. We therefore calculated three habitat indices, with the first being simply the Euclidean distance from each sampling site to the nearest band of riverine forest (demarcated from a Landsat-derived GIS map layer provided by park management; GWD 2005). Our second and third habitat indices were based on the normalized difference vegetation index (NDVI), a measure of vegetation productivity (Fensholt & Sanholt 2005; Pettorelli et al. 2005) that has been linked to occurrence patterns for many wildlife species (Mueller et al. 2008; Pettorelli et al. 2009), including carnivores (Carroll et al. 2001). We used the NDVI derived from the MODIS sensor (Global MOD13Q1 product from the Terra satellite, 16-day composite image at 250m resolution, downloaded from <http://lpdaac.usgs.gov>) to calculate both seasonally specific and longer-term measures of vegetation biomass in MNP. The former captured seasonal variation and corresponded to the 16-day composite NDVI value most closely matched to the period over which a given camera station was sampled (using the average of multiple composite values for

stations sampled for more than 16 days or over a period split across two or more composite time frames). Our longer-term or “integrated” measure represented more stable spatial variation in vegetation biomass (i.e., different habitat types) and consisted of the sum of all 16-day composite NDVI values at a sampling location over the entire period of our survey (Oct. 2006—Jan. 2009; Pettorelli et al. 2005).

We did not explicitly test the effect of intraguild interactions on carnivore occurrence patterns, though we note its potential importance (Caro & Stoner 2003) and suggest it as a factor for future investigation (e.g., MacKenzie et al. 2004; Harmsen et al. 2009).

### *Covariates of carnivore detectability*

Our modeling framework for estimating carnivore occurrence patterns (described below) explicitly accounts for heterogeneity in carnivore detection probability. In addition to species-level heterogeneity, we anticipated that several site-level factors may have affected the probability of detecting a carnivore species (given its occurrence), so we included them as covariates in our model-based hypotheses to control for such “nuisance” effects on the estimation of occurrence probability. Firstly, we hypothesized that heavy hunting pressure and human disturbance may not only decrease the probability of carnivore occurrence, but could also make carnivores wary and thus more difficult to detect where they do occur. We therefore included the indices of relative hunting pressure and distance from park edge (see above) as covariates on detection as well as occurrence. We further hypothesized that certain aspects of our sampling design could have introduced spatial heterogeneity in detectability. Many of our camera stations were set on dirt roads or tracks ( $n = 90$ ), which could have been used or avoided by certain species more often than adjacent areas lacking such features. We therefore tested for such an effect of roads by including a binary covariate on detection indicating whether or not a station was set along a park road. A small subset of camera stations ( $n = 17$ ) consisted of a paired set of two camera units rather than the typical single unit (as part of a concurrent study on density estimation), raising the possibility that such paired stations had higher detection probabilities, so we included another indicator covariate distinguishing them from single-camera stations. While most of our stations were set by one field team that I led for consistency, a portion was established by a second field team ( $n = 65$ ), potentially introducing variation in detectability due to differences in set technique, so we included a third binary covariate indexing the set team. Finally, to account for marked variation between wet and dry seasons in factors that could affect camera performance at a site—such as ambient temperature or density of background vegetation—we included a fourth binary covariate on detection indexing the season in which a station was sampled (“dry” = median sampling date within October–April, “wet” = median date within May–September).

Prior to analysis, all continuous variables were examined for outliers, normalized with a fourth-root transformation (except for edge and the two NDVI variables), and standardized to have mean zero and unit variance (to improve convergence of model estimates and facilitate interpretation of relative effect sizes; McCarthy 2007; Kéry 2010). We tested variables for collinearity using correlation coefficients (Spearman  $r_s$  for all variables and Pearson  $r$  for normalized continuous variables) and the variance inflation factor (Quinn & Keough 2002; Zuur et al. 2009). All statistical tests were performed in program R version 2.11.1 (R Core

Development Team 2010). Our hypothesized covariates of carnivore occurrence and detection probabilities were not strongly collinear ( $|r_s| < 0.57$ ;  $|r| < 0.65$  variance inflation factor  $< 3.3$ ), suggesting that they represented different attributes of the MNP environment (e.g., variation in seasonal vs. long-term prey or vegetation biomass).

### *Background on modeling framework*

We applied a multi-species occupancy modeling framework (Royle & Dorazio 2008) to carnivore detection data from our camera trap survey. This framework represents a hierarchical (or “state-space”) formulation and extension of the single-species occupancy modeling approach described by MacKenzie et al. (2002), and is essentially a robust adaptation of the logistic regression model frequently applied to species “presence-absence” data (Guisan & Zimmerman 2000; MacKenzie et al. 2006). A key advantage of the occupancy modeling approach is the explicit estimation of detection probability, providing a means to overcome the problematic assumption of perfect detection (i.e., species always being detected where they occur). The framework requires repeated sampling of a site over a period considered closed to changes in occupancy status, and uses this temporal replication to estimate the probability that a species not detected at a site could have in fact been present (i.e., false absence). We treated consecutive trap days as repeat surveys at a given camera station and considered the occurrence of a species at a station equivalent to its use of the habitat at that site (rather than considering sites to be permanently “occupied” during the sampling period; MacKenzie et al. 2006. By “use” we include dispersal through a habitat). We also treated our entire survey period as one “season” in that most sites were not re-sampled across seasons, the carnivore community was assumed to be closed (i.e., no species extinctions or colonizations), and we did not wish to estimate site-specific probabilities of extinction or colonization over time (cf. MacKenzie et al. 2003).

The multi-species model extends the single-species approach by capitalizing on additional information contained in multiple species’ detection histories across a sampled community, simultaneously estimating occurrence and detection probabilities for all species. It assumes that an individual species’ response comes from a common community-level distribution of responses. Species-specific parameters are thus treated as random effects governed by an associated community-level “hyper-parameter” (i.e., the hierarchical component). In this way, collective data on the entire carnivore community can improve species-specific estimates of occurrence, even for those species rarely observed and for which a single-species approach would likely yield unreliable results (Zipkin et al. 2009). This approach also facilitates robust estimation of patterns of species richness across sites (i.e., the number of carnivore species using different sites), accounting for species that may have been unobserved during sampling (Dorazio et al. 2006; Kéry & Royle 2008; Zipkin et al. 2009).

### *Model structure*

Our model assumes that site-specific occurrence for species  $i = 1, 2, \dots, N$  at site  $j = 1, 2, \dots, J$ , is an imperfectly observed (latent) random variable,  $z(i,j)$ , which is the outcome of a Bernoulli trial,  $z(i,j) \sim \text{Bern}(\psi_{ij})$ , where  $\psi_{ij}$  is the probability that species  $i$  occurs at site  $j$ , and  $z(i,j) = 1$  if it does occur and zero if it does not. Our observation data,  $y(i,j)$ , representing the detection or non-

detection of species  $i$  at site  $j$  during the camera trap survey, are conditional upon the true occurrence state,  $z(i,j)$ , and are also assumed to be Bernoulli random variables if species  $i$  is present (that is if  $z(i,j) = 1$ ) and are fixed zeros if species  $i$  is absent (i.e., if  $z(i,j) = 0$ , then  $y(i,j) = 0$  with probability 1). This observation model is specified as  $y(i,j) \sim \text{Bern}(p_{ij} \cdot z(i,j))$  for  $k_j$  independent trials, where  $p_{ij}$  is the probability of detecting species  $i$  at site  $j$  if it is present, and  $k_j$  is the number of trap days for which the camera station at site  $j$  was active. We assumed that all species present in the MNP carnivore community were detected at least once during the survey, and we therefore did not estimate the probability of there being additional species that went completely undetected. Previous work suggests only a low probability of additional carnivore species occurring in the park (Chapter 3), and we focused our attention on confirmed species toward which management attention could be directed (cf. Russell et al. 2009; Zipkin et al. 2010).

As noted above, we hypothesized that occurrence and detection probabilities would vary by species and be affected by anthropogenic and natural features of the park (as well as effects of sampling on detection). We incorporated these effects into the model linearly using the logit link function, with the general form of  $\text{logit}(\psi_{ij}) = \varphi_i + \alpha_j$  and  $\text{logit}(p_{ij}) = \eta_i + \beta_j$ , where  $\varphi_i$  and  $\eta_i$  are species-level effects and  $\alpha_j$  and  $\beta_j$  are site-level effects on occurrence and detection, respectively (Kéry & Royle 2009; Zipkin et al. 2009, 2010). We also modeled a correlation ( $\rho$ ) between occurrence and detection based on the assumption that both are affected by species abundance, such that more abundant species would likely be both easier to detect and more prevalent across the landscape, and vice versa (Royle & Dorazio 2008; Zipkin et al. 2009). We further hypothesized that, despite our attempt to achieve independence among sampled sites (through separation in space or time), the occurrence of a species at a site might be affected by the occurrence of that species at neighboring sites, independently of modeled covariates (i.e., due to unmeasured environmental features or intrinsic processes such as animal movement behavior; Augustin et al. 1996; Wintle & Bardos 2006). Preliminary analysis of our camera trap detections also indicated the potential for some spatial autocorrelation in site occurrences (Appendix 4.2). Such spatial autocorrelation could potentially bias inference, yet common tests of autocorrelation (e.g., spatial correlograms of model residuals) are difficult to apply given that our response variable of interest—species occurrence at a site—was only partially observed. We therefore extended our model to accommodate the possibility of spatial autocorrelation among sampling sites using an adaptation of the auto-logistic model described by Royle & Dorazio (2008: 314-321; cf. Augustin et al. 1996; Sberze et al. 2010). We defined a spatial neighborhood around each sampling site as a 5-km radius circle (i.e., an area of approximately 79 km<sup>2</sup>, assumed to encompass short-term movements of individual animals; Appendix 4.2) and specified an autocovariate,  $\text{autocov}_j$ , such that the occurrence of species  $i$  at site  $j$  could be influenced by species  $i$ 's occurrence at all  $g$  sites within the neighborhood, with the magnitude of influence inversely proportional to the distance between the focal station and particular neighboring station (further detail in Appendix 4.2).

The most general model of occurrence for species  $i$  at site  $j$  was therefore specified as:

$$\text{logit}(\psi_{ij}) = \varphi_i + \alpha_1 \text{patrol}_j + \alpha_2 \text{hunting}_j + \alpha_3 \text{NDVI1}_j + \alpha_4 \text{NDVI2}_j + \alpha_5 \text{edge}_j + \alpha_6 \text{river}_j + \alpha_7 \text{prey1}_j + \alpha_8 \text{smallprey1}_j + \alpha_9 \text{prey2}_j + \alpha_{10} \text{smallprey2}_j + \delta_i \text{autocov}_j$$

where  $\varphi_i$  is a species-level effect, the coefficients  $\alpha_{1_i}, \alpha_{2_i}, \dots, \alpha_{10_i}$  represent effects of the associated covariates (Table 1) on species  $i$ , and  $\delta_i$  is the effect of the autocovariate on species  $i$ . Similarly, the full detection model was specified as:

$$\text{logit}(p_{ij}) = \eta_i + \beta_{1_i}\text{road}_j + \beta_{2_i}\text{paired}_j + \beta_{3_i}\text{team}_j + \beta_{4_i}\text{hunting}_j + \beta_{5_i}\text{edge}_j + \beta_{6_i}\text{season}_j$$

where  $\eta_i$  represents the species-level effect on detection and  $\beta_{1_i}, \dots, \beta_{6_i}$  are effects of the respective covariates on detection (details above).

Species-specific occurrence and detection processes were linked to one another through the additional hierarchical model component in which species-level parameters were treated as random effects governed by community-level hyper-parameters. Specifically, we assumed that for a given effect (e.g., influence of patrol effort on occurrence), species-level parameters were drawn from a normal distribution described by the community mean ( $\mu$ ) and standard deviation ( $\sigma$ ) hyper-parameters (e.g.,  $\alpha_{1_i} \sim N(\mu_{\alpha_1}, \sigma_{\alpha_1})$ ). We only considered additive, linear effects of covariates on occurrence and detection since we did not have strong *a priori* reasons for expecting non-linear or interactive effects and felt the additional model complexity was unwarranted given the available sample of observation data.

### *Model selection*

We considered all possible combinations of covariates to be candidate models representing competing hypotheses about significant influences on the MNP carnivore community (or its assessment in the case of detectability). Our *a priori* full model included 10 site-level covariates and an autocovariate for occurrence probability and 6 covariates for detection probability (yielding a candidate set with a daunting  $2^{17} = 131,072$  possible models). Given that several covariates represented similar features (e.g., 4 different prey indices), we anticipated that this model was likely overparameterized and therefore implemented a Bayesian approach to model simplification (Congdon 2005). Information-theoretic approaches are commonly used to distinguish among competing models; for instance, the Akaike Information Criterion (AIC; Burnham & Anderson 2002) or analogous Bayesian Deviance Information Criterion (DIC; Spiegelhalter et al. 2002) balance model fit and complexity by ranking models using deviance and a penalty term weighted by the number of parameters. However, these criteria are not easily or reliably calculated for complex hierarchical models with latent variables, such as our multi-species occupancy model (Celeux et al 2006; Millar 2009). For this reason, we used an alternative approach to model evaluation. We assessed the strength of evidence for covariate effects at the community-level (i.e., across all species) by calculating posterior model probabilities for the candidate set with a mixture modeling approach in which each covariate is multiplied by an “inclusion parameter” (Kuo & Mallick 1998; Congdon 2005: section 3.2; Royle 2008; Royle & Dorazio 2008:72-73). The inclusion parameters ( $w_c$ , for all  $C$  covariates in the model) were latent binary variables with uninformative prior probabilities of 0.5 (i.e., equal probability of a given covariate being included or not in the model). Their posterior probabilities

corresponded to the estimated probability that a particular covariate was included in the “best” model; that is, the degree of support for an effect of that covariate across all carnivore species in the community. The posterior probability of a given candidate model (i.e., combination of covariate effects) was thus calculated as the probability that  $w_c = 1$  for all coefficients included in that model and  $w_c = 0$  for all coefficients not included. In other words, each of the  $2^{17}$  candidate models had a corresponding unique vector of inclusion parameter values, and posterior probabilities for each of these vectors were calculated from their relative frequency in the posterior sample. For occurrence and detection parameters (i.e.,  $\phi_i, \eta_i$ ), posterior probabilities from the mixture model represented model-averaged estimates (i.e., averaged across the different models included in the posterior sample). Model-averaged estimates could also be obtained for covariate coefficients by averaging across posterior samples where the corresponding  $w_c = 1$  (Royle & Dorazio 2008:72-73).

Anticipating that different species may not show consistent responses, we also assessed the importance of covariates on individual species occurrence and detection probabilities by inspecting posterior distributions for all parameters from the full model (i.e., with no inclusion parameters, since these were only applied at the community-level). Species-level parameters (i.e., coefficients  $\alpha_{1i}, \alpha_{2i}$ , etc.) with posterior masses concentrated away from zero were considered indicative of an effect of the corresponding covariate on that particular species (e.g., zero not contained within credible intervals at 95%, or less conservatively, 80% probability thresholds).

We implemented all models in program WinBUGS version 1.4.3 (Lunn et al. 2000), using the package R2WinBUGS (Sturtz et al. 2005) to interface with program R. Inference was made from 3,000 samples of the posterior distribution obtained from 50,000 Markov Chain Monte Carlo (MCMC) iterations after a burn-in of 50,000 and with a thin rate of 50. We used vague priors and random initial values, although achieving acceptable convergence in the MCMC chains required less diffuse prior specifications and other minor adjustments (sample code in Appendix 4.3; see also Royle & Dorazio 2008 and Kéry & Royle 2009). Convergence was assessed by visual assessment of MCMC chains and using the Gelman-Rubin statistic (“Rhat” in R2WinBUGS, with values  $< 1.1$  indicating convergence; Gelman et al. 2004; Kéry 2010).

## Results

We detected 9 carnivore species during the camera trap survey in MNP (Table 2). Spotted hyena (*Crocuta crocuta*) was detected at the greatest proportion of sampling sites (a “naïve” measure of occurrence without accounting for detectability; MacKenzie et al. 2006), followed by leopard (*Panthera pardus*) and white-tailed mongoose (*Ichneumia albicauda*), whereas Gambian mongoose (*Mungos gambianus*) and side-striped jackal (*Canis adustus*) were detected at the fewest sites (Table 2). Model-estimated occurrence probabilities accounting for imperfect detection were higher than uncorrected estimates, but did not change the order of relative abundance across species. Species’ occurrence and detection probabilities were significantly positively correlated (posterior mean of covariance parameter  $\rho = 0.47$ ), suggesting both were related to underlying patterns of species abundance. The model-averaged community-level (i.e., across species) probabilities of site occurrence and per-survey detection were estimated to be

0.22 (posterior SD 0.09) and 0.12 (SD 0.04), respectively (based on the corresponding hyper-parameter posterior probabilities from the mixture model).

### *Community-level covariate effects*

Parameter estimates from our fully parameterized multi-species model were generally imprecise, with most posterior probabilities being widely distributed around their respective means and 95% CIs broadly overlapping 0 (Table 3, Appendix 4.4), indicating that there was not a consistent response across the carnivore community to most site covariates. Posterior distributions for community-level hyper-parameters from the full model indicated the most consistent covariate effect on carnivore occurrence was a positive association with small prey biomass (Table 3, Appendix 4.4). There was also evidence of a consistent “observer effect” on detection probability (i.e., the “team” covariate), with higher mean community-level detectability associated with camera stations set by the primary sampling team (Table 3, Appendix 4.4).

Posterior probabilities for inclusion parameters on site covariates from the mixture model confirmed that small prey biomass was an important occurrence covariate for the MNP carnivore community (having an estimated probability of inclusion in the best model equal to 1; Table 3). They also highlighted the important community-level effect of proximity to riverine forest (mean posterior probability of inclusion,  $Pr = 1.0$ ; Table 3), which was not apparent from the diffuse posterior of the full model due to the varied direction of species responses (Table 2; Fig. 2). There was some support for a community-wide edge effect on occurrence ( $Pr = 0.73$ , posterior  $SD = 0.44$ ; Table 3), and weak evidence for a potential effect of patrol intensity ( $Pr = 0.22$ ,  $SD = 0.41$ ; Table 3). Contrary to our primary hypothesis, there was little evidence of a consistent effect of hunting activity on carnivore occurrence, nor was there any indication of significant community-level effects of vegetation biomass (as measured by NDVI), total prey biomass, or spatial autocorrelation ( $Pr < 0.03$ ; Table 3).

With regard to carnivore detectability, the importance of the “team” covariate was strongly supported at the community-level by the posterior inclusion probability from the mixture model ( $Pr = 0.98$ ,  $SD = 0.15$ ; Table 3). A significant influence of roads was also indicated ( $Pr = 0.91$ ,  $SD = 0.29$ ; Table 3), and there was limited support for an edge effect on detection probability ( $Pr = 0.48$ ,  $SD = 0.50$ ; Table 3). Accordingly, combinations of these occurrence and detection covariates comprised the candidate models with the highest posterior model probabilities (Table 4). A total of 64 candidate models appeared in the posterior sample, but the four highest-ranked models had 70% of the support, and 90% of the posterior model probability was captured by 11 candidate models (Table 4). The top-ranked model contained additive effects of edge, riverine forest and small prey biomass on occurrence, and of road and team on detection ( $Pr = 0.335$ ; Table 4, Fig. 2).

### *Species-level effects*

We examined posterior probability distributions for all species-level parameters in the full model to identify potential species-specific effects that might be obscured at the community level. Posterior means for the effect of seasonal small prey biomass were positive for all 9 carnivore species, and 95% CIs overlapped 0 for only spotted hyena and caracal (*Caracal caracal*; Table 2,

Appendix 4.4). There was weak species-level support for an effect of riverine forest habitat, both in terms of attraction (higher occurrence probabilities nearer to riverine forest for spotted hyena and leopard) and avoidance (lower occurrence probability near riverine forest for caracal; Fig. 2). The model indicated little evidence of an edge effect on occurrence probability for most species, although spotted hyena occurrence probability was marginally higher further away from the park edge, and the opposite was true for large-spotted genet (*Genetta pardina*; Fig. 2). Consistent with community-level estimates, there was little evidence for significant species-level effects of patrol effort, poaching activity, or vegetation biomass on carnivore occurrence, although some potential weak effects were indicated (Table 2, Appendix 4.4). In contrast, a signal of spatial autocorrelation in site occurrence probabilities was indicated for several species (i.e., positive posterior estimates of the autocovariate coefficient; Appendix 4.4).

In agreement with indications at the community-level, sampling-related heterogeneity in detection probabilities was evident at the species level. Posterior probabilities suggested most carnivore species had higher detectabilities at stations set by the primary sampling team (given occurrence), and that leopard and white-tailed mongoose were more likely to be detected at camera stations set on roads, whereas marsh mongoose was less likely to be detected on roads. Hunting activity and seasonality did not appear to affect species' detectabilities, but there was evidence of an edge effect, with posterior distributions for large-spotted genet, marsh mongoose (*Atilax paludinosus*) and spotted hyena suggesting lower detectability near the park edge, while those for leopard, Gambian mongoose and caracal indicated higher edge detectability. Predicted occurrence probabilities from the best model indicated significant heterogeneity among species in the direction and magnitude of their responses to site covariates (Fig. 2).

## Discussion

### *Factors influencing carnivore occurrence*

Our results provide insight into the relative influence of anthropogenic and natural landscape features on the dynamics of a poorly studied carnivore community. The hierarchical multi-species modeling approach identified patterns across the entire community while also highlighting species-specific variation. Our models indicated that availability of suitable prey had the most consistent effect on the MNP carnivore community, with carnivore species' occurrence probabilities positively linked to the relative biomass of smaller prey species (particularly at a seasonal scale). While variation in vegetation biomass (as measured by NDVI) did not appear to significantly influence carnivore occurrence, our mixture model identified a community-level effect of riverine corridors, reflecting an aggregate of varied species responses to this important natural landscape feature. Contrary to expectation, heterogeneity in carnivore occurrence patterns was not associated with measured variation in illegal hunting activity, suggesting that hunting is not a dominant influence on carnivore species' use of park habitats. Our models did point to an effect of proximity to park edge on occurrence, implying that human disturbance may indeed exert influence on the carnivore community. However, this edge effect was not uniformly negative but rather highly variable across species (Fig. 2; unrelated to body mass or home range size), indicating that a simple model of increasing disturbance at the park edge is not appropriate.

Heterogeneity in species' responses to extrinsic stressors is to be expected, and consequently some inconsistency in aggregate responses interpreted at the community level should be anticipated (i.e., diffuse posterior distributions for community hyper-parameters). Nevertheless, uncertainty in our multi-species model also reflects the considerable amount of species-level variation in occurrence patterns unexplained by the spatial covariates we included (Appendix 4.4). Inference for rare species will always be limited by small sample sizes, and parameters were indeed less precisely estimated for carnivore species with few detections in our survey (e.g., Gambian mongoose, side-striped jackal; Appendix 4.4). All the same, the multi-species approach produced useful estimates of occurrence and detection probabilities for these species, and it is more powerful than single-species models that frequently fail to yield reliable estimates for rare species (McShea et al. 2009; Zipkin et al. 2009; C. Burton unpublished data).

Even with the improved ability to estimate occurrence and detection probabilities, our modeling identified few effects of measured landscape covariates for the rarest carnivores in MNP (although some responses were strongly indicated, such as the negative association between caracal occurrence and proximity to riverine forest; Fig. 2). Responses to landscape factors were more discernable for species with a greater number of detections (e.g. spotted hyena, large-spotted genet), and these likely had a significant influence on community-level inference. Since little is known about carnivore ecology in MNP, or more generally across much of West Africa (Ray et al. 2005a), it is difficult to make a comparative assessment of patterns of occurrence indicated by our study (particularly for smaller carnivores). Single-species studies from other areas agree with some of our findings while also highlighting the frequently complex relationships between landscape heterogeneity and carnivore ecology. For example, Marker & Dickman (2005) found leopard abundance to be correlated with prey biomass, while Balme et al. (2007) reported that leopards hunted preferentially in areas of intermediate vegetation cover where prey were easier to catch but not necessarily more abundant. Boydston et al. (2003) and Kolowski & Holekamp (2009) found that spotted hyenas selected areas with dense vegetation and near seasonal streams, but that their association with higher prey density was influenced by the degree of human disturbance. Negative edge effects on survival and behavior were reported for spotted hyenas (Pangle & Holekamp 2010) and leopards (Balme et al. 2010), although in the latter case leopards did not avoid edge areas (consistent with our results and perhaps indicative of an “ecological trap”).

#### *Factors influencing carnivore detectability*

Our hierarchical model also provided insight into biases associated with the sampling process. Firstly, detection probabilities per survey (i.e., per camera trap day) were estimated to be quite low, and accordingly our “naïve” estimates of occurrence probability were negatively biased by an average magnitude of 126% across all 9 carnivore species (from 7% for large-spotted genet to 434% for side-striped jackal, relative to model estimates; Table 2). This underscores the importance of accounting for imperfect detection in models of animal occurrence, a point which has been made previously by many authors (e.g., MacKenzie et al. 2006) and yet has received relatively little attention in the broader literature on species distribution modeling (Guisan & Thuiller 2005; Elith & Leathwick 2009). Explicit consideration of detectability is particularly

important for rare and elusive species, such as most carnivores, and the largest estimated bias in our sample was associated with those species having the fewest detections (Table 2).

Our model indicated that two aspects of our sampling design introduced significant spatial heterogeneity to the probability of detecting a carnivore species given its occurrence. The potential bias of sampling on roads has been noted elsewhere (Henschel & Ray 2003; Larrucea et al. 2007). Yet, given access difficulties, we chose to set many camera stations at or near park roads (although roads in MNP are dirt tracks with relatively little vehicle traffic), and the explicit estimation of detection heterogeneity allowed us to address this sampling effect within the model. Similarly, despite our use of a standardized protocol for setting camera traps, we detected an “observer effect”, where detection probabilities differed between camera stations established by two field teams. Without an analytical method explicitly accounting for detectability, and recording of the relevant sampling covariate, this effect may have been erroneously interpreted as a difference in occurrence probability. The apparent influence of proximity to park edge on detectability could be related to behavioral responses of carnivores to variation in human disturbance (e.g., increased vigilance in closer proximity to human settlement), and, if unaccounted for, may have distorted inference of edge effect on occurrence. Finally, our modeling results suggest that we adequately achieved independence among camera stations by separating them in space and time, since inclusion of the spatial autocovariate term was not supported at the community level. Nevertheless, posterior probability distributions for the autocovariate coefficient were suggestive of spatial autocorrelation in occurrence probabilities for several species (Appendix 4.4), so its potential importance should not be ignored in future work. Sampling design of future carnivore surveys in MNP (and elsewhere) will benefit from careful consideration of the detection biases indicated by our analysis.

### *Study limitations*

Limitations of our study that might affect the strength of inference must be carefully considered. Due to logistical constraints, we were unable to access many portions of the park or to implement a random sampling design, so our camera stations (and resulting detections) may represent a biased sample yielding incomplete information on carnivore occurrence patterns in relation to park features. Nevertheless, we were able to sample across gradients in our hypothesized factors of influence, and we attempted to control for the effects of spatial and temporal sampling features, such as roads and season, on detectability. We infrequently detected several of the carnivore species in MNP, a common challenge in surveys of rare and elusive species, and despite advantages of the multi-species modeling approach, stronger inference is ultimately achieved only by greater sampling effort (including more targeted, species-specific sampling).

Our indices representing anthropogenic and natural landscape features of hypothesized importance were generated from the best available information, but their reliability is diminished by considerable associated uncertainty. For instance, our measures of illegal hunting activity and longer-term prey biomass are dependent on the reliability of data generated by the patrol monitoring system, which is subject to an unknown amount of error (Chapter 2). Hunting pressure is particularly difficult to estimate given that hunters seek to avoid detection by patrols. Patrol data also underestimated the occurrence and abundance of smaller prey species (Chapter

2; Appendix 4.1), so corresponding biomass indices are dominated by the larger and better-detected species. Prey indices derived from our camera-trap survey are subject to the same sampling limitations noted above for the carnivore data, and while the camera data included more small prey items (Appendix 4.1), the diet range for several of the smaller carnivores is poorly represented. Important variation in carnivore habitat quality may not have been adequately described by NDVI, which might be more tightly linked to the ecological characteristics of certain herbivores (Mueller et al. 2008; Pettorelli et al. 2009). While such remote sensing products show great promise for improving ecological understanding across large spatial and temporal scales (Cohen & Goward 2004; Pettorelli et al. 2005), they are not a substitute for detailed, field-based assessments of habitat that are largely lacking for MNP. Even an index as seemingly simple as distance to the park edge is subject to uncertainty associated with inconsistent boundary demarcation (GWD 2005), and its reliability as a proxy for human disturbance is affected by spatial variation in population density and land use around the park (C. Burton, unpublished data). Nevertheless, such limitations are common to many protected areas, particularly in developing nations like Ghana, and our study highlights a novel and conservation-relevant approach to characterizing a park landscape. Future work should seek to test and improve upon these measures of landscape heterogeneity and address other important factors (such as effects of fire, e.g., Klop & van Goethem 2008, or of intra- and interspecific competition, e.g., Durant 1998), as well as consider interactive and non-linear effects. A more thorough examination of our modeling assumptions is warranted (e.g., prior sensitivity, distributional forms), and the analytical framework could be extended to address error in predictor variables and other sources of uncertainty (Cressie et al. 2009). Response variables other than site occurrence could also be considered (e.g., abundance; Royle et al. 2007b) and a more thorough assessment of model adequacy is needed (e.g., Congdon 2005).

### *Conservation implications*

MNP's historical carnivore community has been heavily impacted over recent decades, with the decline and potential extirpation of several species (Chapter 3; Burton et al. in press). Assessing and maintaining the viability of persisting carnivore populations should therefore be of significant management concern, and our study provides useful information to that end. While illegal hunting pressure within the park is severe, we found no evidence that it exerts a direct influence on current patterns of carnivore occurrence. Assuming this result to be accurate (i.e., not due to mismeasurement of hunting pressure), it could relate to the elusive nature of carnivores or the lack of hunter preference for these species. While there is evidence that many carnivore species are killed for local consumptive uses (Chapter 3), MNP enforcement teams rarely report evidence of carnivore remains confiscated from arrested hunters (C. Balangtaa, pers. comm.). It is possible that carnivore species persisting in the park have proven themselves more resilient to direct human impacts like hunting, having passed through the "extinction filter" that apparently claimed other species (Chapter 3; Balmford 1996).

Assessing the indirect impacts of human activity on carnivore populations is more difficult. For instance, the positive association between carnivore occurrence and prey biomass is expected from natural predator-prey dynamics, but could also be indirectly influenced by hunting impacts to prey populations. Nevertheless, the relative dominance of prey availability on

carnivore occurrence suggested by our model may be an encouraging reflection of the prominence of natural influences on the park's carnivore populations, and it provides a tangible target for park managers (i.e., protection of prey populations). Similarly, the lack of a strong or consistent edge effect on carnivore occurrence suggests that elevated impacts around the park are not undermining its effectiveness in protecting carnivore habitat (at least for the populations that persist). Indeed, MNP appears to effectively protect natural habitats such as the riverine forest corridors that our modeling indicated to be of importance to carnivore occurrence patterns. However, in assessing the effectiveness of MNP's protection of carnivore populations, it is important to note the uncertainty reflected in our results, which ultimately represent a fairly coarse and preliminary assessment. Several species were rarely detected in our survey, limiting inference on their dynamics and suggesting that they could be perilously close to local extinction. Even among more frequently detected species, the long-term viability of their populations has not yet been appraised. In fact, preliminary mark-recapture estimates of population density for leopard and spotted hyena—two of the most frequently detected species in our survey—suggest that they persist at low abundances relative to conspecific populations (C. Burton, unpublished data). A reliable assessment of carnivore population viability in MNP, and a better understanding of the nature of human impacts on these populations, will require continued and detailed monitoring of species-specific occurrences and demographic rates.

Though further work is needed, our approach provides a valuable framework for assessment of wildlife communities subject to anthropogenic impact. Few studies capitalize on the powerful information available across entire communities, despite the fact that many surveys generate data for a range of species. In particular, a rapidly growing number of camera-trap surveys produce data on many species, both rare and common, which may not be fully utilized as attention is typically focused on one or a few target species (Rowcliffe & Carbone 2008; O'Brien et al. 2010). We have shown how such camera-trap data are well-suited to a multi-species hierarchical modeling framework, resulting in robust estimation of occurrence and detection probabilities across focal communities. We demonstrated that a community-level approach can facilitate inference on individual species while providing more comprehensive insight at a scale relevant to ecosystem-level management. Furthermore, we showed how data that may be readily available for many protected areas, such as patrol-based monitoring observations and remotely sensed vegetation indices, can be used to test hypotheses about relative influences on protected wildlife populations. This approach may be particularly valuable for guiding management efforts in developing nation parks that lack established research programs but face pressing conservation needs.

**Table 1.** Factors hypothesized to influence patterns of carnivore occurrence in Mole National Park (MNP), with the corresponding index used, predicted direction of effect (i.e., negative or positive influence on occurrence, or both), source of data, and range of values across sampled sites.

<b>Factor</b>	<b>Index</b>	<b>Predicted effect</b>	<b>Source</b>	<b>Range of values<sup>a</sup></b>
Hunting pressure	Relative frequency of poaching observations	-	MNP patrol system	0 - 0.20 obs./unit patrol effort
Human disturbance	Distance from park edge	-	GIS data layer	0 – 22.4 km
Patrol protection	Relative anti-poaching patrol effort	+	MNP patrol system	1.3 – 245.5 units of patrol effort
Prey biomass <sup>b</sup>	Relative biomass of potential prey	+	MNP patrol system (multi-season) and camera trap detections (seasonal).	0 – 1722.1 kg/ unit patrol effort 0 – 781.4 kg/trap-day
Small prey biomass <sup>b</sup>	Relative biomass of smaller prey (< 18kg)	+	MNP patrol system (multi-season) and camera trap detections (seasonal)	0 – 41.0 kg/unit patrol effort 0 – 69.0 kg/trap-day
Riverine forest	Distance from nearest corridor of riverine forest	+/-	GIS data layer derived from Landsat image (GWD 2005)	0.01 – 7.2 km
Vegetation productivity	NDVI <sup>c</sup>	+/-	MODIS/Terra (MOD13Q1, 250m, lpdaac.usgs.gov)	1882 – 7720 (seasonal) <sup>d</sup> 230,608 – 322,297 (integrated) <sup>d</sup>

<sup>a</sup> Range of values for sampled camera stations. Data were normalized and standardized prior to analysis.

<sup>b</sup> Prey species are listed in Appendix 4.1. Species average adult body masses were taken from Jones et al. (2009). Total prey biomass was expected to have a greater influence on larger carnivores given the relative dominance of larger prey species. See Methods for details on the calculation of different indices from patrol and camera-trap data.

<sup>c</sup> NDVI = Normalized Difference Vegetation Index

<sup>d</sup> See Methods for details on the seasonal and integrated measures of NDVI.

**Table 2.** Carnivore species detected during the camera trap survey in Mole National Park, Ghana (scientific names in Appendix 4.1). The proportion of 224 sampling sites at which they were detected reflects observation data (i.e., “naïve” estimate of occurrence), whereas species occurrence ( $\psi$ ) and detection ( $p$ ) probabilities are model-averaged estimates from the multi-species hierarchical occurrence mixture model (means and standard deviations from posterior probability distributions for species-specific parameters). Site covariates of occurrence are shown for cases where the posterior probability distribution from the full model for the corresponding species-specific coefficient indicated a potential effect (i.e., posterior mass not concentrated at 0; distributions are given in Appendix 4.4).

<b>Common name</b>	<b>Prop. sites</b>	$\psi$ <b>Mean (SD)</b>	$p$ <b>Mean (SD)</b>	<b>Covariate effects indicated*</b>
Spotted hyena	0.442	0.544 (0.050)	0.173 (0.039)	small prey(+), riverine(+),edge(-), hunting(-), seasonal NDVI(+)
Leopard	0.299	0.526 (0.077)	0.140 (0.038)	small prey(+), riverine(+), patrol(-), hunting(+)
White-tailed mongoose	0.259	0.292 (0.039)	0.119 (0.031)	small prey(+), riverine(-), seasonal NDVI(-), patrol(-)
Large-spotted genet	0.246	0.263 (0.037)	0.146 (0.041)	small prey(+), edge(+), hunting(+), seasonal NDVI(+)
African civet	0.098	0.189 (0.062)	0.123 (0.047)	small prey(+)
Caracal	0.054	0.096 (0.045)	0.100 (0.047)	riverine(-), small prey(+)
Marsh mongoose	0.049	0.095 (0.053)	0.124 (0.060)	small prey(+)
Gambian mongoose	0.018	0.075 (0.073)	0.094 (0.053)	small prey(+)
Side-striped jackal	0.013	0.072 (0.089)	0.087 (0.054)	small prey(+)

\* Direction of effect indicated as either positive (+) or negative (-) association of species occurrence probability with the particular covariate. For the different prey biomass covariates, only the strongest effect is indicated.

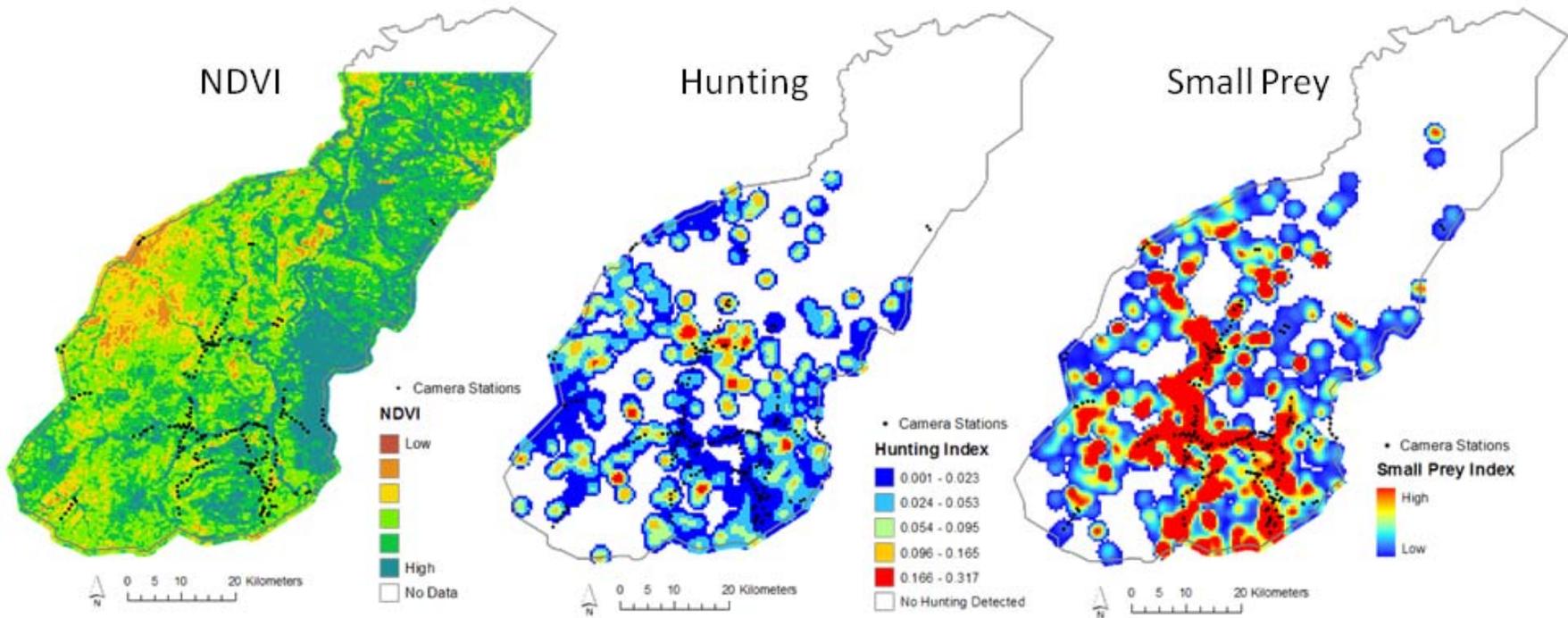
**Table 3.** Posterior probability summaries of hyper-parameters for mean community-level effects of hypothesized site covariates on occurrence ( $\alpha$  and  $\delta$  coefficients) and detection ( $\beta$  coefficients; see Methods for covariate details). Posterior mean, standard deviation (SD) and 95% credible interval (CI) were estimated from the full model, while the corresponding inclusion probability from model selection using a mixture model is also shown (representing the posterior probability of that covariate effect being included in the best model). Posterior distributions for these hyper-parameters as well as species-level parameters are given in Appendix 4.4.

Parameter (covariate)	Mean	SD	95% CI	Inclusion probability
$\alpha_1$ (patrol effort)	-0.19	0.29	-0.77, 0.39	0.219
$\alpha_2$ (hunting activity)	-0.04	0.32	-0.76, 0.56	0.015
$\alpha_3$ (seasonal NDVI)	0.04	0.25	-0.45, 0.51	0.028
$\alpha_4$ (integrated NDVI)	-0.08	0.20	-0.48, 0.32	0.001
$\alpha_5$ (edge distance)	-0.03	0.32	-0.67, 0.62	0.732
$\alpha_6$ (riverine distance)	-0.003	0.34	-0.69, 0.72	1.0
$\alpha_7$ (prey biomass, long-term)	0.13	0.29	-0.47, 0.65	*
$\alpha_8$ (small prey biomass, long-term)	0.33	0.26	-0.20, 0.81	*
$\alpha_9$ (prey biomass, short-term)	-0.26	0.31	-0.92, 0.33	0.010
$\alpha_{10}$ (small prey biomass, short-term)	1.18	0.40	0.51, 2.10	1.0
$\delta$ (spatial autocovariate)	0.76	1.12	-1.36, 3.28	0
$\beta_1$ (road)	-0.12	0.43	-1.01, 0.69	0.910
$\beta_2$ (paired stations)	0.10	0.27	-0.43, 0.63	0.011
$\beta_3$ (set team)	-0.93	0.50	-2.08, -0.03	0.976
$\beta_4$ (hunting activity)	-0.01	0.14	-0.27, 0.26	0.001
$\beta_5$ (edge distance)	-0.16	0.29	-0.79, 0.34	0.479
$\beta_6$ (season)	0.22	0.32	-0.42, 0.83	0.038

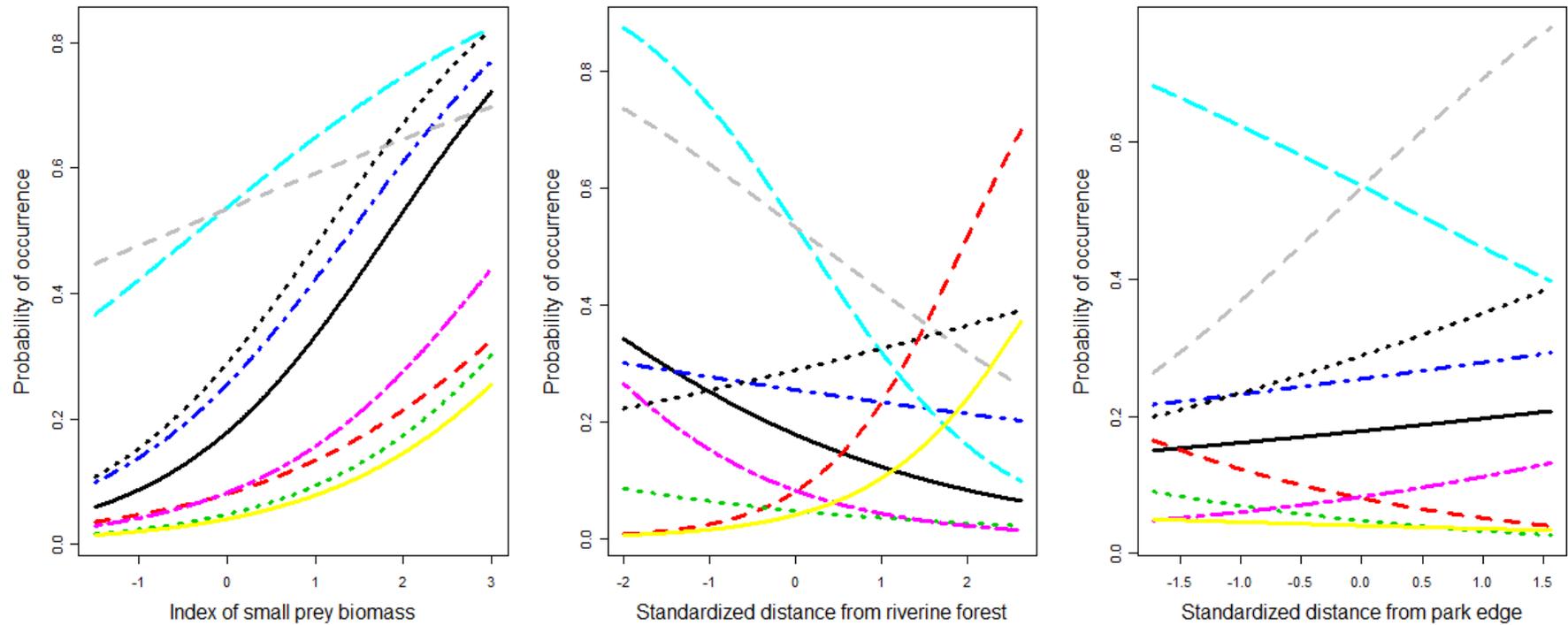
\* The two prey indices derived from patrol data were not included in the final mixture model as they were considered redundant to (but less informative than) the comparable short-term prey indices derived from camera trap data (based on results of the full model and a preliminary mixture model).

**Table 4.** Posterior model probabilities for the top 11 models that had 90% of the posterior support across all candidate models for community-level effects on carnivore occurrence ( $\psi$ ) and detection ( $p$ ), as estimated from the mixture modeling approach to model selection (53 additional models appeared in the posterior sample but all with probabilities  $< 0.01$ ).

<b>Model</b>	<b>Poster probability</b>
$\psi(\text{edge} + \text{river} + \text{small prey}) p(\text{road} + \text{team})$	0.335
$\psi(\text{river} + \text{small prey}) p(\text{road} + \text{team} + \text{edge})$	0.139
$\psi(\text{edge} + \text{river} + \text{small prey}) p(\text{road} + \text{team} + \text{edge})$	0.124
$\psi(\text{patrol} + \text{edge} + \text{river} + \text{small prey}) p(\text{road} + \text{team} + \text{edge})$	0.103
$\psi(\text{patrol} + \text{edge} + \text{river} + \text{small prey}) p(\text{road} + \text{team})$	0.043
$\psi(\text{river} + \text{small prey}) p(\text{road} + \text{team})$	0.040
$\psi(\text{edge} + \text{river} + \text{small prey}) p(\text{team})$	0.032
$\psi(\text{patrol} + \text{river} + \text{small prey}) p(\text{road} + \text{team} + \text{edge})$	0.030
$\psi(\text{river} + \text{small prey}) p(\text{road} + \text{edge} + \text{season})$	0.022
$\psi(\text{patrol} + \text{edge} + \text{river} + \text{small prey}) p(\text{team})$	0.018
$\psi(\text{edge} + \text{river} + \text{small prey}) p(\text{team} + \text{edge})$	0.016



**Figure 1.** Mole National Park, Ghana, showing the location of 224 camera-trap stations from which occurrence data on carnivores (and prey) were obtained, as well as three example covariate surfaces. “NDVI” (left) is the normalized difference vegetation index (from MODIS/Terra sensor) summed over the study period (i.e., integrated NDVI, Oct. 2006 – Jan. 2009; we did not obtain data for the white area in the north); “Hunting” (middle) is an index of illegal hunting activity detected by park law enforcement patrols (observations per unit patrol effort); and “Small Prey” (right) is a patrol-based, multi-season index of biomass for prey species weighing less than 18 kg (standardized by patrol effort). For the hunting and small prey surfaces, no observations were made in the white areas within the park boundary, which generally reflects low or no patrol sampling effort (see Chapter 2: Fig. 1).



**Figure 2.** Model-predicted carnivore responses (i.e., marginal probabilities of occurrence) relative to variation in the three site covariates included in the best occurrence model: small prey biomass, distance from riverine forest, and distance from park edge (Table 4). Species are: African civet (solid black), caracal (dashed red), Gambian mongoose (dotted green), large-spotted genet (dot-dash blue), leopard (dashed light blue), marsh mongoose (dot-dash purple), side-striped jackal (solid yellow), spotted hyena (dashed grey), white-tailed mongoose (dotted black; scientific names and details of model selection are given in the text).

## **Supporting Information for Chapter 4**

**Appendix 4.1:** Scientific names and mean body mass for all species, with relative abundance for prey species detected by patrol and camera-trap surveys in Mole National Park, Ghana (2006-2009).

**Appendix 4.2:** Further detail on the assessment of spatial autocorrelation in carnivore occurrence patterns.

**Appendix 4.3:** Example segments of WinBUGS model code for the hierarchical multi-species carnivore occurrence model

**Appendix 4.4:** Posterior distributions for community-level hyperparameters and species-level parameters from the full multi-species occurrence model.

**Appendix 4.1:** Scientific names and mean body mass for all species, with relative abundance for prey species detected by patrol and camera-trap surveys in Mole National Park, Ghana (2006-2009).

Scientific name	Common name	Body mass (kg)	Camera detections	Patrol count
Potential prey species				
<i>Syncerus caffer</i>	African buffalo	592.7	99	1692
<i>Hippotragus equinus</i>	Roan antelope	264.2	73	1557
<i>Kobus ellipsiprymnus</i>	Waterbuck	204.4	144	6155
<i>Alcelaphus buselaphus</i>	Hartebeest	160.9	253	5542
<i>Phacochoerus africanus</i>	Warthog	82.5	278	4716
<i>Kobus kob</i>	Kob	80.0	553	19621
<i>Orycteropus afer</i>	Aardvark	56.2	86	0
<i>Tragelaphus scriptus</i>	Bushbuck	43.3	345	2071
<i>Papio anubis</i>	Olive baboon	17.7	467	9589
<i>Ourebia ourebi</i>	Oribi	17.2	3	279
<i>Sylvicapra grimmia</i>	Grey Duiker	15.6	45	366
<i>Hystrix cristata</i>	Crested Porcupine	13.4	135	0
<i>Cephalophus rufilatus</i>	Red-flanked Duiker	12.1	64	217
<i>Erythrocebus patas</i>	Patas Monkey	8.0	66	2372
<i>Colobus vellerosus</i>	Geoffroy's black and white colobus	7.7	0	70
<i>Thryonomys swinderianus</i>	Marsh cane rat (grasscutter)	3.8	23	0
<i>Chlorocebus sabaesus</i>	Green Monkey	3.7	171	3580
<i>Lepus saxatilis</i>	Scrub Hare	2.6	52	0
<i>Cricetomys gambianus</i>	Giant Rat	1.3	2	0
<i>Xerus erythropus</i>	Striped Ground Squirrel	0.6	6	0
<i>Galago senegalensis</i>	Senegal Galago	0.2	3	0
<i>Bucorvus abyssinicus</i>	Abyssinian Ground Hornbill	4.0	30	0
<i>Neotis denhami</i>	Denham's Bustard	4.8	1	0
<i>Lissotis melanogaster</i>	Black-bellied Bustard	1.2	2	0
<i>Streptopelia spp/Turtur abyssinicus</i>	Dove species	0.1	32	0
<i>Francolinus bicalcaratus</i>	Double-spurred Francolin	0.4	41	0
<i>Numida meleagris</i>	Helmeted Guineafowl	1.3	168	0
<i>Ptilopachus petrosus</i>	Stone Partridge	0.2	28	0

<b>Scientific name</b>	<b>Common name</b>	<b>Body mass (kg)</b>
Carnivore species		
<i>Crocuta crocuta</i>	Spotted hyena	63.4
<i>Ichneumia albicauda</i>	White-tailed mongoose	3.6
<i>Panthera pardus</i>	Leopard	52.4
<i>Genetta pardina</i>	Large-spotted genet	2.0
<i>Civettictis civetta</i>	African civet	12.1
<i>Atilax paludinosus</i>	Marsh mongoose	3.6
<i>Caracal caracal</i>	Caracal	12.0
<i>Mungos gambianus</i>	Gambian mongoose	1.6
<i>Canis adustus</i>	Side-striped jackal	10.4

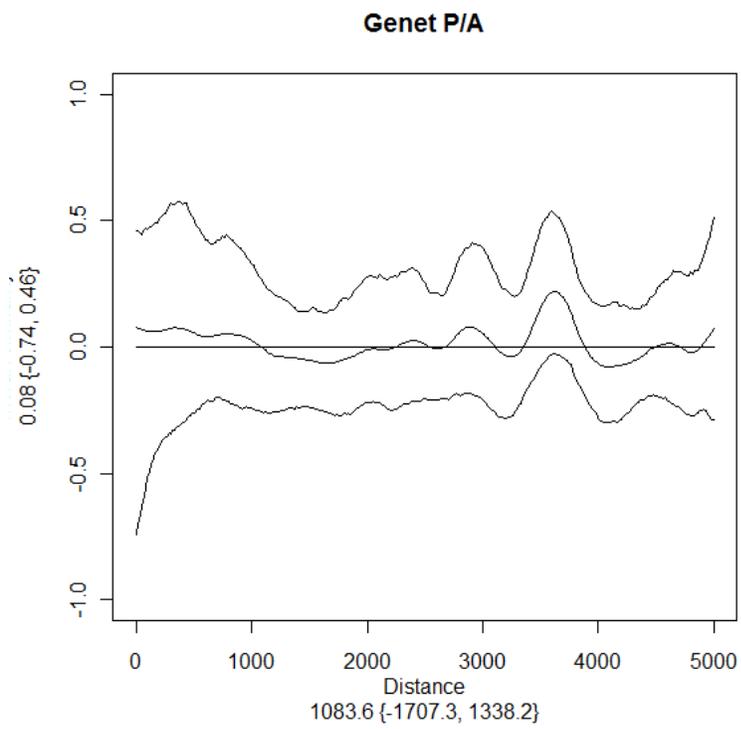
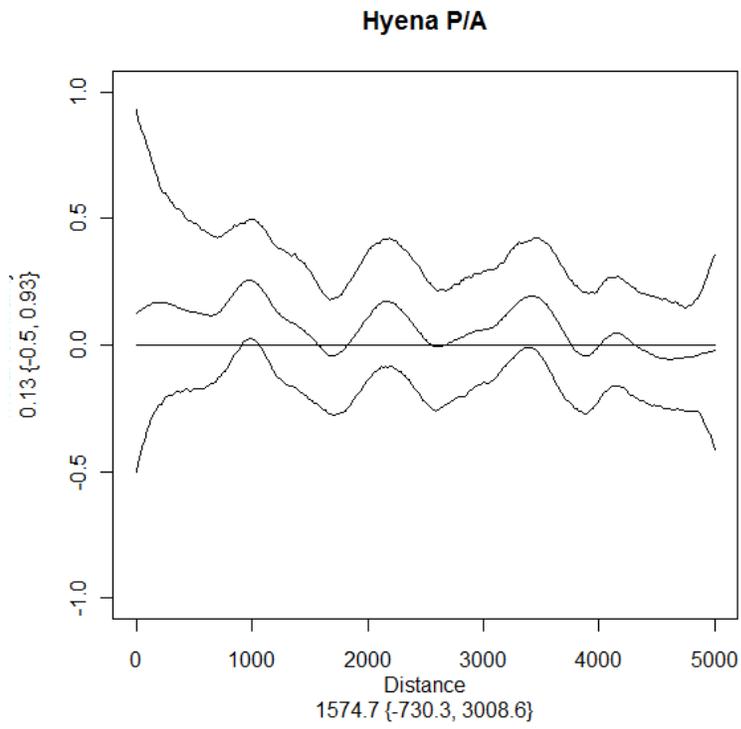
**Appendix 4.2:** Further detail on the assessment of spatial autocorrelation in carnivore occurrence patterns.

### Part I: Potential for spatial autocorrelation

We aimed to achieve spatial independence in our sampling design by spacing camera stations at intervals of approximately 1 km. Nevertheless, for logistical reasons some sites were within 1 km of each other (including a small number of sites that were re-sampled with different stations in different years). Furthermore, endogenous ecological processes such as ranging or dispersal behavior could be expected to span across distances greater than 1 km for most carnivore species in MNP. For instance, estimated home range sizes average about 40 km<sup>2</sup> across the nine species detected (Chapter 3), indicating that one individual of a particular species could use habitats across several adjacent sites, thereby reducing the likelihood that nearby sites were independent samples of species occurrence.

On the basis of two types of preliminary evidence, we felt that including spatial autocorrelation in our model was warranted. Firstly, as part of a concurrent mark-recapture analysis of population density, we calculated that the mean maximum distance moved by 15 spotted hyena individuals (identified by spotting patterns) was approximately 5 km, with similar results for individually identified leopards. This suggested that the range of individual movements for the period over which a site was sampled could have encompassed several adjacent stations (at least for such larger species). Secondly, preliminary examination of species detections (i.e., raw observations of “presence-absence” at camera sampling sites) using spline correlograms (Bjørnstad & Falck 2001) and Moran’s I correlograms (Dormann et al. 2007) suggested some evidence of spatial autocorrelation. For example, the two plots below show spline correlograms (with outer lines giving 95% pointwise bootstrap confidence intervals) for detections of spotted hyena and large-spotted genet as a function of distance between camera stations (in meters. Correlograms implemented in the R package *ncf*). The x-intercept is interpreted as the distance at which site occurrences are no more similar than expected by chance for the sample area. There is thus an indication of positive spatial autocorrelation over short distances, although it may not be significant as 95% CIs overlap 0.

Spline correlograms for spotted hyena and large spotted genet detections at camera stations (i.e., presence-absence or "P/A"; plot details in previous paragraph):



## Part II: Neighborhood size

We initially defined four different sizes of spatial neighborhood as all stations within 1, 3, 5, or 10 km of a focal station, and compared the fit of multi-species models with each of the corresponding autocovariate terms as the only covariate (based on estimated deviance returned from R2WinBUGS). These distances represented neighborhood sizes of approximately 3, 28, 79 and 314 km<sup>2</sup>, respectively, providing a gradient comparable to the range of home range sizes (and thus expected individual movements) for the nine carnivore species. Models with autocovariates based on a 5- and 10-km radii neighborhoods had similar estimated deviances which were substantially lower than those with 1- and 3-km radii neighborhoods. We used the 5-km radius (79 km<sup>2</sup>) neighborhood for our autocovariate specification in subsequent modeling as we felt it represented a reasonable compromise for the varying home ranges sizes across the different species (see Chapter 3). Further work could attempt a more systematic assessment of the effect of neighborhood size on the interpretation of spatial autocorrelation in this system.

## Part III: Form of the modeled spatial autocovariate

Specification of the autocovariate for our hierarchical multi-species occurrence model is illustrated in the following segment of R code (for a 5-km radius spatial neighborhood):

```
# load library spdep for neighborhood calculations and define X-Y
coordinates
library(spdep)
coords <- as.matrix(cbind(site.cov$east/1000,site.cov$north/1000))
# define neighbors at threshold distance = n.dist (in kilometers, UTM)
n.dist <- 5
nb.5km <- dnearneigh(coords,0,n.dist)
# calculate vector nummn[j] specifying the number of neighbors of site j
nummn <- rep(0,J)
for (j in 1:J) nummn[j] <- length(nb.5km[[j]])
# calculate distances for the neighbors
nb.5km.d <- nbdists(nb.5km, coords)

# Construct matrix NN[j,g] which identifies the G neighbors of site j
NN <- matrix(rep(0,J*max(nummn)),nrow=J)
for (j in 1:J) {
  NN[j,] <- append(as.vector(nb.5km[[j]]),rep(NA,max(nummn)-nummn[j]))
}

# Construct matrix D[j,g] specifying the distance between site j and ...
# ... neighboring site g (with NAs filled in as needed)
D <- matrix(rep(0,J*max(nummn)),nrow=J)
for (j in 1:J) {
  D[j,] <- append(as.vector(nb.5km.d[[j]]),rep(NA,max(nummn)-nummn[j]))
}
```

**Appendix 4.3:** Example segments of WinBUGS model code for the hierarchical multi-species carnivore occurrence model. A hash mark (#) precedes annotation remarks. Refer to Methods for symbol equations and parameter definitions.

```
# specify prior probabilities
# include prior on covariate inclusion parameters for mixture model, w[c] ~
dbern(0.5)
psi.mean ~ dunif(0,1)
alpha <- log(psi.mean) - log(1-psi.mean)

mu.delta ~ dunif(-5,5)
sigma.delta ~ dunif(0,5)
tau.delta <- (1/(sigma.delta*sigma.delta))

mu.a1 ~ dunif(-5,5)
tau.a1 ~ dgamma(0.1,0.1)
# ... same specification for all 10 occurrence covariate coefficients
mu.b1 ~ dunif(-5,5)
tau.b1 ~ dgamma(0.1,0.1)
# ... same specification for all 6 detection covariate coefficients

p.mean ~ dunif(0,1)
beta <- log(p.mean) - log(1-p.mean)

sigma.u ~ dunif(0,10)
sigma.v ~ dunif(0,10)
tau.u <- pow(sigma.u,-2)
tau.v <- pow(sigma.v,-2)
rho ~ dunif(-1,1)
var.eta <- tau.v/(1.-pow(rho,2))

# species-level parameters for n species. Note truncation trick for MCMC convergence

for (i in 1:n) {
  phi[i] ~ dnorm(alpha, tau.u)I(-10,10)
  mu.eta[i] <- beta + (rho*sigma.v/sigma.u)*(phi[i] - alpha)
  eta[i] ~ dnorm(mu.eta[i], var.eta)I(-10,10)
  delta[i] ~ dnorm(mu.delta, tau.delta)I(-10,10)
  al[i] ~ dnorm(mu.a1, tau.a1)I(-5,5)
# ... same basic specification for all 10 occurrence covariate coefficients
```

```

    b1[i] ~ dnorm(mu.b1, tau.b1)I(-5,5)
# ... same basic specification for all 6 detection covariate coefficients

# specify autocovariate and occurrence and detection functions across J sites
    # note that inclusion parameters w[c] would be included on regression
    coefficients ...
    # ... for mixture model selection approach, e.g., w[1]*a1[i]*patrol[j]

for (j in 1:J) {

    x[i,j,1] <- 0
    for (g in 1:numnn[j]) {
        x[i,j,g+1] <- x[i,j,g] + Z[i,(NN[j,g])]/D[j,g]
    }

    lpsi[i,j] <- phi[i] + a1[i]*patrol[j] + a2[i]*hunting[j] +
        a3[i]*ndvi1[j] + a4[i]*ndvi2[j] + a5[i]*edge[j] + a6[i]*river[j] +
a7[i]*prey1[j] +
        a8[i]*smallprey1[j] + a9[i]*prey2[j] + a10[i]*smallprey2[j] +
        delta[i]*(x[i,j,numnn[j]+1]/numnn[j])

    psi[i,j] <- 1/(1+exp(-lpsi[i,j]))

    Z[i,j] ~ dbern(psi[i,j])

    lp[i,j] <- eta[i] + b1[i]*road[j] + b2[i]*paired[j] + b3[i]*team[j] +
b4[i]*hunting[j]
        + b5[i]*edge[j] + b6[i]*season[j]

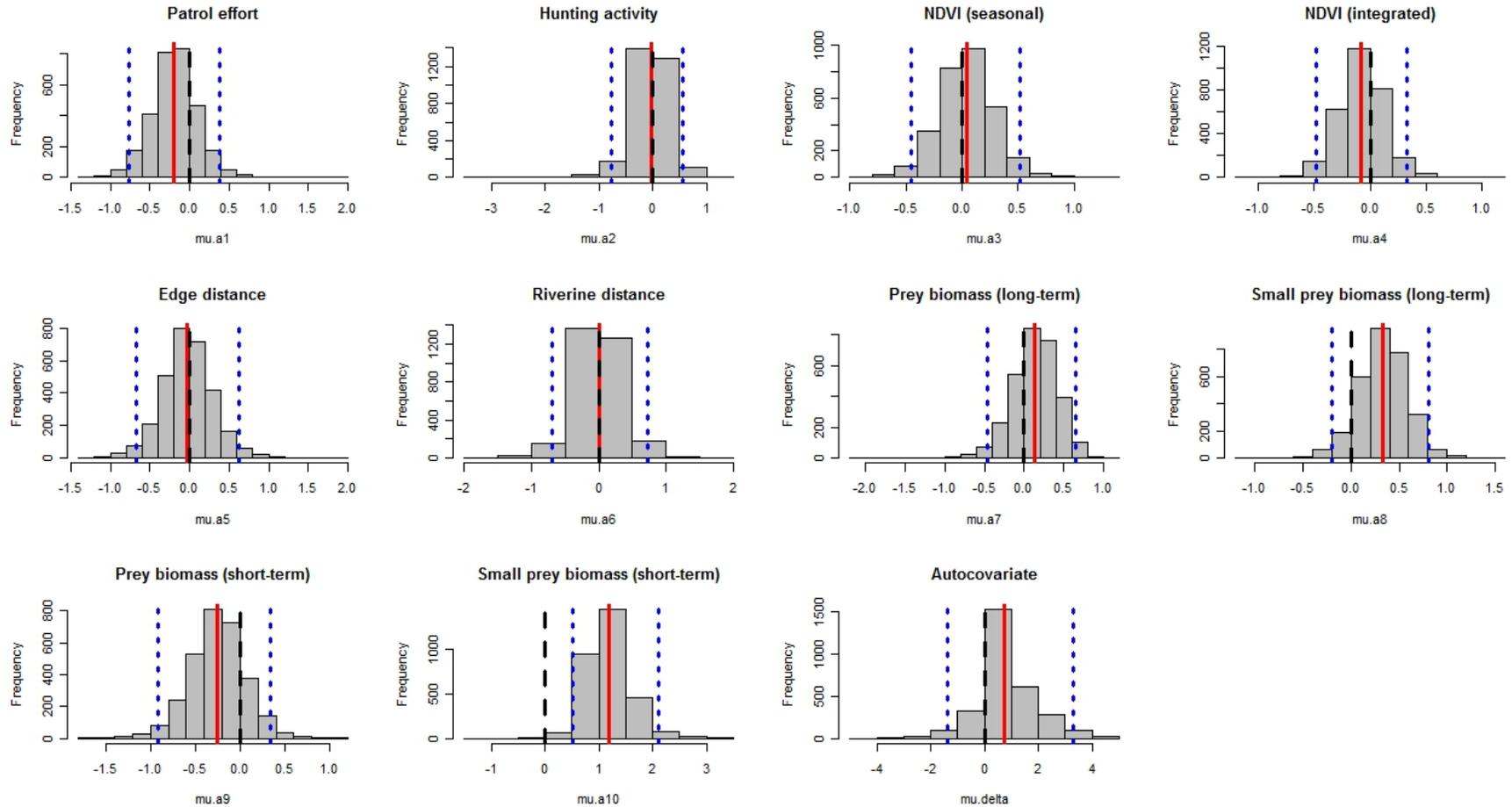
    p[i,j] <- 1/(1+exp(-lp[i,j]))

    mu.p[i,j] <- p[i,j]*Z[i,j]

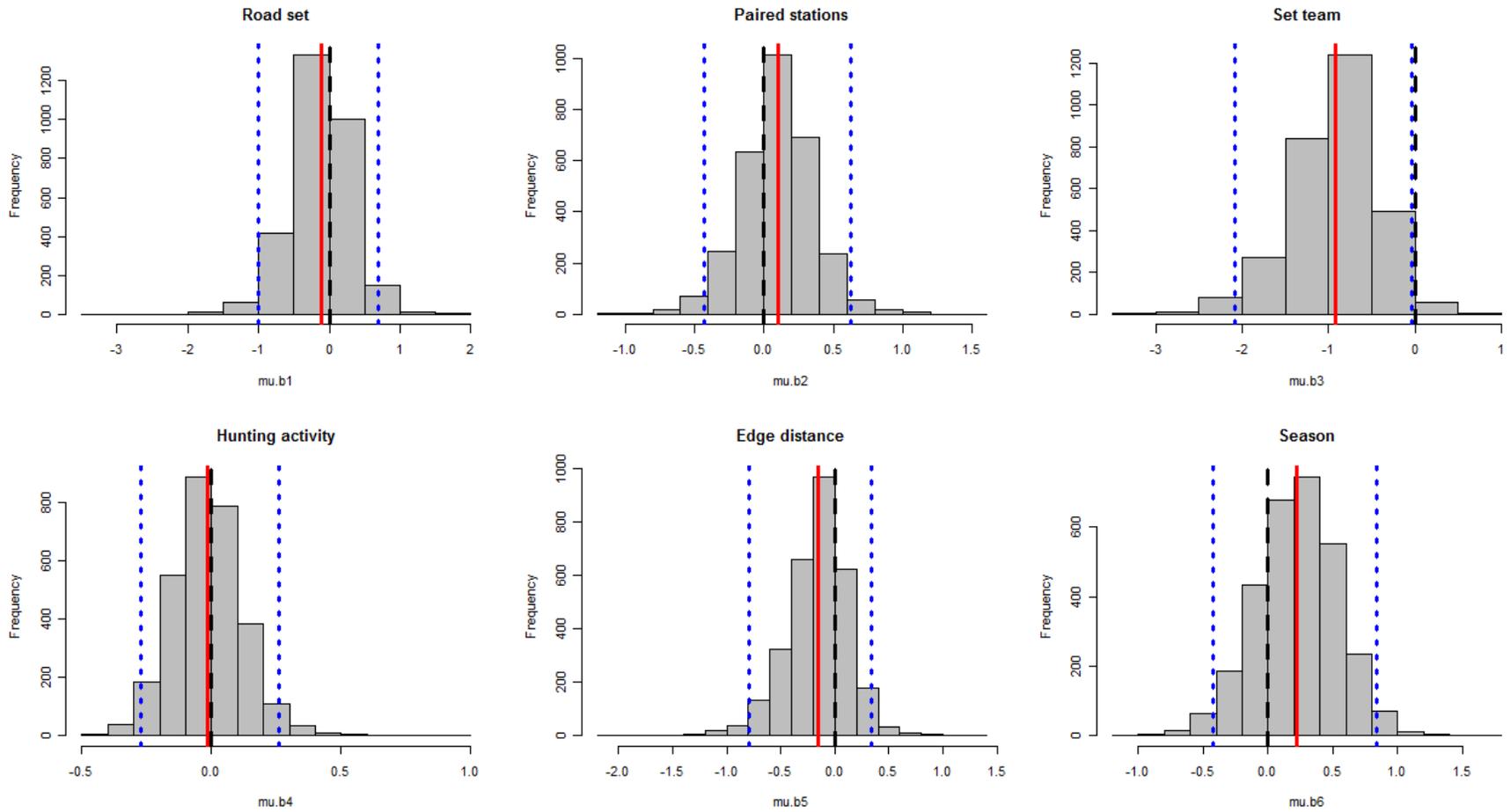
    Y[i,j] ~ dbin(mu.p[i,j], K[j])
}
}
# calculate site-specific estimate of species richness
for (j in 1:J) {
    Nsite[j] <- sum(Z[1:n,j])
}}

```

**Appendix 4.4:** Posterior distributions from the full model for community-level hyperparameters on occurrence and detection probabilities, and species-level parameters on occurrence probability.

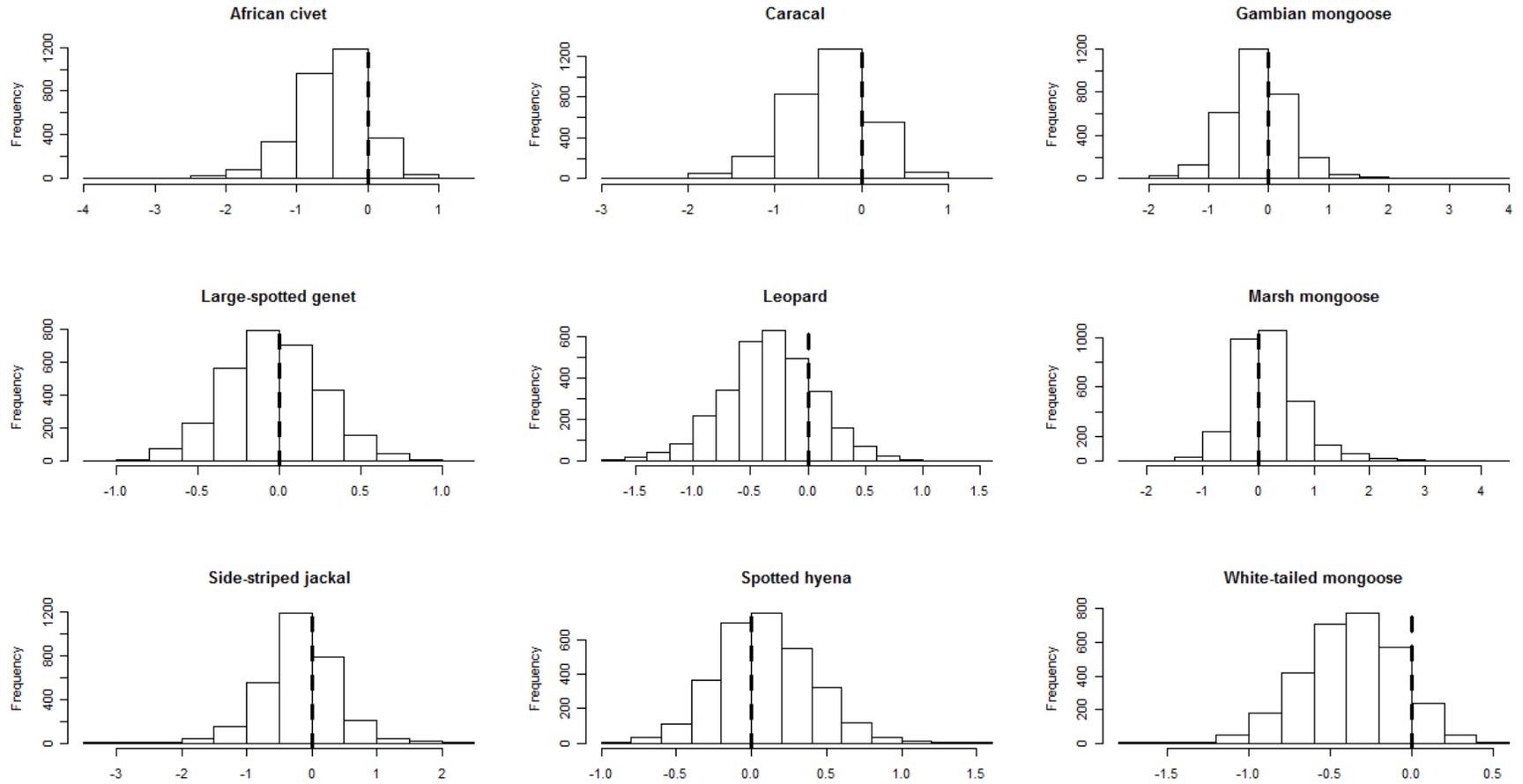


Posterior probability distributions for mean **community-level hyperparameters corresponding to site-level covariates on occurrence** probability. Vertical lines indicate 0 (i.e., no effect; black long-dash), the hyperparameter mean (red solid) and the 95% credible interval (blue short-dash).

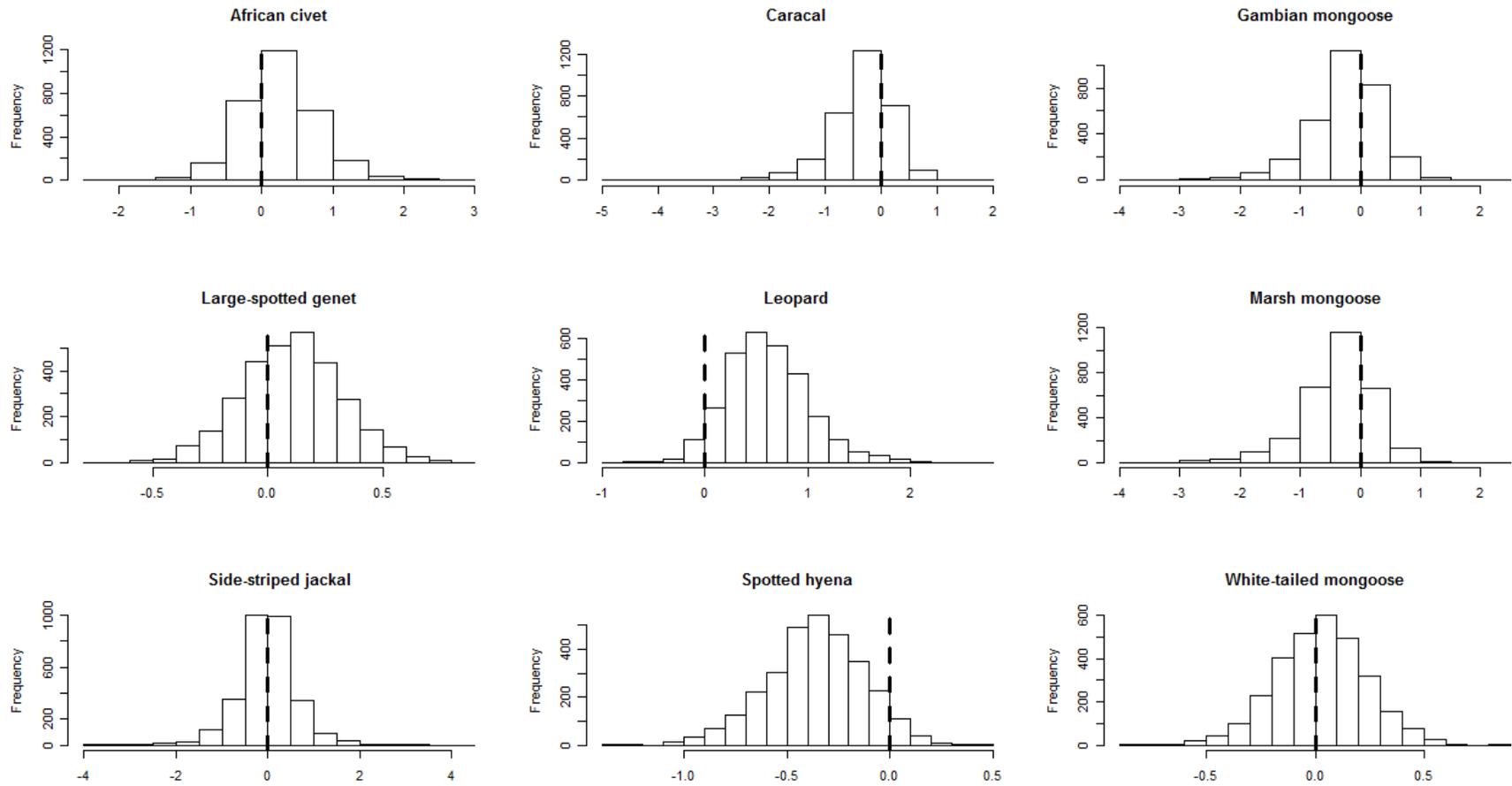


Posterior probability distributions for mean **community-level hyperparameters corresponding to site-level covariates on detection probability**. Vertical lines indicate 0 (i.e., no effect; black long-dash), the hyperparameter mean (red solid) and the 95% credible interval (blue short-dash).

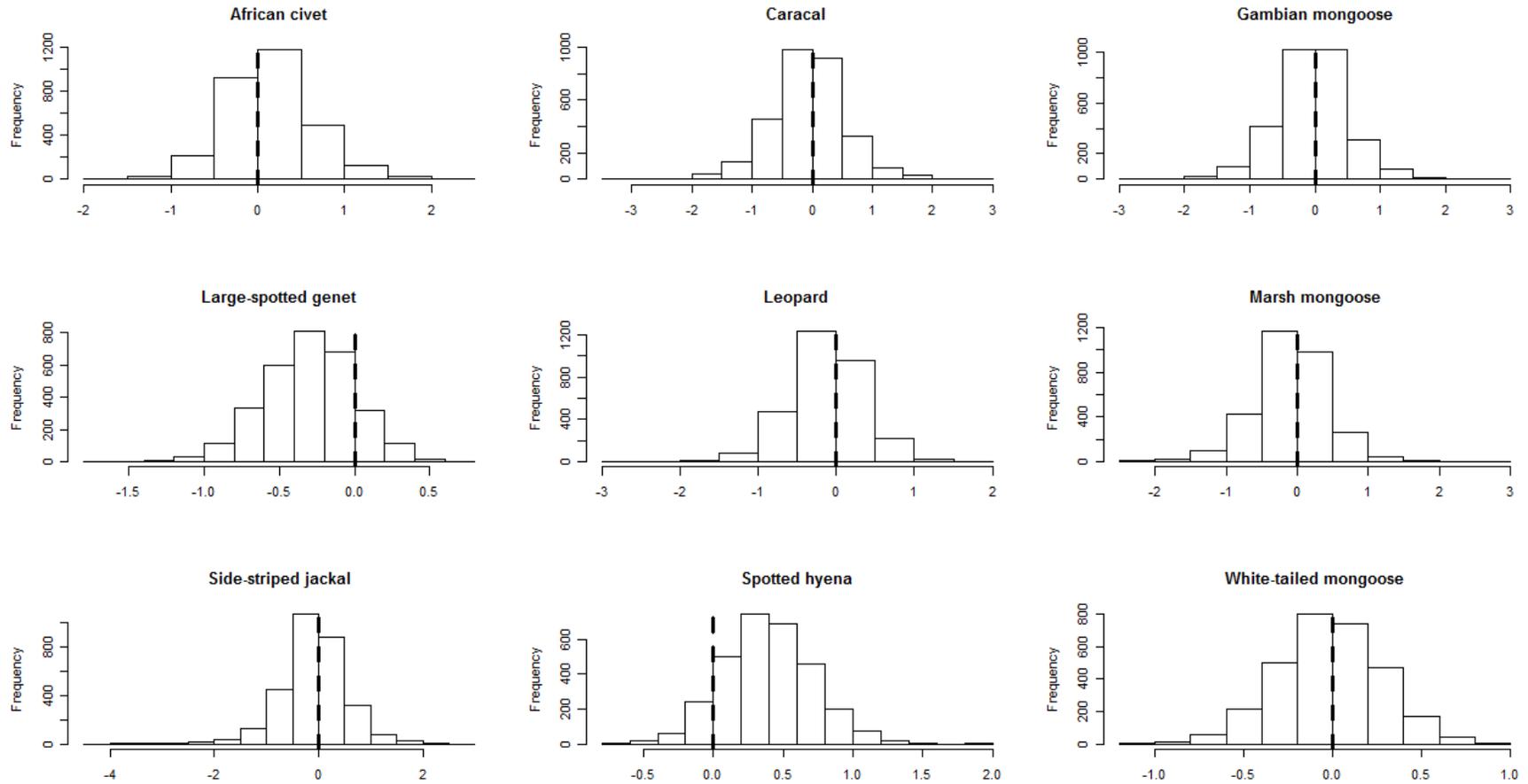
Posterior probability distributions from full model for species-level occurrence coefficients on effect of **patrol effort** ( $\alpha_{1i}$ ; vertical line at 0, i.e., no effect)



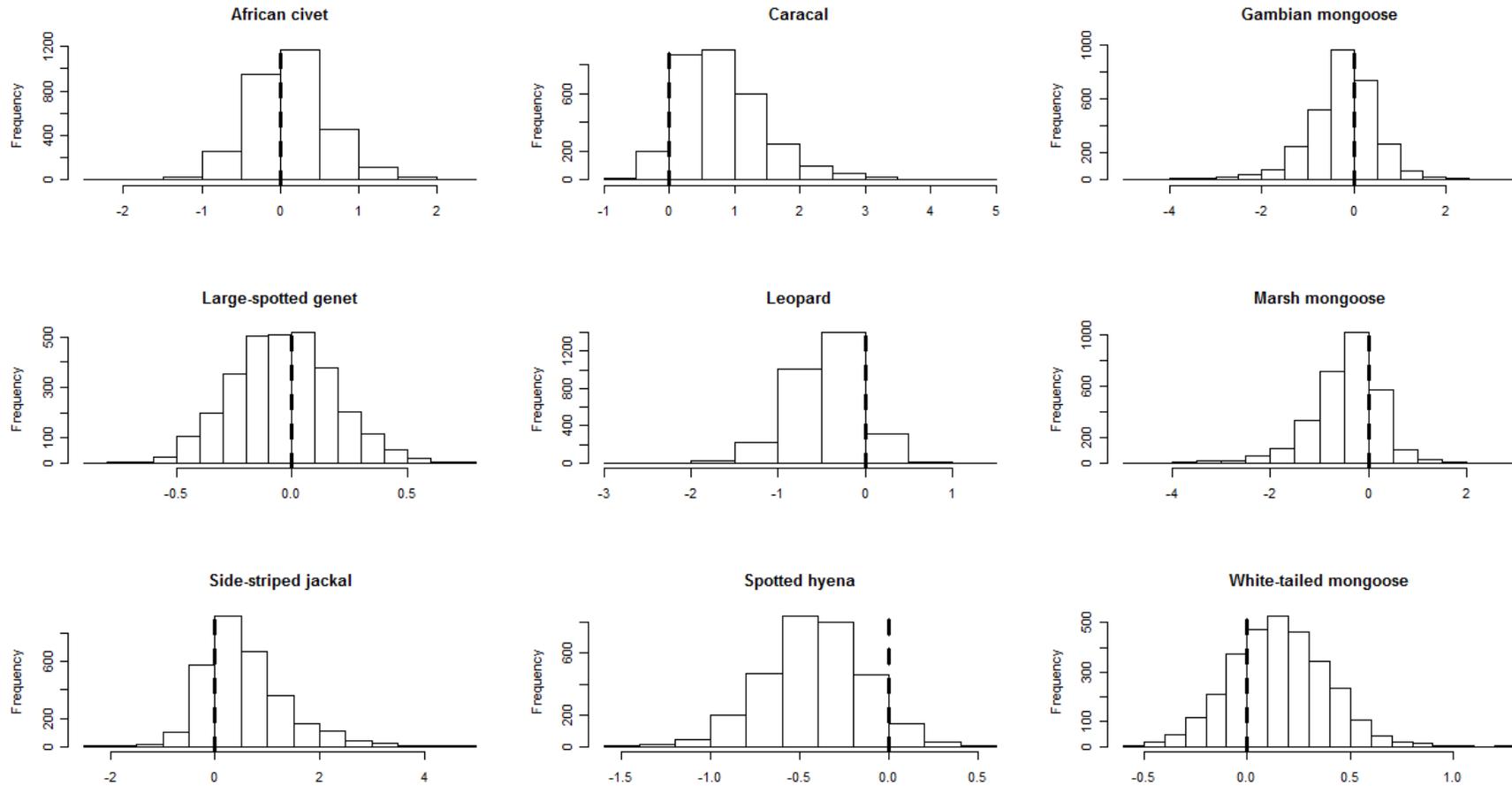
Posterior probability distributions from full model for species-level occurrence coefficients on effect of **hunting activity** ( $\alpha_{2i}$ )



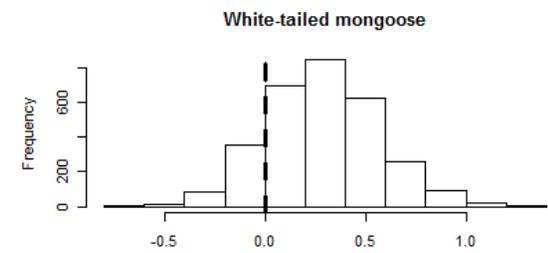
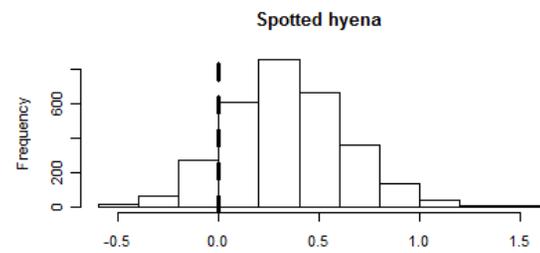
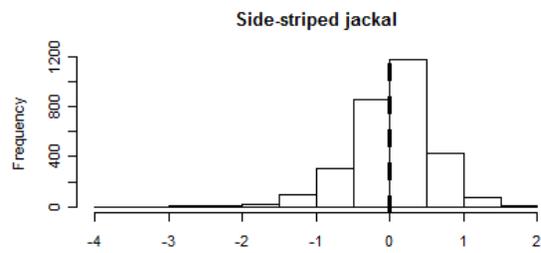
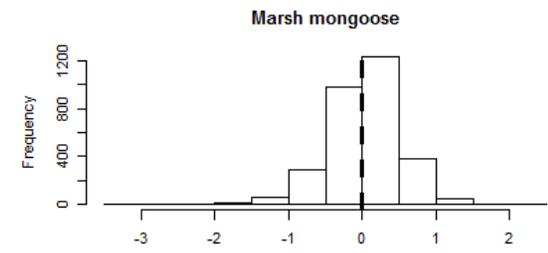
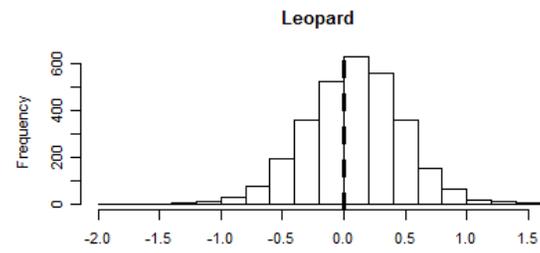
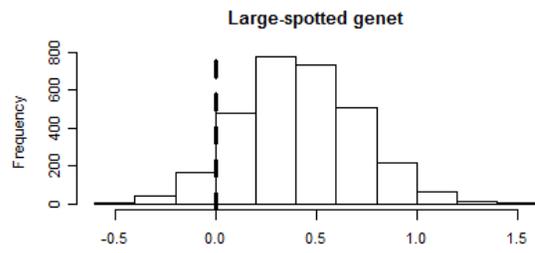
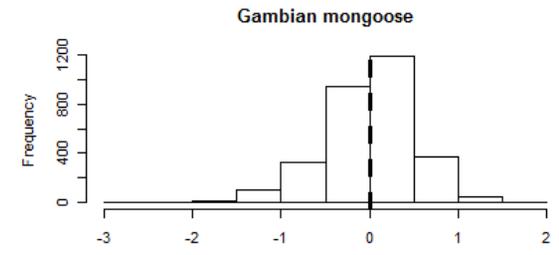
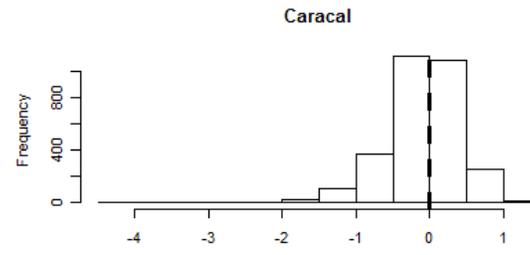
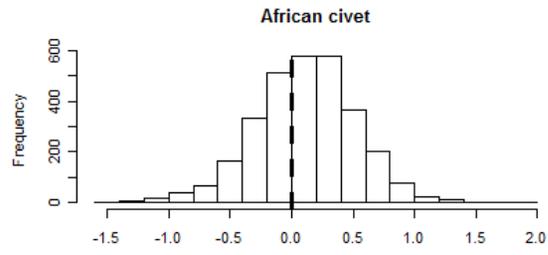
Posterior probability distributions from full model for species-level occurrence coefficients on effect of **distance from park edge** ( $\alpha_{5i}$ )



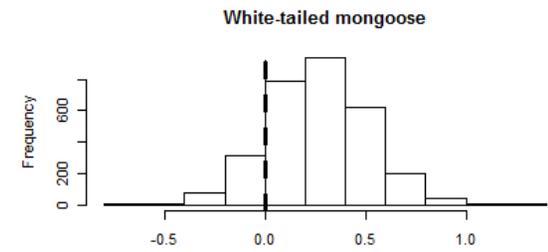
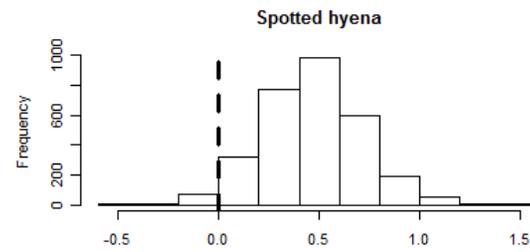
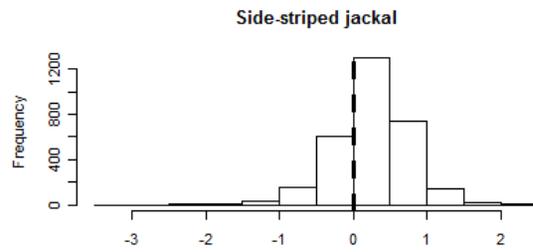
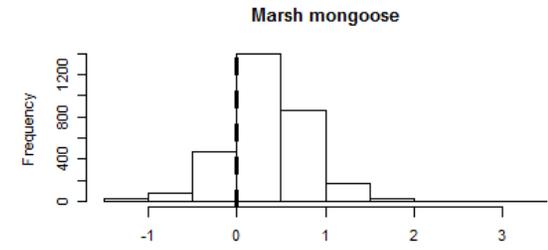
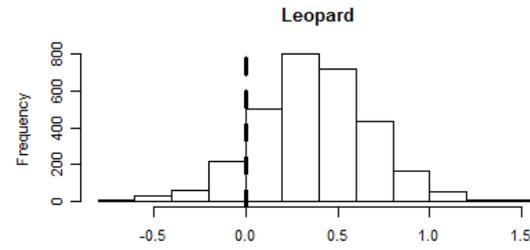
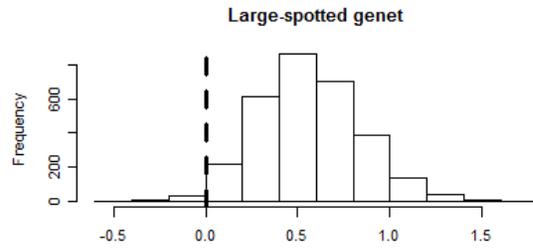
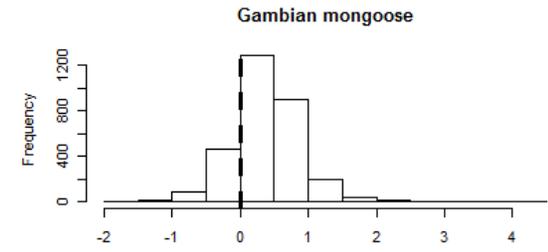
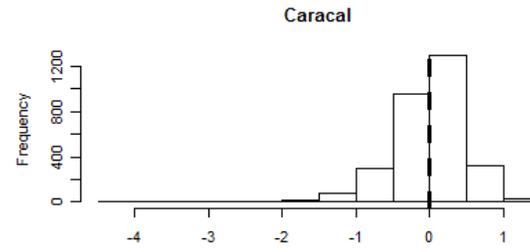
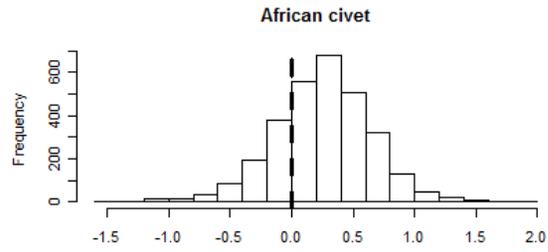
Posterior probability distributions from full model for species-level occurrence coefficients on effect of **distance from riverine forest** ( $\alpha_i$ )



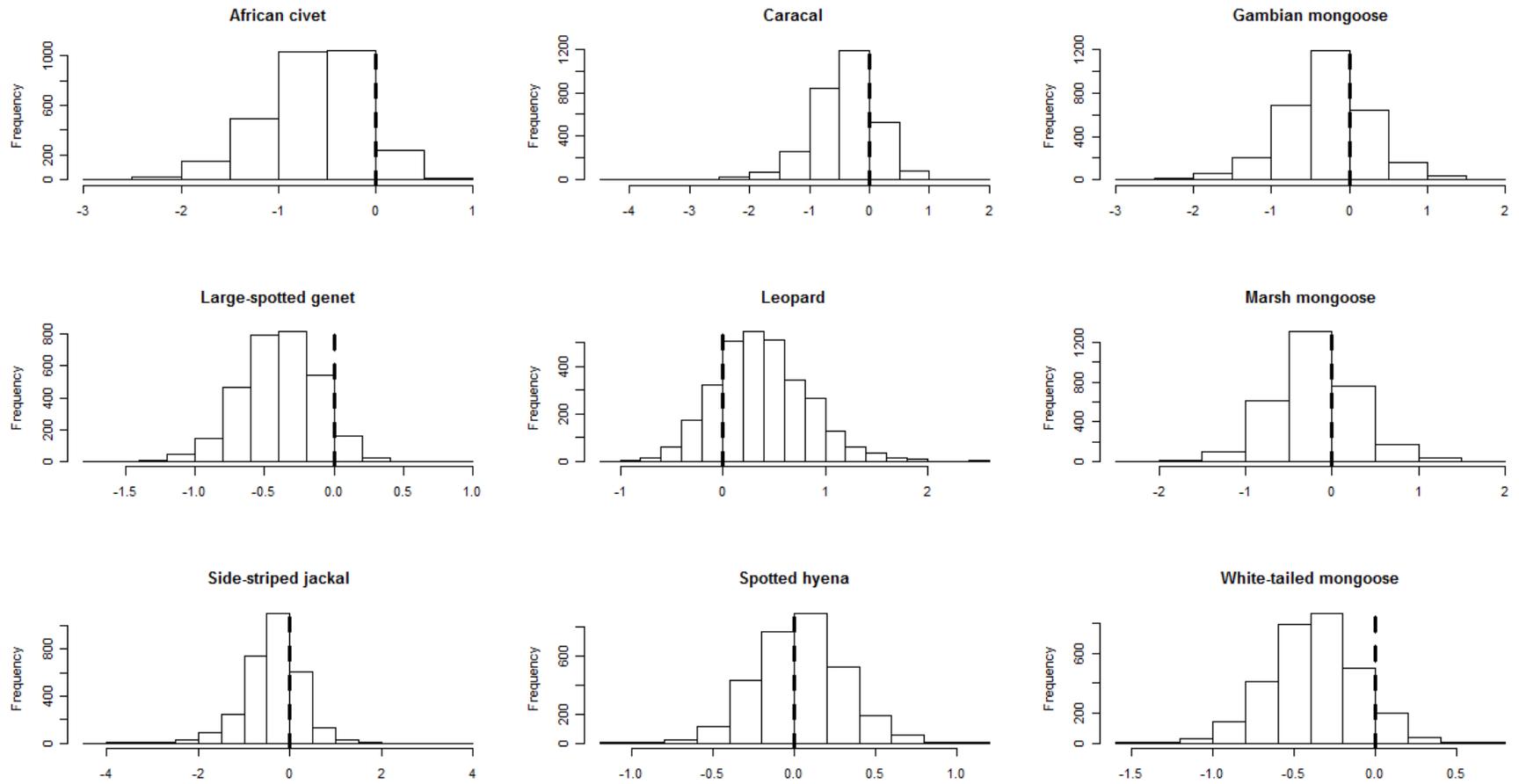
Posterior probability distributions from full model for species-level occurrence coefficients on effect of **longer-term prey biomass** ( $\alpha_i$ )



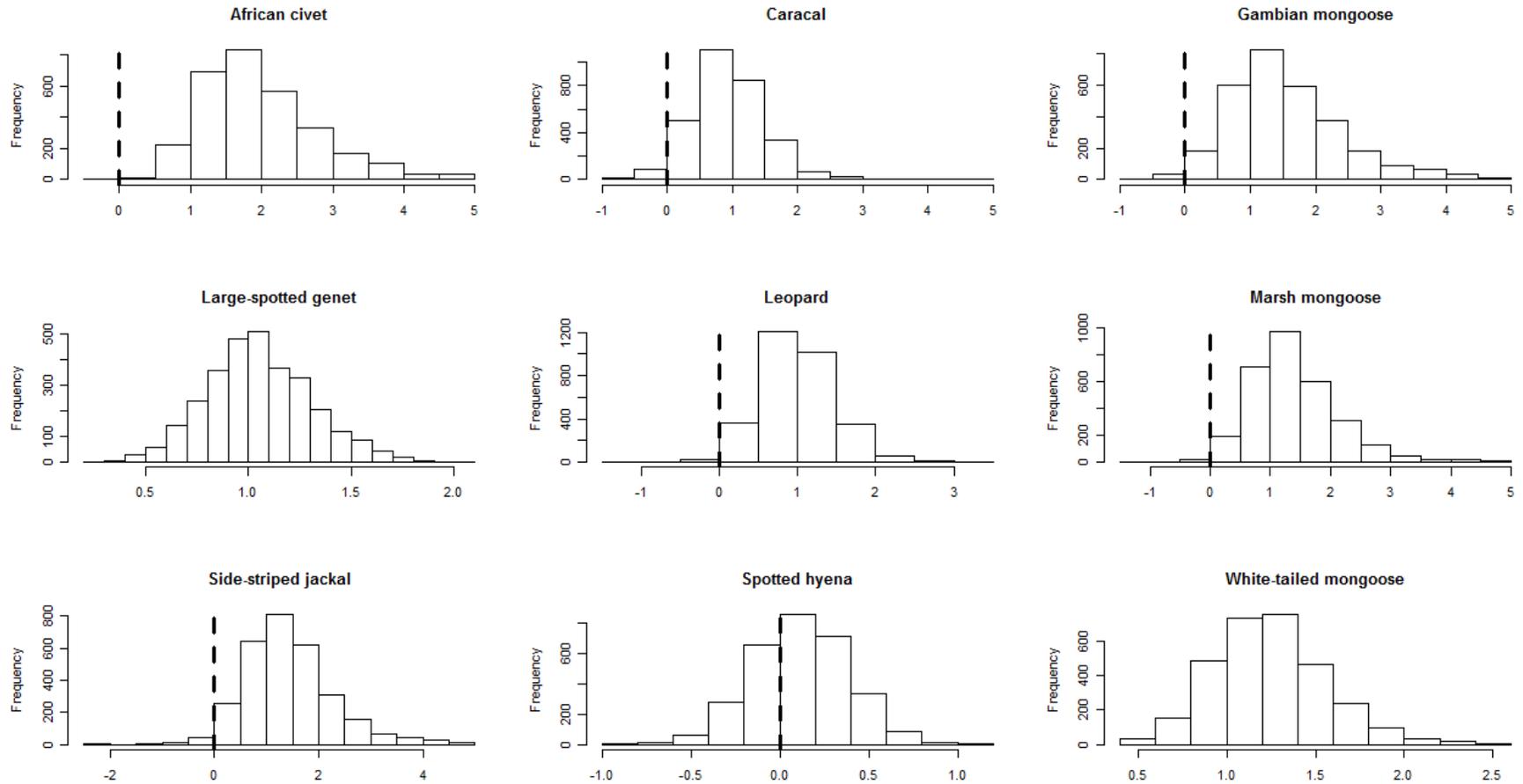
Posterior probability distributions from full model for species-level coefficients on effect of **longer-term small prey biomass** ( $\alpha\delta_i$ )



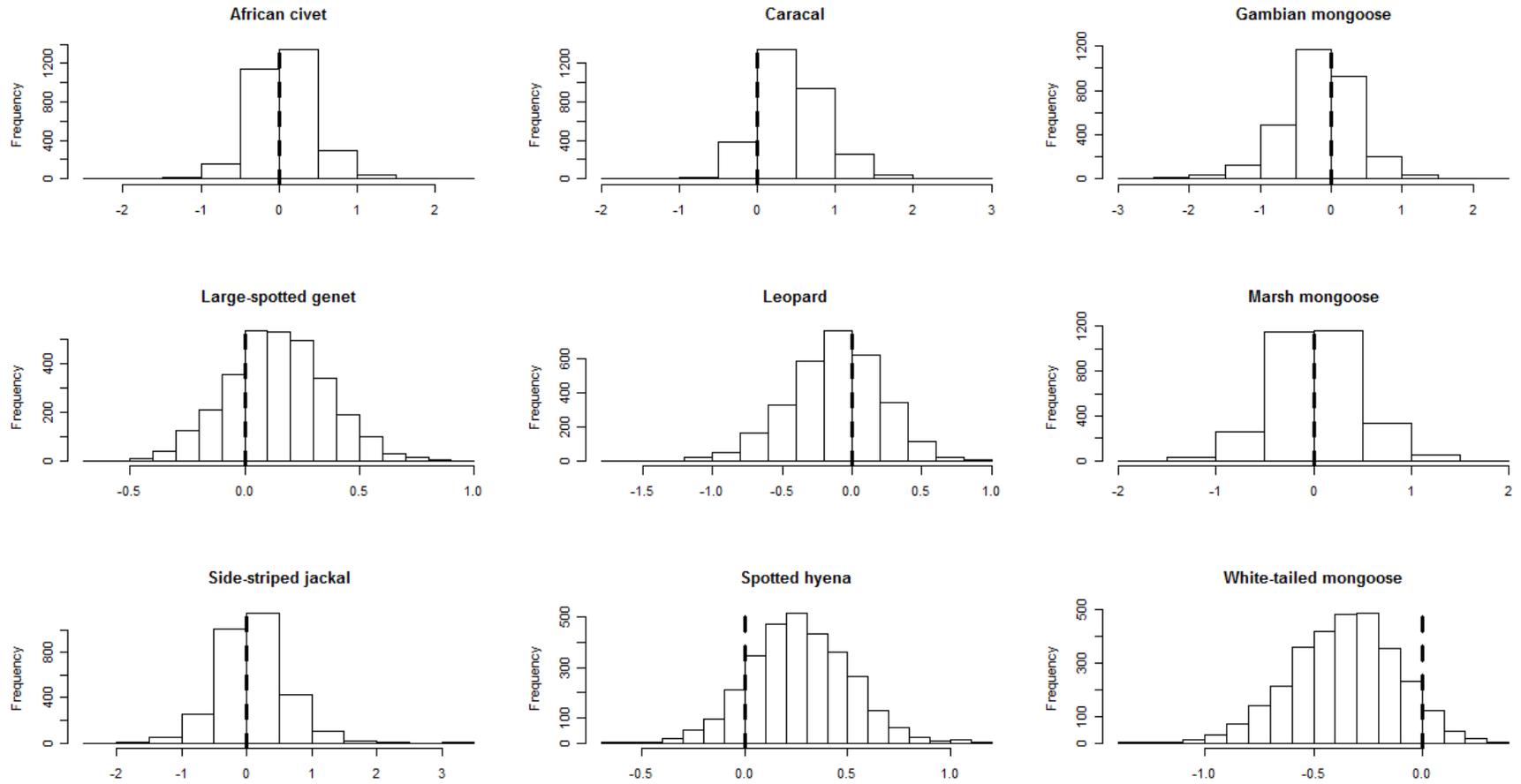
Posterior probability distributions from full model for species-level occurrence coefficients on effect of **seasonal prey biomass** ( $\alpha_{9i}$ )



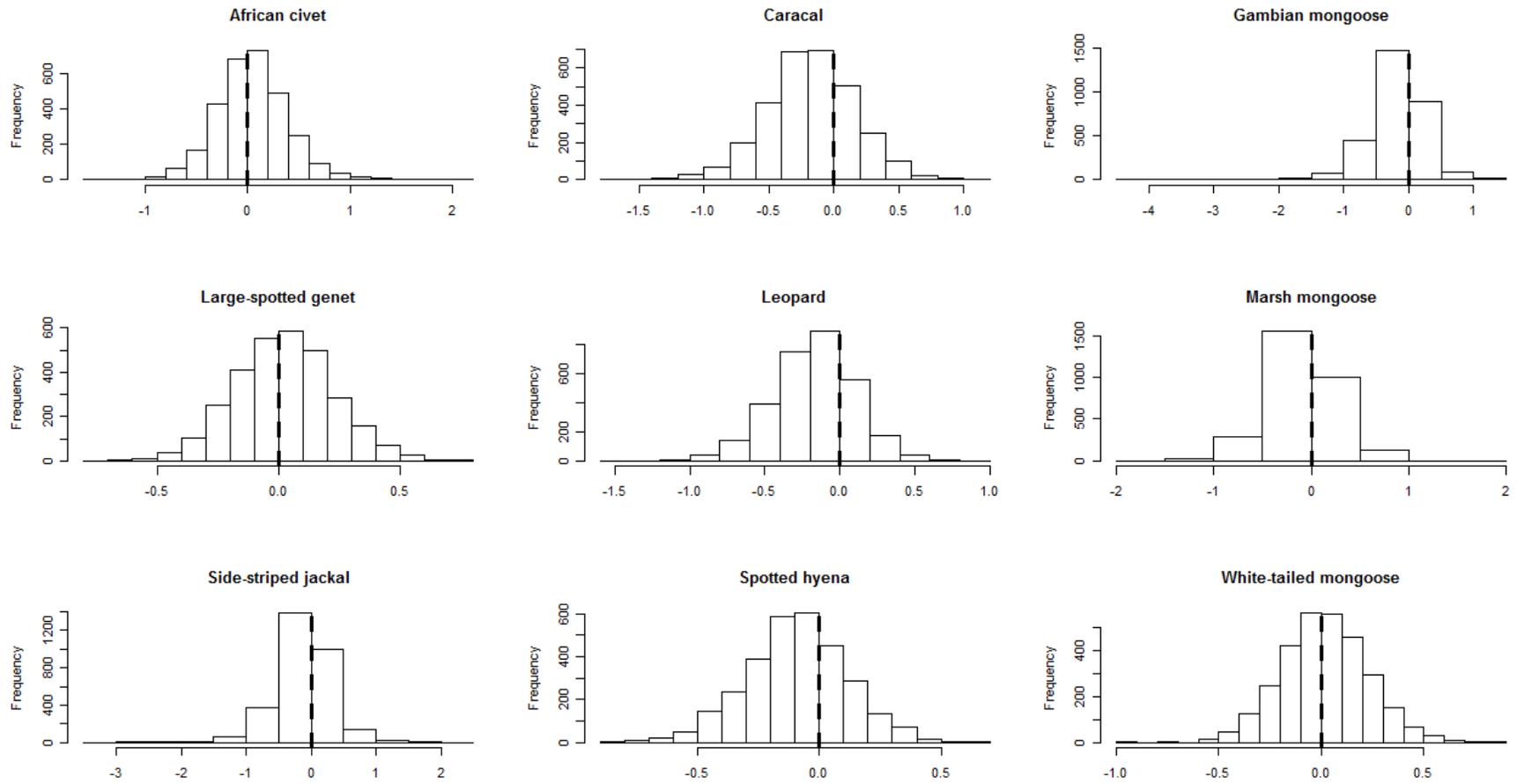
Posterior probability distributions from full model for species-level occurrence coefficients on effect of **seasonal small prey biomass** ( $\alpha_{10i}$ )



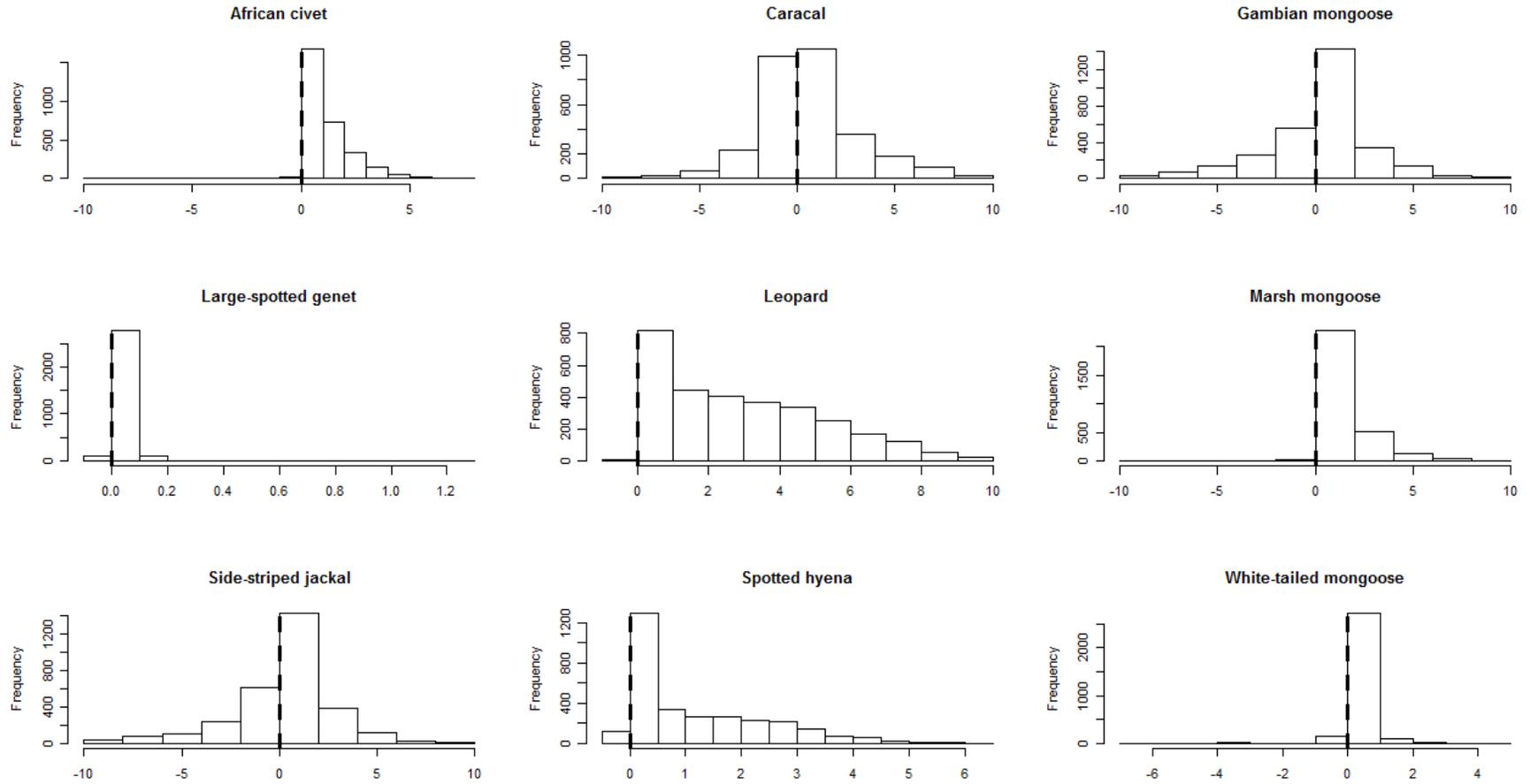
Posterior probability distributions from full model for species-level occurrence coefficients on effect of seasonal NDVI ( $\alpha_{3i}$ )



Posterior probability distributions from full model for species-level occurrence coefficients on effect of **integrated NDVI** ( $\alpha_4$ )



Posterior probability distributions from full model for species-level coefficients on effect of **spatial autocovariate** ( $\delta_i$ )



## CHAPTER 5

### Conclusion & Directions for Future Research

In this dissertation, I investigated aspects of the conservation ecology of carnivores and other mammals in Mole National Park, Ghana. The work was broadly motivated by a desire to better understand the nature of anthropogenic threat to the persistence of wildlife populations, as well as the consequences of uncertainty for understanding human-wildlife dynamics and options for conservation success. Working within the context of a large tropical savanna wildlife reserve—situated in a developing country and region undergoing considerable conservation conflict—I explored themes of protected area effectiveness, monitoring efficiency, extinction vulnerability, and human-carnivore conflict. My specific objectives were to: (i) investigate the degree of uncertainty in data from a long-term, locally-based mammal monitoring program in Mole National Park (MNP); (ii) evaluate patterns of persistence and extinction vulnerability among historically occurring carnivore species in the park; and (iii) examine the extent to which anthropogenic and natural park features influence current occurrence patterns among extant carnivore species. I also endeavored to test the utility of recently developed field and analytical tools—specifically camera trapping and hierarchical occupancy modeling—for improving inference on rare and elusive species. My results provide valuable insight for conservation efforts in this understudied park and region, and have broader implications for the understanding of human-wildlife dynamics and protected area effectiveness in an increasingly human-dominated world. In this concluding chapter, I summarize and discuss the key findings of my three research studies, and highlight several important directions for future research.

#### *Summary of key findings*

In my first study (Chapter 2), I assembled and reviewed 40 years (1968-2008) of observations of mammal species and illegal hunting made by MNP wildlife guards during regular law enforcement patrols. These observations form part of an ecological monitoring program implemented by the Ghana Wildlife Division (GWD) within its wildlife protected areas, and they have been used to make inference on the status of, and impacts to, MNP's larger mammal community. I first compared a modern subset of patrol monitoring data (2006-2008) to results of a concurrent camera-trap survey, and found that patrol observations underrepresented the park's mammal community, recording only two-thirds as many species as camera traps. Patrol and camera data agreed fairly well with respect to the occurrence and relative abundance of larger, diurnal and social species, such as many larger ungulates and primates (e.g., kob antelope, *Kobus kob*, and olive baboon, *Papio anubis*). By contrast, camera traps were much more effective at detecting smaller, solitary and nocturnal species, particularly carnivores (e.g., spotted hyena, *Crocuta crocuta*, and white-tailed mongoose, *Ichneumia albicauda*). I then evaluated the potential effects of sampling error on the interpretation of long-term trends in MNP's mammal populations. The distribution of sampling effort underlying patrol observations (in terms of the number of patrols conducted) was highly variable in both time and space, and counts uncorrected for effort presented a biased picture of temporal trends when compared with an index of count per unit effort. Patrol counts were also highly variable over short time periods within single sampling units (e.g., consecutive patrols from the same management sector), indicating that

sampling error confounds true variation in MNP's mammal community dynamics. I suggested that the ability of GWD's monitoring program to reliably detect true trends in mammal populations may have been previously overstated, and I argued—within the context of recent literature debates—that more careful attention to robust methodological design and analysis is needed if this and similar programs are to satisfy an objective of dependable wildlife monitoring. I further considered the challenges of effective biodiversity monitoring within a developing economy, and highlighted the pressing need for greater international support in the creation and maintenance of local technical capacity in ecological monitoring.

Given evidence from Chapter 2 that most of MNP's carnivore species have not been adequately detected by the patrol monitoring system, I looked more closely at the status of this ecologically and culturally important group of mammals in Chapter 3. I first established a baseline historical carnivore community using reliable records of species occurrences, and then evaluated evidence for the persistence of these species using data from several survey methods (camera traps, sign transects, call-in stations, village interviews and patrol observations). I found camera-trap data to be most reliable as it provided unambiguous evidence of carnivore occurrence, whereas other methods resulted in more equivocal results. Camera-trap data were also well suited to a repeated sampling analytical framework that allowed explicit accounting of imperfect detection, a frequently confounding factor for surveys of rare and elusive species. Only 9 of 16 historically occurring carnivore species were detected by the camera survey, and results of a hierarchical multi-species occupancy model indicated a low overall likelihood of the occurrence of additional undetected species. This implies that several species have been locally extirpated from MNP (or are at least very rare), including the ecosystem's top predator, lion (*Panthera leo*). While drivers of observed declines remain uncertain, evidence of local human-carnivore conflict was documented, including hunting of carnivores for traditional use and in retaliation for livestock depredation. Contrary to predictions based on theory and empirical evidence from other areas, species ecological and life-history traits—such as body mass, home range size, and fecundity—did not explain patterns of persistence. I argued that our perception of carnivore extinction vulnerability may be biased by a disproportionate focus on larger carnivores, and that smaller species may be more vulnerable than previously anticipated. I suggested that more studies looking across entire carnivore communities within a common environmental context could improve our ability to predict extinction risk under increasing anthropogenic pressures.

While the results of Chapter 3 indicated that MNP's carnivore community has been heavily impacted over recent decades, it did not directly address extrinsic drivers of community disassembly. In Chapter 4, I tested hypotheses about factors potentially impacting occurrence patterns among the park's nine extant carnivore species. I extended the multi-species hierarchical modeling approach presented in Chapter 3 to accommodate spatial covariates on site-specific carnivore occurrence and detection probabilities, including spatial autocorrelation, and used a form of Bayesian model selection to assess support for competing hypotheses. While there was considerable variation across species in their estimated responses to examined features of the MNP landscape, there was little indication that carnivores were negatively influenced by illegal hunting pressure (in terms of their use of park habitats). By contrast, occurrence patterns of most carnivore species were positively associated with the biomass of smaller prey species, and several species had either positive or negative associations with riverine forest (but not with other indicators of habitat heterogeneity). Influences of sampling design on carnivore

detectability were also identified and addressed within this modeling framework (e.g., road and observer effects), and the analytical approach facilitated inference on even the rarest carnivore species in the park.

In conclusion, my dissertation results generally concur with previous suggestions that wildlife populations in West Africa are subject to significant anthropogenic pressure, particularly from hunting. Many carnivore populations have apparently declined to the point of local extinction, even within a flagship protected area like MNP. Nevertheless, I showed that human-wildlife relations are complex and inadequately explained by common models of anthropogenic impact, such as those predicting ordered extinction of large-bodied species or simple edge effects in parks. I demonstrated that existing wildlife monitoring data may be subject to important biases that confound interpretation of population or community dynamics over time and space, and I argued that local ecological monitoring should be strengthened by additional attention to objectives and methodology. My results demonstrated the utility of camera trapping as a survey method capable of yielding important insight into mammal community dynamics in tropical savannas. Camera data are particularly valuable when combined with robust analytical tools (such as hierarchical occupancy modeling) that explicitly address common sources of bias like heterogeneity in detection probability. Applying this approach, I uncovered complex dynamics of carnivore community disassembly within Mole National Park and highlighted the relative influence of prey availability on current carnivore occurrence patterns. Efforts to improve wildlife conservation in Ghana and elsewhere should include a greater emphasis on obtaining and effectively using reliable monitoring data, and on ensuring that impacts to carnivore populations are addressed within an ecosystem management framework.

### *Directions for future research*

The results and themes of this research raise many questions for which further work is needed. As is typical of problems in applied conservation science, wildlife conservation efforts in Mole National Park (and more generally in Ghana, West Africa, and elsewhere) would benefit from locally-grounded and complementary research into methodological, ecological, and socio-economic themes. Ideally, future work should be interdisciplinary (or at least multidisciplinary) and involve broader collaboration across diverse scientists, managers, and stakeholders. Research in Ghana, as in many tropical regions, typically lacks the practical, infrastructural support (e.g., research stations, transportation networks) and intellectual benefits that are often amassed by previous study, and it therefore requires extra effort to overcome logistical hurdles and establish necessary baselines of information.

One important avenue for further research is a more detailed assessment of the potential for the Ghana Wildlife Division's long-term monitoring data to yield reliable inference on trends in wildlife and illegal hunting. The promise of, and need for, effective locally-based ecological monitoring has been highlighted by Danielsen et al. (2005a) and was discussed in Chapter 2, as were the considerable limitations facing reliable use of the GWD data. Recently developed analytical approaches that explicitly model observation dynamics distinctly from latent ecological processes may prove useful in providing more robust inference on changes in local wildlife communities (e.g., Clark & Bjørnstad 2004; Cressie et al. 2009; Kéry & Royle 2010; Kéry et al. 2010). Given the dearth of information for most wildlife populations in West Africa, and the urgent need for informed conservation action, successful application of such methods

might be used to test hypotheses and improve predictions about the direction and drivers of past and future wildlife change in MNP and other PAs. In particular, understanding the influence of local anthropogenic impacts (e.g., hunting, burning) relative to more diffuse or indirect ecological effects (e.g., climate change, trophic cascades, species interactions) would be of considerable importance to both science and management. Even so, no amount of analysis will eliminate uncertainty, and research is needed to explore effective ways of adapting and optimizing monitoring efforts so that they can more explicitly incorporate uncertainty and better inform management decision-making (e.g., Field et al. 2005; Nichols & Williams 2006; McCarthy & Possingham 2007).

Irrespective of outcomes from further analysis of patrol monitoring data, there is a clear need for more focused field research on the MNP ecosystem. Data from the 2006-2009 camera trap survey can provide useful background for directing further work, and more detailed analyses remain to be completed. For example, the existing camera data can be used to describe animal activity patterns and habitat use (Bowkett et al. 2007; Ridout & Linkie 2009), test hypotheses about co-occurrence and interspecific interactions (MacKenzie et al. 2004; Harmsen et al. 2009; Richmond et al. 2010), and estimate population densities (e.g., Karanth & Nichols 1998; Rowcliffe et al. 2008; Royle et al. 2009). Preliminary density estimates have been made for MNP's leopard and spotted hyena populations but should be further refined (Burton et al. 2007; Takahashi & Burton 2010). Repeated implementation of camera surveys in MNP can be used to test the generality of results obtained during this initial survey, and could also be used as an alternative approach to monitoring wildlife changes over time (particularly for species like carnivores that are poorly monitored by the patrol system). Data on other survey methods deployed in MNP during this study, such as sign transects and interviews, have yet to be analyzed in detail, and doing so may further inform the design of a more effective wildlife monitoring program. Similarly, explicit comparison of other methods used in MNP would be instructive (e.g., aerial surveys, Bouché 2006), and the evaluation of additional methods could be of considerable value, particularly non-invasive genetic surveys (Eggert et al. 2003; Boulanger et al. 2004; Gompper et al. 2006; Ruell & Crooks 2007; Castro-Arellano et al. 2008).

Importantly, the viability of mammal populations persisting in MNP has not been adequately assessed. Basic information on demographic parameters is lacking (i.e., rates of reproduction and survival), and, as noted, available trend data are associated with considerable uncertainty. Telemetry is a powerful tool for wildlife research that has yet to be used in Ghana, and one that could generate important data on animal survival rates, sources of mortality, species interactions, and patterns of movement and habitat selection (Fischer & Linsenmair 2001b; Johnson et al. 2004; Hopcraft et al. 2005; Aarts et al. 2008; Balme et al. 2010). Individuals of wide-ranging species, like leopard and spotted hyena, are likely to move across park boundaries and interact with adjacent human communities, and more direct monitoring of such interactions through telemetry could be of enormous benefit in addressing human-wildlife conflict. Cross-boundary management will be critical to the long-term viability of most park wildlife populations, and telemetry studies could help identify important unprotected habitats and direct planning of conservation corridors (Forbes & Theberge 1996; Chetkiewicz & Boyce 2009). Furthermore, demographic data obtained from telemetry could be used to parameterize population viability models that, in turn, would be useful for examining extinction risk and evaluating alternative management scenarios (Beissinger & McCullough 2002; Morris & Doak 2002; Carroll et al. 2003; Larson et al. 2004; Schumaker et al. 2004; Linkie et al. 2006; Beissinger et al. 2008).

Regardless of whether or not telemetry studies are pursued, data are needed on sources of mortality for park populations, particularly from potentially important but poorly studied anthropogenic threats (such as hunting and disease, e.g., Cleaveland et al. 2007; Metzger et al. 2010).

Detailed data on habitat quality and vegetation dynamics are also lacking for MNP and most other Ghanaian protected areas. In a previous study (Burton & Brashares 2006) I examined the potential of several remote sensing products for describing wildlife habitat in Ghana's parks (e.g., land cover maps from SPOT VEGETATION and AVHRR satellite data; Hansen & Reed 2000; Mayaux et al. 2003), but found them to be too coarse or inaccurate to be very useful at a local scale. While the utility of other remote sensing products for this purpose requires further study (e.g., MODIS NDVI data used in Chapter 4 or VGT4AFRICA data available at [www.vgt4africa.org](http://www.vgt4africa.org)), finer-scale habitat maps are needed and could be derived from available Landsat and ASTER satellite imagery (e.g., Braimoh & Vlek 2005). Field studies of vegetation change are also needed to complement remote sensing data, particularly for understanding potential impacts to wildlife of widespread seasonal wildfires and variation in water availability (e.g., Klop & van Goethem 2008), as well as the broader consequences of changing wildlife communities for ecosystem functioning (e.g., trophic cascades and associated changes in herbivore foraging). However, accurate landscape-level descriptors of land cover and land use will be needed to identify and monitor potential wildlife corridors that are critical to restoring connectivity across the region's isolated protected areas (Parren et al. 2002; Bouché 2007).

Successful conservation in the West African landscape will ultimately depend on a better understanding of complex socio-ecological dynamics (Homewood et al. 2001; Wardell et al. 2003; Brashares et al. 2004; Agyemang et al. 2007; Borgerhoff Mulder et al. 2007). The landscape is generally dominated by anthropogenic activity (Sanderson et al. 2002; Norris et al. 2010), and relationships between parks and local people have typically been antagonistic (e.g., Mason 1993; Murphree 2002). The Ghana Wildlife Division is moving toward collaborative management with communities living around protected areas, working to devolve authority for wildlife to local Community Resource Management Areas (CREMAs; GWD 2000). While ecological data will be critical to this endeavor (such as in understanding wildlife habitat use and demographics on community lands; e.g., Daily et al. 2003; Naughton-Treves et al. 2003), relevant sociological data are of utmost importance. I collected data on human-wildlife relations during this study, some of which were described in Chapter 3, but much of which requires further analysis. A better understanding of local knowledge and perceptions of wildlife, and attitudes toward conservation, is vital to planning and supporting collaborative management (Newmark et al. 1993; Lyon 2000; Bauer 2003; Gadd 2005). This includes understanding local variation in attitudes and behaviors, such as differences between villages, between individuals or groups within villages, or between long-term residents and recent immigrants or nomadic pastoralists.

More knowledge of the dynamics of illegal hunting in and around MNP is also urgently needed. There are many outstanding questions related to who is hunting and why. For instance, is hunting primarily motivated by economic needs or cultural traditions? What species and areas are most targeted, and what hunting techniques are used? Is harvested bushmeat destined for local consumption or distant markets? What is the importance of hunting for ceremonial or medicinal purposes relative to nutritional or economic needs (e.g., skins for chiefs, bones and other body parts for traditional healing)? What alternative sources of income or sustenance might

be locally available or desirable? And how have these various factors or dynamics changed over time? Answers to such questions could greatly influence the design of conservation interventions for reducing the negative impacts of hunting (Milner-Gulland et al. 2003; Campbell 2005; Damania et al. 2005; Wilkie et al. 2005; Crookes et al. 2007; van Vliet & Nasi 2008). Similarly, more study into the dynamics of rule enforcement and compliance would also be valuable (Keane et al. 2008), such as assessing likelihoods of detection, punishment, and repeat offense for hunters (C. Balangtaa, unpublished data).

More generally, the various impacts of MNP to local livelihoods—both positive and negative—need to be better assessed. Wildlife and other park resources can undoubtedly provide benefits to local communities. The sustainable harvest of wildlife for bushmeat has long been promoted but not successfully realized in Ghana (Asibey 1966, 1971, 1974; Asibey & Child 1990), and wildlife tourism has considerable potential for generating income (Archabald & Naughton-Treves 2001; Lindsey et al. 2005; Balmford et al. 2009; but see also Nepal 1997; Kiss 2004). The MNP ecosystem delivers other important natural resources—including clean water, thatching grass, fuelwood, and medicinal plants—although their availability for local use is unclear (GWD 2005). By contrast, the park entails considerable costs for local communities—such as those related to wildlife crop-raiding, livestock depredation, or the opportunity costs of foregone use—and these can provide powerful disincentives for local support of conservation. A better accounting of costs relative to current and potential future benefits of protecting the park and adjacent community reserves is needed (Naidoo & Adamowicz 2005; Naidoo & Ricketts 2006). Moreover, research is required on effective methods for mitigating human-wildlife conflict and thereby reducing local costs (e.g., Ogada et al. 2003; Adjewodah et al. 2005; Woodroffe et al. 2005).

An ecosystem services framework may provide a promising approach for better linking park protection to local livelihoods and poverty alleviation, as well as for creating new sources of conservation financing (Balmford et al. 2002; Ferraro & Kiss 2002; Goldman et al. 2008; Tallis et al. 2008; Harvey et al. 2010; Nelson et al. 2010). However, previous attempts at integrating conservation and development have often failed (Barrett & Arcese 1995; Oates 1999; Newmark & Hough 2000; Wells & McShane 2004), and potential limitations of an economic welfare approach to biodiversity conservation have been widely noted (Rees 1998; Norgaard et al. 1998; Chee 2004; Mertz et al. 2007; Child 2009; Hansen et al. 2009). Research is warranted into the potential merits and drawbacks of utilitarian (i.e., market-based) approaches to conservation in Ghana, relative to approaches focused more on intrinsic, educational or aesthetic values of wildlife (including traditional totems, sacred groves, and other cultural values, e.g., Fargey 1992; Decher 1997; CI-Ghana 2002; Bossart et al. 2006; Sheppard et al. 2010). Another important and related avenue of socio-political research is that of evaluating the effectiveness of different governance structures for achieving conservation in Ghana. For instance, an assessment of advantages or disadvantages of traditional forms of local governance relative to top-down models of state control over natural resources is important for informing collaborative wildlife management and implementation of the CREMA approach (e.g., Mason 1993; Barrett et al. 2001; Robinson 2010).

Finally, more work will be needed to assess the generality of the results of this study in Mole National Park—as well those from future studies in the area—for other protected areas in Ghana and West Africa. MNP is a flagship park in Ghana, being the largest and one of the better funded, so it might be expected to have achieved better conservation outcomes than other parks

(e.g., Brashares et al. 2001). Patrol-monitoring data exist for GWD's other protected areas and should be similarly assessed, and field research on wildlife populations in other parks is badly needed. Likewise, a synthesis of data from recent surveys on diverse taxa (and using diverse methods) in Ghana and neighboring countries would be informative (e.g., Beier et al. 2002; Eggert et al. 2003; Holbech 2005; Leache et al. 2006; Sam et al. 2006, 2007; Wong & Sicotte 2006; Bouché 2007; Thiollay 2007; Dowsett et al. 2008; Kumordzi et al. 2008; Larsen 2008; Aalangdong 2009; Shirley et al. 2009; Phalan 2009; Henschel et al. 2010; Thompson et al. 2010). Research needs are particularly urgent for parks subject to major development impacts (e.g., dam construction in Bui National Park) and human encroachment (e.g., settlement in Digya National Park), as well as those situated within Ghana's heavily fragmented rainforests that are increasingly influenced by a matrix of competing land uses (e.g., timber extraction, cocoa agroforestry, oil palm plantations; Jeffrey 1970; Asibey & Owusu 1982; Holbech 2009; Phalan 2009; Norris et al. 2010). To that end, data from patrol-based monitoring, sign transects, camera trapping, and village interviews were also collected during this project for a key rainforest reserve (Ankasa Conservation Area; see Burton 2009), and comparative analyses of this and other wildlife datasets can help build our knowledge of conservation challenges and opportunities in this region.

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