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Evaluating persistence and its predictors in a West African carnivore community

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ABSTRACT

Carnivore extinctions frequently have cascading impacts through an ecosystem, so effective management of ecological communities requires an understanding of carnivore vulnerability. This has been hindered by the elusive nature of many carnivores, as well as a disproportionate focus on large-bodied species and particular geographic regions. We use multiple survey methods and a hierarchical multi-species occupancy model accounting for imperfect detection to assess extinction risk across the entire carnivore community in Ghana's Mole National Park, a poorly studied West African savanna ecosystem. Only 9 of 16 historically occurring carnivore species were detected in a camera-trap survey covering 253 stations deployed for 5469 trap days between October 2006 and January 2009, and our occupancy model indicated low overall likelihoods of false absence despite low per-survey probabilities of detection. 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 questions about the predictability of carnivore community disassembly. Our results imply an urgent need for new initiatives to better protect and restore West Africa's embattled carnivore populations, and they highlight a broader need for more empirical study of the response of entire carnivore communities to anthropogenic impact.

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1. 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 and Chellam, 2009). More than one-quarter of mammalian carnivore species (hereafter "carnivores") are currently considered threatened by extinction, with many more undergoing 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 (Prugh et al., 2009; Ray et al., 2005b). 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 (Cardillo et al., 2004, 2005; Purvis et al., 2000). 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 (Fritz et al., 2009; Isaac and Cowlshaw, 2004).

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, and typically a larger-bodied species (e.g., 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. Moreover, effort to research and conserve carnivores is unevenly distributed across the globe. Attention on carnivores in Africa has focused intensively on East and southern Africa and few data exist for populations in West or Central Africa (Bauer et al., 2003; Ray et al., 2005a), despite acute threats to wildlife there entailed by high human densities and widespread hunting for

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bushmeat (Brashares et al., 2001). What little data exist for carnivores in West Africa reveal discouraging trends; for instance, the lion (*Panthera leo*) has been classified as regionally endangered (Bauer and Nowell, 2004) and the African wild dog (*Lycaon pictus*) is thought to have been largely eradicated (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).

In this study, we assessed patterns of persistence across the carnivore community in Ghana's Mole National Park (MNP), a protected savanna ecosystem that is a central piece of strategies for biodiversity conservation in West Africa (e.g., IUCN, 2006). Specifically, we used results of camera trapping, sign and call-in surveys, village interviews, and patrol records to compare current and historical carnivore occurrences in MNP. We applied a multi-species occupancy model to camera-trap data to account for imperfect detection and 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. Based on theory and available literature, we predicted that large-bodied and wide-ranging carnivores would be at

greatest risk of extinction in MNP, and we tested the relationship between persistence and 17 characteristics of species representing these and other common predictors of vulnerability (Table 1). We also considered the causes and consequences of carnivore community collapse in this West African ecosystem, as well as the broader implications for understanding carnivore extinction risk elsewhere.

2. Methods

2.1. Study area

MNP is the largest of Ghana's protected areas, covering approximately 4600 km² in the country's Northern Region (09°11'–10°06'N and 01°22'–02°16'W; Fig. 1). Open savanna woodland is the dominant habitat type and mean annual rainfall is ~1100 mm, with >90% falling during the April-to-October wet season (GWD, 2005). Most of the park's rivers are seasonal and water is a limiting factor during the dry season. There have been few published wildlife studies conducted in MNP, and none focused on carnivores, but previous surveys indicate the presence of regionally significant populations of savanna ungulate and primate species (Bouché, 2006; Wilson and Kpelle, 1993). 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 (GWD, 2005; Jachmann, 2008a).

2.2. Survey methods

Our primary means of assessing the status of carnivores in MNP was through the use of camera traps, a technique that has proven useful in surveying other populations of cryptic carnivores (Balme et al., 2009; 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.

2.2.1. Camera trapping

We obtained data on carnivore occurrence from 253 camera stations established within MNP between October 2006 and January 2009 (Fig. 1). Stations were distributed across much of the park, targeting areas where carnivores were expected to occur (based on reported sightings and local knowledge of prey and habitat) while also sampling gradients in key park features (e.g., proximity to boundary, potential prey abundance, water availability). The northernmost portion of MNP was not sampled because of extremely limited access and reports of low prey densities (GWD, 2005). Camera stations were deployed in 20 spatially and temporally differentiated groups targeting different portions of the park and different seasons (Fig. 1; mean = 12.5 stations per group). 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, and water sources. Stations consisted of a single passive infra-red DeerCam DC-300 film unit (Non Typical, Park Falls, WI, USA), set at a height of ~40 cm facing perpendicular to the expected direction of animal travel and ~3 m from the anticipated site of capture. A 1-min delay between subsequent photographs and 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. Stations were active for a mean of 21.6 days (SD 12.8), yielding a total

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 Section 2 and Appendix S2 for details).

Variable	Predicted direction of greater extinction vulnerability	Range of values
Adult body mass	Larger mass	0.5–158.6 kg
Activity period	Diurnal activity ^a	Diurnal, Nocturnal, Mixed
Home range size	Larger home range	0.8–817 km ²
Gestation length	Longer gestation	56.8–112.3 days
Weaning age	Older age	20.9–371.4 days
Population density ^b	Lower density	0.01–3.7 individuals/km ²
Group size	Larger groups ^c	1–9.3
Diet breadth ^d	Narrower diet range	1–3 diet categories
Habitat breadth	Fewer habitat types	2–20 IUCN habitat categories ^e
Distribution in Ghana ^f	Restricted distribution	3–55 occurrence grid cells
West African range ^g	Smaller range	36,509–6196,580 km ²
Threats	More threat factors	0–19 IUCN threat factors ^h
Human conflict ^h	Prone to conflict	Yes or No
Adaptability ^e	Not adaptable to human habitats	Yes or No
Local use ⁱ	Greater local use	6–73% reported use
Livestock conflict ⁱ	More livestock conflict	0–45% reported livestock conflict
Local perception ⁱ	Less positive perception	8–36% reported positive perception

^a Species exhibiting diurnal activity were expected to be more vulnerable to hunting.

^b No population density value was available for *Genetta thierryi*.

^c Species with larger social groups were expected to be more vulnerable to hunting and Allee effects.

^d Four possible diet categories: plant, invertebrate, small vertebrate, large vertebrate.

^e IUCN Habitats Classification Scheme v3.0 (adaptability inferred from use of the "Artificial–Terrestrial" category).

^f Based on Grubb et al. (1998) where known occurrences were mapped in grid cells of 15 min of latitude by 15 min of longitude.

^g Calculated in ArcGIS 9.3.1 from IUCN (2009) extent of occurrences (Appendix S1).

^h IUCN Threat Classification Scheme v3.0 (conflict inferred from threat categories of Agriculture, Livestock, and Hunting/Persecution).

ⁱ Based on responses from village interviews for the subset of nine larger carnivores (see Appendix S3).

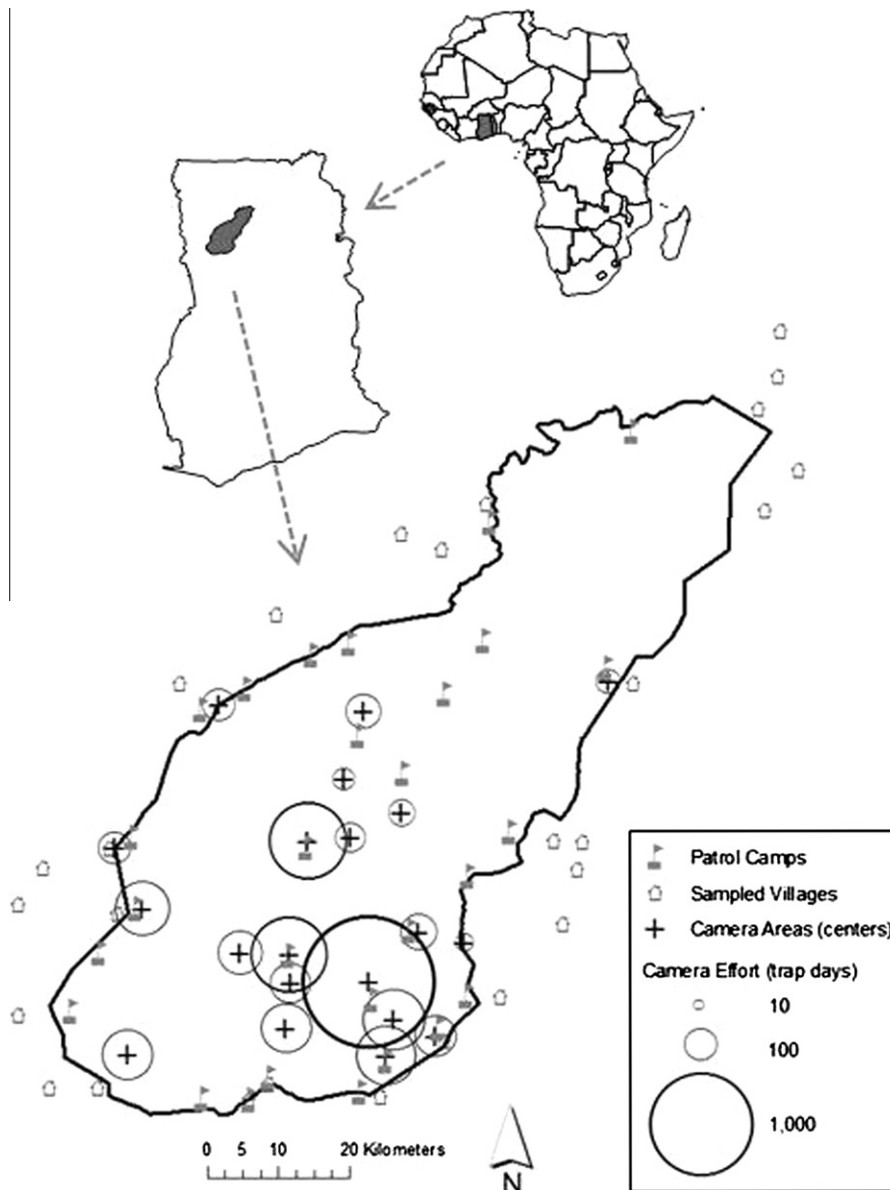


Fig. 1. Map of Mole National Park, showing its location and the spatial distribution of camera-trap sampling, village interviews, and law enforcement patrol camps (from which long-term records were available). Camera-trap sampling is represented by the centroid of cameras within a spatio-temporal group and a circle proportional to the total number of trap-days for that group. Sign and call-in surveys were conducted primarily within the circles depicting camera sampling effort.

survey effort of 5469 trap-days. Effort was highest in the central and southeastern portions of the park (Fig. 1), where prey and water were expected to be most available (Bouché, 2006; GWD, 2005), and during the dry season months of November to March, when access for surveys was greatest and water sources most attractive for wildlife.

2.2.2. Sign, call-in and spotlight surveys

Observations of carnivore tracks and scat (i.e., sign or spoor) were recorded both systematically and opportunistically during foot and vehicle travel around and between camera sampling sites (Fig. 1). Variable length transects totaling ~330 km (mean = 6 km) were surveyed by foot, and routes totaling ~1400 km were surveyed by vehicle (mean = 33 km, driven at 10–20 km/h). Most routes were repeated within and between seasons over the period of camera-trap sampling (October 2006–January 2009).

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 and Dublin (1998). Surveys lasted ~1 h

(between 1900–2230 and 0530–0630 h) and consisted of two cycles of the following sequence broadcast from two horn speakers (45 W, 8 Ω, 285 mm) mounted at 180° on top of a truck: 3 min warthog distress squeals, 5 min silence, 3 min buffalo distress bleats, 6 min spotted hyena vocalizations, and 10 min of silence. A 2-million candlepower spotlight was used to scan for animals responding to calls. We also completed three nighttime vehicle spotlight transects of ~10 km along sections of road in the south-eastern portion of the park. The number of call-in and spotlight surveys was limited by poor visibility and access (i.e., dense vegetation, hazardous or non-existent roads).

2.2.3. Patrol records

Mole National Park management has implemented large mammal monitoring based on observations made by field staff during regular law enforcement patrols (GWD, 2005; Jachmann, 2008b). Monitoring records covering October 2004 to May 2008, and including data from ~2800 patrols spread across the park, were examined for sightings of carnivore species. To estimate longer-

term trends, we also extracted carnivore sighting records from ~2000 monthly reports containing data from 28,000 + patrols distributed across the park from 1968 to 2001 (Fig. 1). Counts from modern and historical patrols were combined and an annual index of abundance was calculated as the number of individuals observed in a year standardized by a unit of effort set at 100 patrols (i.e., catch-per-unit-effort; see Burton, 2010 for more details on the patrol data).

2.2.4. Interviews

We conducted 68 semi-structured interviews with key informants living in 27 villages adjacent to MNP (Fig. 1; Appendix S3). Respondents were asked to name all 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.

2.3. Historical carnivore occurrence and traits

We established a list of 16 species representing the recent historical or “intact” carnivore community for MNP (i.e., from park establishment ca. 1960; Table 2) based primarily on the detailed occurrence records assembled and assessed by Grubb et al. (1998; Appendix S1). We then 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 for trait values were the PanTHERIA database (Jones et al., 2009) and species accounts from the IUCN Red List of Threatened Species (IUCN, 2009), but we also used other sources for certain variables and species (Table 1; Appendix S2).

2.4. Estimating carnivore occurrence, relative abundance, and richness

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 (cf. O'Brien et al., 2003). We also considered evidence of carnivore occurrence from our other survey methods, although resulting data were generally less reliable or verifiable and not as well-suited to our analytical framework (see Section 4).

A significant challenge to surveying rare and elusive species and documenting local extinctions is the problem of imperfect detection (MacKenzie et al., 2006). We therefore applied a multi-species site-occupancy modeling framework (Royle and 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 (=site) and used this temporal replication to estimate the probability that a species not detected at a site was truly absent (with occurrence of a species considered equivalent to its use of the habitat at that site). Briefly, the multi-species model involves a three-level hierarchical framework in which the observation data, representing detections of different species at different 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 depends on the specification of a hypothetical “supercommunity” expected to contain the real community and is key to robust estimation of community attributes like species richness. Further details of the modeling framework are given in Appendix S4 and Royle and Dorazio (2008, pp. 379–389).

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). We specified a “supercommunity” of 20 carnivore species from which our detections were sampled (encompassing the estimated historical community size of 16 while allowing for the possibility of additional species; Appendix S1), with 11 “zero detection” spe-

Table 2

Evidence for the occurrence of carnivore species in Mole National Park from 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. Indices derived from camera-trap data are also given. Historical occurrence was ascertained from evidence compiled in Grubb et al. (1998; Appendix S1). Evidence for the persistence of the seven species listed at the bottom is weak and they are presumed to now be extremely rare or extirpated from the park.

Scientific name	Common name	Body mass (kg)	Evidence ^a	Detection frequency ^b	Prop. sites ^b	Pr(occurrence) ^c mean (SD)	Pr(detection) ^c 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	– ^a	0	0	–	–
<i>Herpestes sanguineus</i> ^d	Slender Mongoose	0.5	– ^a	0	0	–	–
<i>Genetta thierryi</i>	Hausa Genet	1.4	– ^a	0	0	–	–

^a 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”.

^b Detection frequency (independent detections per 100 trap days) and proportion of sites at which a species was detected across all 253 camera stations.

^c Probabilities of site occurrence and per-survey detection estimated from the multi-species occupancy model based on camera-trap detections across 224 stations. Means and standard deviations are from 5000 samples of the posterior probability distribution.

^d Slender mongoose is also frequently known as *Galerella sanguinea*.

cies added to the nine species detected (see Section 3). We fit the model using a Bayesian approach to parameter estimation implemented in programs R 2.10.1 (R Development Core Team, 2009) and WinBUGS 1.4.3 (Lunn et al., 2000), modifying code provided in Royle and Dorazio (2008, Appendix S4).

2.5. Testing predictors of persistence

We tested the relationship between carnivore persistence and the ecological and life-history traits using decision-tree models and two indices of persistence generated from the camera trap survey: (i) a binary variable indicating species presence/absence (P/A), and (ii) a continuous variable corresponding to the estimated probability of occurrence (ψ_i) for each carnivore from the occupancy model (with a value of 0 for species that were not detected). While occurrence probability does not equate directly to persistence (i.e., species could persist at different frequencies of site occurrence), it better reflects the possibility of imperfect detection.

Decision-tree models have been proposed as effective tools for assessing extinction risk and have several advantages over traditional parametric approaches since they (a) avoid assumptions of distributional form or data independence, (b) identify context-dependent associations among correlated predictor variables, and (c) improve predictive power (Davidson et al., 2009; De'ath and Fabricius, 2000). We used classification and regression trees (for the binary and continuous response variables, respectively) implemented in R package *tree* to assess the ability of species traits to explain variation in estimated persistence among carnivores. Because 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 (Cutler et al., 2007). Using R package *randomForest*, we assessed variable importance and classification error rate (for P/A) or % variance explained (for ψ_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 bivariate relationships between all 17 predictors (Table 1) and the two response variables were assessed with: (i) Fisher's exact test for categorical predictors and P/A, (ii) Spearman's rank correlation test for continuous predictors and ψ_i , or (iii) Wilcoxon rank-sum test comparing values of a continuous variable (e.g., body mass) grouped by a binary variable (e.g., P/A). All statistical tests were implemented in R version 2.10.1.

3. Results

3.1. 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 9 (Table 2). Seven "historical" species, including lion and wild dog, were not detected in the camera trap survey, nor could their presence be confirmed by the sign, call-in or spotlight surveys. 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). 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 few observations (median = 8, range = 1–99). 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 to 2008).

Village interview responses had the greatest associated uncertainty, with ambiguity in the timing and reliability of reported observations making it 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 a few reports of recent sightings (i.e., within 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

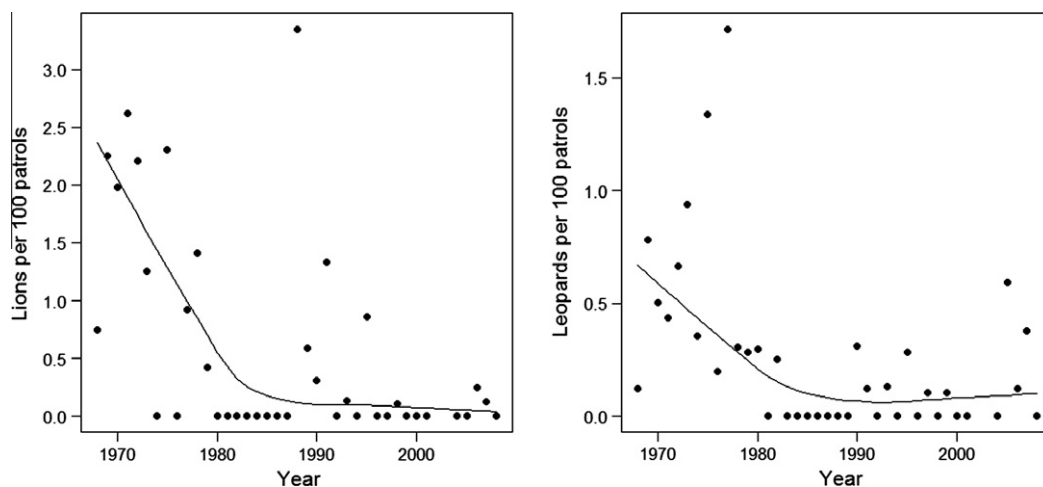


Fig. 2. Relative abundance (individuals counted per 100 patrols) of lions (left) and leopards (right) observed during law enforcement patrols conducted in Mole National Park from 1968 to 2008. Trends (solid lines) were fit with a locally-weighted polynomial regression (*lowess* function in program R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

ceremonial, medicinal or nutritional purposes) ranged from a low of 5% for honey badger to a high of 55% for lion. Lion and spotted hyena were most frequently cited as depredating livestock (45% and 25% respectively), and several instances of retaliatory killing were reported.

3.2. Probabilities of occurrence and detection

Estimates of carnivore occurrence and detection probabilities and species richness were generated from the multi-species occupancy model using camera trap data. Posterior median richness was 9 (Fig. 3), suggesting the camera trap survey detected all car-

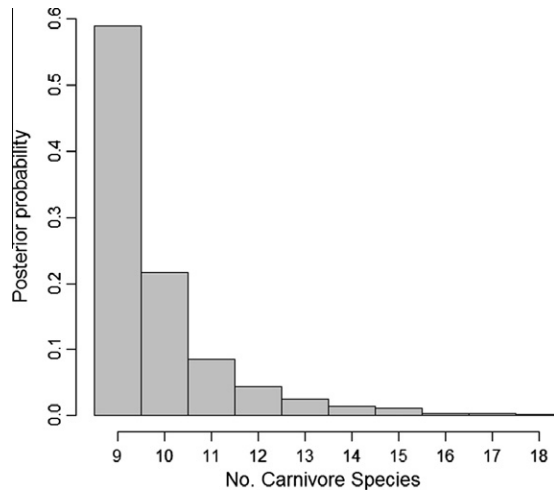


Fig. 3. Posterior probability distribution for the number of carnivore species occurring in the Mole National Park wildlife community, estimated from a hierarchical multi-species occupancy model applied to detection data from 224 camera-trap stations.

nivore 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 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 across the carnivore community was 0.21 (SD 0.10), which can also be interpreted as the estimated proportion of sampled sites used on average by carnivores. The mean probability of detection given occurrence was only 0.058 per site per day (SD 0.030), but this translated into a very low probability of false absence across all sites and trap-days (Appendix S4). 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 $r_s = 0.97$, $P < 0.001$; Table 2). Occurrence and detection probabilities were also 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 and 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).

3.3. 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 S2). Activity

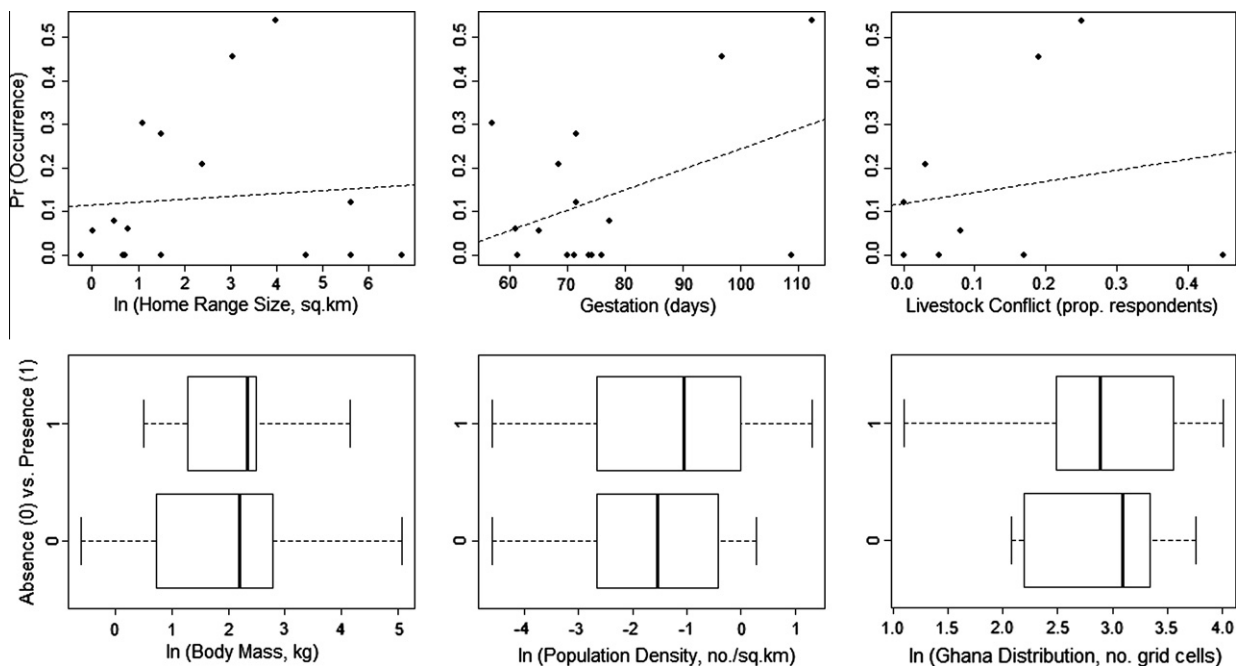


Fig. 4. Bivariate relationships between estimated persistence of carnivore species in Mole National Park and, by example, 6 of 17 species traits tested. The top row shows carnivore probability of occurrence (estimated from the multi-species occupancy model based on camera trap detections) plotted against (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 (from the camera trap survey). None of the 17 variables were significantly associated with either measure of persistence (see Section 3.3).

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, 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 S2); however, the model fit was also poor, explaining only 31% of variation in species occurrence (null deviance = 0.461, residual deviance = 0.318). 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 P/A = 81%; variance in ψ_i explained = 31%; Appendix S2). Similarly, tests of association between P/A or ψ_i and each of the 17 variables did not provide 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).

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 fully extinct in the park. In addition, low estimated probabilities of occurrence and evidence from patrol records and village interviews indicate populations of many species still persisting 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.

4.1. 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., Pettorelli et al., 2010). Camera-trap data also were well-suited to the occupancy modeling framework 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 S4), as is consideration of the spatial and temporal scope of sampling. Our survey effort was highest in the central and south-eastern 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). Our 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). Recent patrol records 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 sightings 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.

4.2. 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, a result unlikely to be driven by detection bias since a species' estimated detection probability was uncorrelated with body mass (or with other traits). There is thus little evidence from MNP to support the premise that large carnivores are consistently more vulnerable to extinction and smaller carnivores correspondingly increase via trophic release (Prugh et al., 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 (Ray et al., 2005a; Woodroffe and Ginsberg, 1998). Nevertheless, most carnivore species lost from MNP do not represent extremes in their ecological or life-history traits or in their interaction with humans. 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 imply they may be more vulnerable than expected or previously appreciated.

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 (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 (Brashares et al., 2001; Woodroffe, 2000), 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/km², which roughly corresponds to densities in the area surrounding MNP (Jachmann, 2008a). 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; Jachmann, 2008a; Fig. 5), and there was no apparent correlation between carnivore persistence and variation in local threats estimated from interview data. Elucidating rules of community disassembly is key to accurate prediction of anthropogenic effects on ecosystem functioning (Woodroffe and Ginsberg, 2005; Zavaleta et al., 2009), so 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.

4.3. Extrinsic drivers of decline

Considering the evidence of decline and probable extirpation within MNP's historical carnivore community, there is a need to identify extrinsic factors upon which management 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 (Brashares et al., 2001), and illegal hunting is pervasive in and around MNP (Jachmann, 2008a; Fig. 5). Nevertheless, many medium- and larger-sized prey appear to be relatively abundant within portions of the park (Bouché, 2006; Burton, 2010), so it is not clear that larger carnivores are limited by an inadequate prey base, and little is known about the



Fig. 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.

availability of prey for smaller carnivores. Our village interviews suggested that use of carnivore products (i.e., skins, organs) and retaliatory killing for livestock depredation are common around MNP (Fig. 5), implying that direct persecution is an important threat (at least for medium- and large-bodied species). Instances of illegal hunting of carnivores have been recorded by the law enforcement program and mortalities likely result from the widespread use of “gin” (leg-hold) traps in and around the park (Fig. 5).

Habitat degradation in the park is unlikely to be a major factor underlying carnivore declines since MNP’s savanna woodlands are relatively intact. Conversely, habitat surrounding the park is variably altered or degraded by human settlement, farming and livestock grazing, which have undoubtedly increased park isolation and edge effects and thereby constrained the effective size (and viability) of carnivore populations. Interspecific competition also impacts many African carnivores (Caro and Stoner, 2003), and our data hint at its potential role in MNP: an apparent increase in the spotted hyena population may have resulted from, and perhaps contributed to, the decline of lions and other carnivores with which hyenas compete (Ray et al., 2005a). Nevertheless, our understanding of these and other potential drivers of change in MNP’s carnivore community remains largely speculative, and further investigation is urgently needed.

4.4. 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 and Estes, 2010). Using patrol monitoring records from several of Ghana’s protected areas, Brashares et al. (2010) inferred a “mesopredator release” of olive baboons (*Papio anubis*) following large carnivore declines, raising the possibility of significant ecological and socioeconomic damage from an overabundant pest. 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 (Woodroffe and Ginsberg, 2005). 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; Burton, 2010). Nevertheless, functional roles and trophic dynamics require further study in MNP, and it is possible that anthropogenic impacts such as hunting overwhelm 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., 2003; Henschel 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 and Ehrlich, 2002) but also undermines local customs and beliefs (CI-Ghana, 2002) and limits potential economic gains from tourism linked to charismatic carnivores (Lindsey et al., 2005). Remaining populations must be better protected by increasing support for law enforcement programs (Jachmann, 2008a,b) while enhancing efforts to alleviate conflicts between parks and local livelihoods (Woodroffe et al., 2005). Ultimately, a long-term vision for regional-scale conservation is needed to restore these carnivore populations and their embattled ecosystems.

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Appendix A. Supplementary material

Further details on the historical carnivore community (Appendix S1), species traits and associated analysis (Appendix S2), village interviews (Appendix S3), and hierarchical multi-species occupancy model (Appendix S4). Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2011.06.014](https://doi.org/10.1016/j.biocon.2011.06.014).

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