Local-Scale Variation in Land Use Practice Supports a Diverse Carnivore Guild on Namibian Multiple-Use Rangeland ☆

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A B S T R A C T

Many rangelands worldwide are threatened by human population growth, so there is an urgent need for understanding how we can preserve functional diversity across these systems. The conservation and restoration of mammalian carnivores (order Carnivora) is critical because they impart important trophic cascading effects. Land use practice on rangelands may determine carnivore distributions and abundances; thus, to effectively facilitate coexistence between carnivores and humans, it is essential to understand carnivore community functioning in human-dominated landscapes. We conducted a camera trapping survey on multiple-use rangeland in north-central Namibia to investigate the spatial ecology of free-ranging carnivores in a farming system that comprises both livestock farming activities and wildlife-based land uses. We hypothesized that carnivore diversity and occupancy would be determined by farm type and predicted the associations of carnivore distributions with covariates related to resource availability, intraguild interactions, and anthropogenic influence. We considered single-season occupancy models and hypothesized that in this semiarid study system, seasonality had profound effects on the spatial ecology of carnivores. Our results show that Namibian multiple-use rangeland supported a diverse carnivore guild. Carnivore diversity and occupancy were generally similar across farm types, suggesting that the carnivore community assemblage in our study area was homogeneous. Local-scale variation in land use practices did not limit carnivore distributions, which could be key to maintaining ecological integrity of rangelands. The effect of seasonality suggested that carnivore space use on Namibian rangelands was influenced by availability of dry season resources. In addition, carnivores were dependent on natural resources, showed complex interactions with intraguild members, and had seasonally contrasting associations with anthropogenic activities. Namibian multiple-use rangelands may function as viable socioecological landscapes and could act as an important link between core conservation areas.

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Introduction

Although the establishment of protected areas (PAs) throughout Africa has been instrumental for the conservation of biodiversity, many large mammal populations continue to decline (Craigie et al. 2010). A comprehensive and interconnected PAs network is often lacking (Fjeldså et al. 2004), and many PAs perform poorly because of insufficient funding and poor management (Lindsey et al. 2017). In addition, edge effects reduce effective reserve size and enhance isolation (Woodroffe and Ginsberg 1998; Newmark 2008). Wide-ranging species often extend their home ranges beyond the administrative boundaries of PAs, so integrative management at the landscape-level is needed to target a more holistic approach to conservation (Newmark 2008; Bowyer et al. 2019).

Many unprotected lands primarily emphasize extensive grazing and pastoralism (Lund 2007; Briske 2017). These rangelands are common in arid and semiarid to dry subhumid areas and are usually dominated by grasses and shrubs (Briske 2017). Rangelands are keystone elements of these landscapes because they offer a livelihood to millions of people while supporting important ecological

regulatory services and biological diversity (Lund 2007). Rangelands can support diverse communities of terrestrial vertebrates (Kinnaird and O'Brien 2012; Msuha et al. 2012; Kiffner et al. 2015; Drouilly et al. 2018a), but livestock farming practices can be difficult to reconcile with biodiversity conservation due to overstocking, large herbivore removal, and carnivore persecution (Du Toit and Cumming 1999; Ogutu et al. 2005; Fynn et al. 2016; Briske 2017). With continued human population growth, functional diversity of rangelands becomes threatened, creating a strong demand for multipurpose management of rangelands to provide sustainable goods and services (Bedunah and Angerer 2012).

Throughout southern Africa, legislative changes in the past decades provided farmers with property rights over wildlife occurring on their land, which encouraged farmers to invest in wildlife as an alternative source of income to livestock (Barnes and de Jager 1996; Barnes et al. 2004; Clements et al. 2019). The development of game farms, with land use practices such as game meat production, ecotourism, trophy hunting, and/or wildlife conservation (i.e., wildlife-based land uses), resulted in substantial increases of wildlife numbers outside state PAs because more habitat became preserved (Barnes et al. 2004). Game farming may be more profitable compared with livestock farming in semiarid areas, which underpinned the transition toward multiple-use landscapes (Lindsey et al. 2013b; Holechek and Valdez 2018; Young et al. 2018). This resulted in a mosaic distribution of livestock farms, game farms, and mixed farms (both livestock production and wildlife-based land uses) across southern African rangelands, and therefore it is vital to understand the effect of local-scale variation in land use practices on patterns of biodiversity and ecosystem health.

Species of the order Carnivora (hereafter named "carnivores") have a disproportionately large effect on ecosystems because of cascading effects across trophic webs and are therefore often referred to as keystone species (Roemer et al. 2009; Ripple et al. 2014). They have been studied extensively worldwide and, despite regional variation, their main patterns of occurrence have been found to be governed by 1) resource availability, such as the density and distribution of prey, water, and/or shelter (Fuller and Sievert 2001; Carbone and Gittleman 2002); 2) intraguild interactions, resulting in spatial, temporal, and/or dietary niche partitioning (Palomares and Caro 1999; Donadio and Buskirk 2006; Edwards et al. 2015) or facilitation (Yarnell et al. 2013; Bashant et al. 2020), and 3) anthropogenic influence, limiting carnivore distributions because of disturbance and/or direct persecution (Woodroffe 2000; Ripple et al. 2014). Human-carnivore conflict has severe impacts on wildlife community structure, frequently imposing cascading effects on trophic webs (e.g., via mesopredator release (Prugh et al. 2009; Ritchie and Johnson 2009), overabundance of herbivores (Ripple and Beschta 2012), or imposing a predator-pit effect (i.e., low-density equilibrium) on staple prey populations (Pech et al. 1992; Fernandez-de-Simon et al. 2015). Consequently, conservation and restoration of carnivore populations may prove crucial in safeguarding ecosystem functioning (Ripple and Beschta 2012; Ripple et al. 2014) and promoting socioeconomic benefits to wildlife-based land uses (Clements et al. 2016). However, unsustainable carnivore management may follow when economic needs of game farming exceed ecological needs of carnivores—hence the importance of carnivore guild-level considerations in conservation strategies (Clements et al. 2016; Curveira-Santos et al. 2021).

The objective of this study was to inform such strategies by gaining a better understanding of mammalian carnivore diversity and community functioning on multiple-use rangelands in north-central Namibia. Particularly, we use occupancy modeling based on camera trapping data to understand patterns of carnivore distributions between different farm types and in relation to seasonal covariates associated with resource availability, intraguild interac-

tions, and anthropogenic influence. We grouped carnivore species with shared characteristics (as defined by Jones et al. 2009) into functional groups to detect prevailing drivers of occupancy of free-ranging carnivores in this mosaic rangeland system (Table 1). We defined functional groups by adult body mass, intermediate-sized (1–15 kg) versus large-sized carnivores (> 15 kg) (Buskirk 1999), and by feeding strategy, specialists (i.e., carnivorous and insectivorous [reliant on one dietary category: vertebrates or invertebrates]) versus generalists (i.e., omnivorous [reliant on multiple dietary categories: vertebrates, invertebrates, fruits and/or plants]) (Jones et al. 2009).

We hypothesized that the carnivore community would be more diverse and with higher species-specific occupancy rates on game farms compared with mixed farms and livestock farms due to a suite of favorable characteristics, namely abundant natural prey, reduced disturbance, and high-quality habitat (Boast and Houser 2012). However, as carnivores may move extensively in search for resources, they may cross less favorable areas, possibly leading to a homogeneous community assemblage across farm types (Curveira-Santos et al. 2021).

We further hypothesized that seasonality would have profound effects on the processes governing the spatial ecology of carnivores in semiarid systems such as ours (Schuette et al. 2013; Rich et al. 2017b). Therefore, we analyzed the strength and direction of seasonal covariate associations related to resource availability, intraguild interactions, and anthropogenic influence. More specifically, we expected resource scarcity during the dry season to restrict space use of free-ranging carnivores due to preferred use of space around resources of limited availability.

We also hypothesized that generalist species would be more common than specialists because they are better suited to persist and thrive in human-dominated landscapes, given their higher ecological plasticity (Fedriani et al. 2001; Davis et al. 2018). Lastly, we expected that the occupancy probability of large-sized carnivores would be lower than intermediate-sized ones because of their typically lower densities and higher vulnerability to local extinction due to human-carnivore conflict (Ripple et al. 2014).

Given the importance of rangelands for wildlife conservation throughout southern Africa, we aimed at providing new empirically based information relevant to the conservation and management of carnivore populations and their habitat across semiarid, multiple-use landscapes.

Methods

This study was conducted on freehold (privately owned) farmland in north-central Namibia and covered an area of 3 153 km² (Fig. 1). These farms surround the Waterberg Plateau National Park (WPNP), which was established in the 1970s to protect native and endangered species (Schneider 1998). For most wildlife, little to no migration exists between the WPNP and surrounding farms, as the plateau rises up 200 m above the landscape with steep cliffs. Agile species (e.g., leopard *Panthera pardus*) may occasionally move between the WPNP and surrounding farmland, but the effect of migration and dispersal is considered negligible. Therefore, the WPNP is not functioning as a source area for the surrounding farmlands (Stein et al. 2011). Livestock production is the dominant land use practice in our study area (i.e., mainly cattle, hereafter livestock farms; 2 206 km²), while other farms support wildlife-based land uses (i.e., game meat production, trophy hunting, ecotourism and conservation, hereafter game farms; 290 km²) or a combination of both livestock production and wildlife-based land uses (hereafter mixed farms; 658 km²).

The area is classified as semiarid and is divided into a wet season (November–April) and a dry season (May–October). Mean annual rainfall is 400–500 mm, mostly falling in the wet season

Table 1
Target species detected during the camera trap survey on freehold farmlands in north-central Namibia between 2016 and 2017. Number of independent detections, mean occupancy, mean local abundance (estimated number of individuals per camera trap site) and detection probability are presented per season. Values between brackets are standard deviations.

Body mass	Feeding strategy	Species	Dry season				Wet season			
			N	$\hat{\psi}$	$\hat{\lambda}$	$\hat{p}$	N	$\hat{\psi}$	$\hat{\lambda}$	$\hat{p}$
Large-sized carnivores	Specialist	Cheetah	2	0.29 (0.19)	2.06 (4.21)	0	1	0.32 (0.19)	4.18 (8.78)	0
		Leopard	67	0.58 (0.12)	1.11 (0.5)	0.02	96	0.45 (0.07)	0.7 (0.15)	0.03
	Generalist	Brown hyena	327	0.71 (0.05)	1.43 (0.2)	0.08	206	0.67 (0.06)	1.35 (0.28)	0.05
Intermediate-sized carnivores	Specialist	Aardwolf	55	0.24 (0.05)	0.32 (0.09)	0.01	13	0.43 (0.18)	3.43 (7.2)	0
		African wildcat	112	0.73 (0.09)	1.65 (0.55)	0.03	98	0.69 (0.08)	1.5 (0.45)	0.03
		Bat-eared fox	72	0.38 (0.07)	0.88 (0.41)	0.02	47	0.16 (0.04)	0.19 (0.06)	0.01
		Caracal	88	0.44 (0.07)	0.8 (0.25)	0.02	40	0.85 (0.13)	5.44 (5.35)	0.01
		Serval	5	0.14 (0.12)	0.28 (0.56)	0	1	0.13 (0.08)	1.39 (2.4)	0
	Generalist	Black-backed jackal	1024	0.8 (0.03)	1.95 (0.19)	0.17	426	0.6 (0.04)	1.08 (0.14)	0.09
		Cape fox	10	0.07 (0.04)	0.24 (1.04)	0	4	0.29 (0.15)	5.55 (9.24)	0

N indicates number of independent detections; $\hat{\psi}$, mean occupancy probability; $\hat{\lambda}$, mean local abundance; $\hat{p}$, species detection probability.
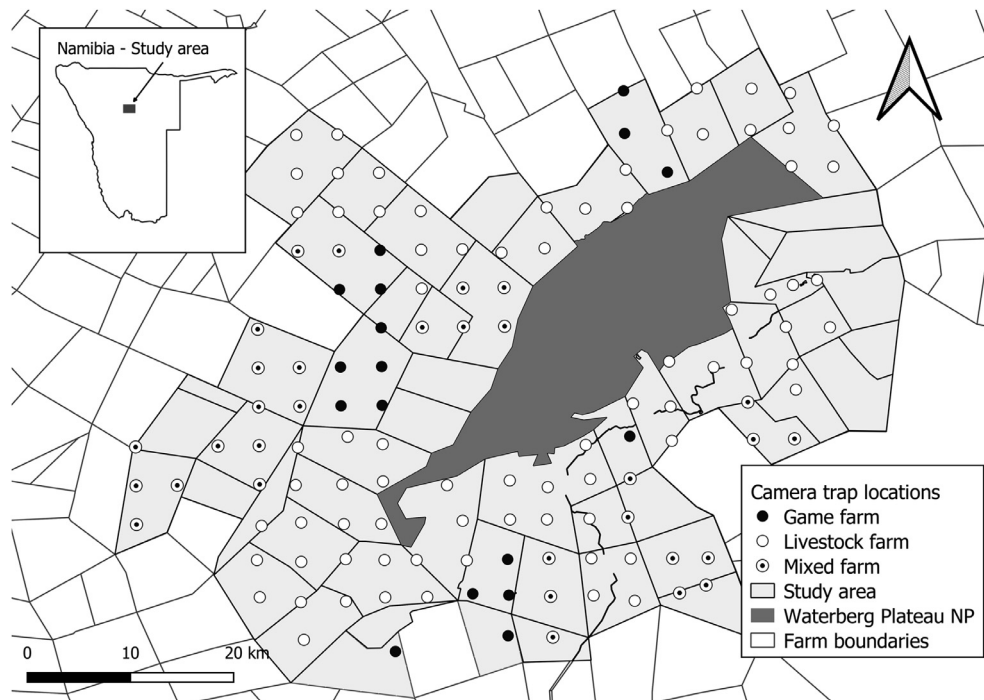

Figure 1. Map of the study area with camera trap locations. Farm type where the camera trap was placed is depicted for game farms as a solid circle, for livestock farms as an open circle, and for mixed farms as a circle with a dot.

(Mendelsohn et al. 2002). Borehole water is often pumped to the surface for livestock and wildlife as there are few natural permanent water sources that hold water year-round. The vegetation is characterized by thornveld biome, with dense *Senegalia mellifera* and *Dichrostachys cinerea* shrublands and woodlands (Barnard 1998; Schneider 1998). Bush encroachment is common as a result of mega-herbivore removal, fire exclusion, and increased pressure from livestock and drought (Kauffman et al. 2007).

Lions *(Panthera leo)*, spotted hyenas *(Crocuta crocuta)*, and African wild dogs *(Lycaon pictus)* were extirpated from the study area in the 1980s (Stein, 2010). Other large carnivores (> 15 kg) known to occur in the area are leopard, cheetah *(Acinonyx jubatus)*, and brown hyena *(Hyaena brunnea)*. Intermediate-sized carnivores (1−15 kg) known to be present are aardwolf *(Proteles cristata)*, African wildcat *(Felis silvestris lybica)*, black-backed jackal *(Canis mesomelas)*, bat-eared fox *(Otocyon megalotis)*, caracal *(Caracal caracal)*, Cape fox *(Vulpes chama)* and serval *(Leptailurus serval)*. Ungulate species, such as common warthog *(Phacochoerus africanus)*, gemsbok *(Oryx gazella)*, kudu *(Tragelaphus strepsiceros)*,

red hartebeest *(Alcelaphus buselaphus),* springbok *(Antidorcas marsupialis),* and steenbok *(Raphicerus campestris),* and smaller prey species, such as scrub hare *(Lepus saxatilis),* springhare *(Pedetes capensis),* murids, and birds, are common throughout the landscape and are mostly nonmigratory (Kauffman et al. 2007). All wildlife species are free roaming across the landscape, except for larger ungulate species (body weight > 100 kg) that are constrained within game farms. We assumed reasonable permeability of game fences for smaller species, including carnivores (Cozzi et al. 2013; Kesch et al. 2015; Pirie et al. 2017).

Camera trap survey

Between February 2016 and October 2017, we deployed remote camera traps (Bushnell Trophy Cam) at 125 locations (see Fig. 1). Per season, we used a rotational system for camera trap deployment where we divided the study area into four subareas and sequentially sampled each area for 30 d (i.e., time cameras were active) (Brassine and Parker 2015; Rich et al. 2017b). We deployed an

average of 31 camera traps within each subarea. Camera trap locations were identified by placing a 4×4 km grid over the study area. The 4-km spacing was selected to target intermediate- to large-sized carnivore species in an effort to establish a uniform sampling effort across the study area, ensuring independence at sampling sites and minimizing spatial autocorrelation (Foster and Harmsen 2012; Van der Weyde et al. 2018). We selected final camera trap deployment sites within 200 m of each grid cell's centroid, along the nearest game trails or two-tire track dirt roads to increase detection probability (Cusack et al. 2015). Camera trap placement and capture efficiency may have limited capture events (Brassine and Parker 2015; Jumeau et al. 2017; Kolowski and Forrester 2017), and sequential sampling of subareas may have violated the model's assumption of geographical closure (MacKenzie et al. 2002), but these limitations were inherent to the study design.

We mounted camera traps on metal fence posts hammered into the ground, positioned at approximately 50–70 cm height, perpendicular to the trail or road. When motion was detected, cameras took pictures every 30 s, with a burst of captures consisting of three 5MP images taken within 1 s. Cameras were active 24 h/d and checked every 10–15 d to replace SD (security digital) cards and batteries and for troubleshooting. We sorted photos to species level. Independent detections of the same species were defined when photo events were separated by more than 30 min as it is unlikely that individuals moving along game trails or roads would stay longer near the camera trap location (Rich et al. 2017b).

State covariates

We hypothesized that seasonal carnivore occupancy in the study area was influenced by three main factors: resource availability, intraguild interactions and anthropogenic influence, and selected covariates according to these drivers based on a priori hypothesis about our target species' biological requirements (Appendix A).

Covariates representing resource availability included 1) vegetation cover, 2) water accessibility, and 3) prey availability. We analyzed vegetation cover using Africa Land Cover data with spatial resolution of 100-m pixels (Buchhorn et al. 2019a, 2019b). We calculated around each camera trap station the mean fractional cover of shrubs, trees, and herbaceous vegetation within a 1-km buffer. This would represent general conditions surrounding the camera trap station applicable to our suite of variably sized species. Fractional cover within a 1-km buffer around the camera trap stations had a correlation coefficient ~1 with fractional cover within a 500-m buffer and a 2-km buffer around the camera trap stations; hence, we selected a 1-km buffer size to portray the habitat characteristics of the area sampled by each camera trap (e.g., Rich et al. 2017b). We excluded fractional cover of herbaceous vegetation from further analyses as it was negatively correlated with both the fractional cover of shrubs and trees. Fractional cover of trees was also higher at camera trap locations closer to the WPNP and may prove an indirect measure for the habitat features (i.e., rocks, relief) at the base and escarpment of the Waterberg plateau that may be preferred by certain species (i.e., leopard, caracal).

We identified water sources (i.e., natural waterholes and artificially constructed dams) using Africa Land Cover data (Buchhorn et al. 2019a, 2019b). We obtained distance to the nearest water source by estimating the Euclidean linear distance (km) from each camera trap station to the nearest water source. During the dry season, we only considered permanent water sources (i.e., holding water year-round), while during the wet season, we also accounted for seasonal water sources. We were unable to account for artificial waterpoints (i.e., water troughs) that were set up throughout the study area, particularly in the dry season. Artificial waterpoints

are frequently moved by farmers, and functionality is highly variable due to broken pipes, empty boreholes, livestock location, and weather conditions.

We quantified site-specific prey availability through estimating prey encounter rate, defined as the number of independent detections of a given prey species at that camera station per 100 trap-d (Rich et al. 2017a). We identified preferred prey for each carnivore species within the suite of species known to occur in our study area based on relevant literature and preferred prey body mass (Appendix B).

We assessed the effect of intraguild interactions by quantifying site-specific intensity of use by 1) larger competitors and 2) similar-sized competitors (Appendix C). The asymmetrical relationship between species with body mass ratio larger than 4:1 allows the larger to physically impose dominance, often taking the form of interspecific killing and/or intraguild predation of the subordinate species (Palomares and Caro 1999; Monterroso et al. 2020). On the other hand, similarity of body size has been proposed to lead competitors to seek similar prey, which reduces the likelihood of co-occurrence as a mechanism to avoid direct mortality (Linnell and Strand 2000; Donadio and Buskirk 2006).

Covariates of anthropogenic influence included 1) distance to the nearest urban built-up area, which had mostly farmhouses with permanent residents, 2) livestock availability, and 3) farm type. We identified urban built-up areas using Africa Land Cover data (Buchhorn et al. 2019a, 2019b). We estimated the Euclidean linear distance (km) from each camera trap station to the nearest built-up area as a proxy for human activity. Carnivores may also frequent these areas in search of alternative resources, particularly during the dry season. We quantified site-specific livestock availability through estimating cattle encounter rates defined as the number of independent detections of cattle at that camera station per 100 trap-d. We included farm type (livestock farm, game farm, or mixed farm) where the camera trap was placed as a categorical covariate to investigate the effect of land use practice on carnivore occupancy and biodiversity. Although local differences in wildlife-based land uses may influence occupancy estimates, conditions on game farms are assumed to be more favorable to wildlife conservation than mixed or livestock farms (Lindsey et al. 2013a). In addition, the physical barrier of the Waterberg plateau prevented natural source-sink dynamics with the surrounding farmland; thus, carnivore occupancy in our study area was assumed to be unaffected by the presence of this PA.

We accounted for heterogeneity in carnivore probability of detection by including trail type where the camera trap was placed as a site-specific detection covariate. We hypothesized that detection probability would differ between game trails and two-tire track dirt roads. Seasonal differences in vegetation density may affect probability of detection, but we fitted season-specific models with season-specific detection probabilities. Furthermore, game trails and roads were cleared of vegetation.

Covariates were checked for correlation using Spearman correlation tests. We ensured no strong collinearity existed between covariates ($|r| > 0.7$) and scaled all covariates before analysis to have a mean of 0 and standard deviation of 1. Covariates were derived using the R software v3.4.3 (R Development Core Team 2018).

Modeling framework

We used multiple single-species, single-season occupancy models with the Royle-Nichols (RN) formulation (Royle and Nichols 2003), based on the observed species-specific detection histories of the carnivores recorded in our study area. "Occupancy" was defined as the probability of a species using a particular camera trapping site, even though it may have not been recorded (MacKenzie et al. 2006). In the RN formulation for abundance-induced het-

erogeneity in detection probability, species abundance was represented by α_i and modeled as being governed by a Poisson with rate parameter λ_i. We modeled detection probability as a function of r_{ij} and α_i, whereby r_{ij} represents the probability of detection of an individual, rather than species, and α_i as the number of individuals at each site (see Tobler et al. 2015 for further discussion). Following Royle and Nichols (2003), we modeled occupancy as a function of abundance by:

$$\Psi_i \sim 1 - \exp(-\lambda_i)$$

where Ψ_i denotes the probability site occupancy at site i. We assumed detection to be independent of all spatial covariates, except for trail type, which was fit on daily sampling occasions.

We built the RN occupancy models under a Bayesian framework using *R2Jags* (Su and Yajima 2015) and *rjags* (Plummer 2018) packages in R v3.4.3 (R Development Core Team 2018), with the following formulation:

$$N_i \sim Poisson(\lambda_i) \tag{1}$$

$$\log(\lambda_i) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p$$

$$y_{ij}|N_i \sim Poisson(N_i \phi_{ij})$$

$$logit(\phi_{ij}) = \alpha_0 + \alpha_{season} x_{season}$$

where λ_i denotes the mean local abundance at site i, ϕ_{ij} denotes the detection probability at site i and sampling occasion j, β_1 to β_n denotes the coefficient of each state covariate where p denotes the number of parameters in the abundance sub model, N_i denotes local abundance at site i, and y_{ij} denotes the observed detection/nondetection at site i on occasion j.

We selected prior distributions to be vaguely informative to allow full flexibility in the estimation of model parameters.

$$\alpha_k \sim normal(0, 100)$$

$$\beta_k \sim normal(0, 100)$$

We modeled species-specific occupancy and detection and evaluated the posterior distribution of each parameter for consistency with model assumptions. The Markov chain Monte Carlo was generated using three parallel chains, with 130 000 iterations, a 20 000-iteration burn-in, and a thinning of 20 for the generality of species. Species considered rare at our study area (i.e., that accounted for a naïve occupancy estimate < 0.1), were modeled using 200 000 iterations, a 50 000 burn-in, and a thinning of 30. Furthermore, these species were modeled under a more reduced set of hypotheses (i.e., covariates) to avoid overparameterizing the models and allow numeric convergence (Appendix A). We assessed model convergence from a visual inspection of chain trace plots and from the Gelman-Rubin statistic (i.e., R-hat), where values < 1.1 suggested reliable convergence (Gelman and Rubin 1992).

Covariates were considered to have a robust effect when 95% credible intervals of estimated coefficients did not include zero, while covariates were considered to be informative when 80% credible intervals of estimated coefficients did not include zero (Arnold 2010).

To compare carnivore diversity between farm types and between seasons, we calculated site-specific diversity estimates based on the Shannon Biodiversity Index (Shannon and Weaver 1948; Margalef 1957). The Shannon Biodiversity Index provides information about community composition based on species richness and species evenness. Estimates of species richness were derived from our camera trap survey, while estimates of species evenness were derived from the mean local abundance values estimated by the RN occupancy models. Higher values indicate more diverse carnivore community assemblages.

To allow easy identification of farm-type preference per carnivore species, we calculated seasonal occupancy contrasts between farm types by subtracting species-specific occupancy estimates per pair of farm type (Curveira-Santos et al. 2021).

Results

General patterns

We detected 2 694 independent records of 10 intermediate- and large-sized carnivore species over 7 605 camera trap nights. In addition, we detected 10 315 records of 33 other mammalian wildlife species and 1 769 records of cattle. Three target species (i.e., Cape fox, cheetah, and serval) yielded low numbers of independent detections and hence were considered as rare in our study area (see Table 1). Overall mammalian species richness was similar across farm types and between seasons (range 37–43 species). Site-specific diversity of carnivores based on the Shannon Biodiversity Index was slightly lower in the wet season compared with the dry season but was generally similar across farm types (Fig. 2). For the wet season, the mean Shannon Biodiversity Index for camera trap locations on game farms was 1.51 (0.77–1.87 [95% credible interval]), on livestock farms 1.65 (1.04–1.94), and on mixed farms 1.53 (0.74–1.97). For the dry season, the mean Shannon Biodiversity Index for camera trap locations on game farms was 1.66 (0.64–1.90), on livestock farms 1.79 (1.63–1.95), and on mixed farms 1.85 (1.58–2.02).

Mean seasonal occupancy estimates were highest for caracal (0.85; wet season), African wild cat (0.69–0.73), brown hyena (0.67–0.71), and black-backed jackal (0.60–0.80) (Fig. 3; see Table 1). Mean seasonal occupancy estimates were lowest for serval (0.13–0.14), Cape fox (0.07–0.29), bat-eared fox (0.16–0.38), cheetah (0.29–0.32), and aardwolf (0.24; dry season). Mean seasonal occupancy estimates were intermediate for leopard (0.45–0.58), caracal (0.44; dry season), and aardwolf (0.43; wet season). The mean probability of occupancy was higher in the dry than wet season for leopard, brown hyena, African wild cat, bat-eared fox, serval, and black-backed jackal. The opposite pattern was found for cheetah, aardwolf, caracal, and Cape fox.

During the dry season, carnivore occupancy tended to be higher on game farms than livestock farms and mixed farms, except for caracal and bat-eared fox (see Figs. 3 and 4). During the wet season, carnivore occupancy tended to be similar or higher on livestock farms and mixed farms compared with game farms, except for serval.

Mean local abundance tended to be similar or higher during the dry season compared with the wet season (see Table 1). Species with higher mean local abundance values during the wet season were estimated with less precision. For most species, mean local abundance was similar across farm types, or estimates had wide and overlapping credible intervals (Appendix D). Only during the dry season, brown hyena and black-backed jackal tended to be more abundant on game farms (2.15 and 2.11 individuals per site, respectively) compared with mixed farms (1.1 and 1.73 individuals) and livestock farms (1.16 and 1.58 individuals). Bat-eared fox tended to be less abundant on game farms during both seasons (wet season: 0.03 individuals; dry season: 0.15 individuals) compared with mixed (wet season: 0.13 individuals; dry season: 0.35 individuals) and livestock farms (wet season: 0.22 individuals; dry season: 0.54 individuals).

Detection probability was higher on two-tire track dirt roads than on game trails, except for bat-eared fox and Cape fox in the wet season, and for cheetah and serval in the dry season.
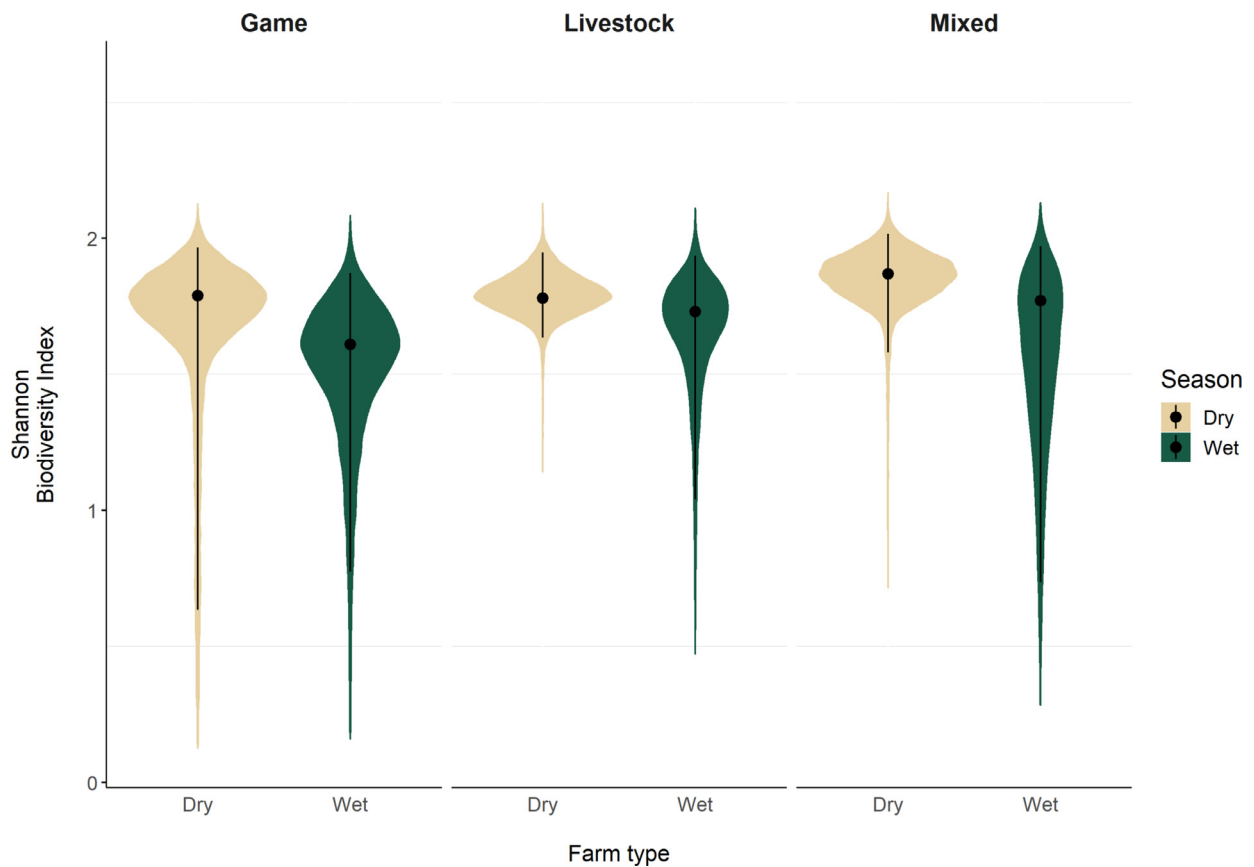
Figure 2. Site-specific seasonal carnivore diversity per farm type based on the Shannon Biodiversity Index.

A summary of the most relevant parameter estimates of site co-variates is presented in Table 2 and further described in the next sections. The full set of model parameter estimates is summarized in Appendix E.

Resource availability

The fractional cover of shrubs had a positive effect on the probability of occupancy of Cape fox, caracal (dry season* [asterisk indicates "95% credible interval did not include zero, i.e., robust effect"], wet season), bat-eared fox (wet season), and African wild cat (wet season) and had a negative effect on the probability of occupancy of serval (dry season, wet season*), brown hyena (dry season), bat-eared fox (dry season*), African wild cat (dry season), and cheetah (wet season) (Fig. 5). The fractional cover of trees had a positive effect on the probability of occupancy of leopard, brown hyena (wet season), and caracal (wet season) and had a negative effect on the probability of occupancy of bat-eared fox (dry season*, wet season), black-backed jackal*, brown hyena (dry season), African wild cat, aardwolf (dry season*) and caracal (dry season*).

During the dry season, distance to water had a positive effect on the probability of occupancy of caracal and leopard and had a negative effect on the probability of occupancy of brown hyena. During the wet season, distance to water had a negative effect on the probability of occupancy of leopard, brown hyena, and caracal (Fig. 5).

Wild prey availability had a positive effect on the probability of occupancy of leopard, brown hyena (dry season, wet season*), and black-backed jackal and had a negative effect on the probability of occupancy of caracal and African wild cat (wet season) (see Fig.

5). The strength of association tended to be stronger in the wet season.

Intraguild interactions

The encounter rates of larger competitors had a positive effect on the probability of occupancy of bat-eared fox (dry season*), caracal (dry season), aardwolf (wet season), and black-backed jackal (wet season) and had a negative effect on the probability of occupancy of serval, aardwolf (dry season), black-backed jackal (dry season), Cape fox (dry season), African wild cat (wet season), and caracal (wet season) (see Fig. 5). The association was generally stronger in the dry season, except for African wild cat.

The encounter rates of similar-sized competitors had a positive effect on the probability of occupancy of serval, brown hyena (dry season), Cape fox (dry season), aardwolf (wet season), and leopard (wet season) and had a negative association with the probability of occupancy of black backed jackal (dry season*, wet season), caracal (dry season*, wet season), African wild cat (dry season), aardwolf (dry season), leopard (dry season), brown hyena (wet season), and cheetah (wet season) (see Fig. 5).

Anthropogenic influence

Distance to urban built-up areas positively influenced the probability of occupancy of aardwolf (dry season), leopard (wet season), brown hyena (wet season), caracal (wet season), and African wild cat (wet season) and negatively affected the probability of occupancy of bat-eared fox (dry season*, wet season), brown hyena (dry season), caracal (dry season), and African wild cat (dry season) (see Fig. 5).
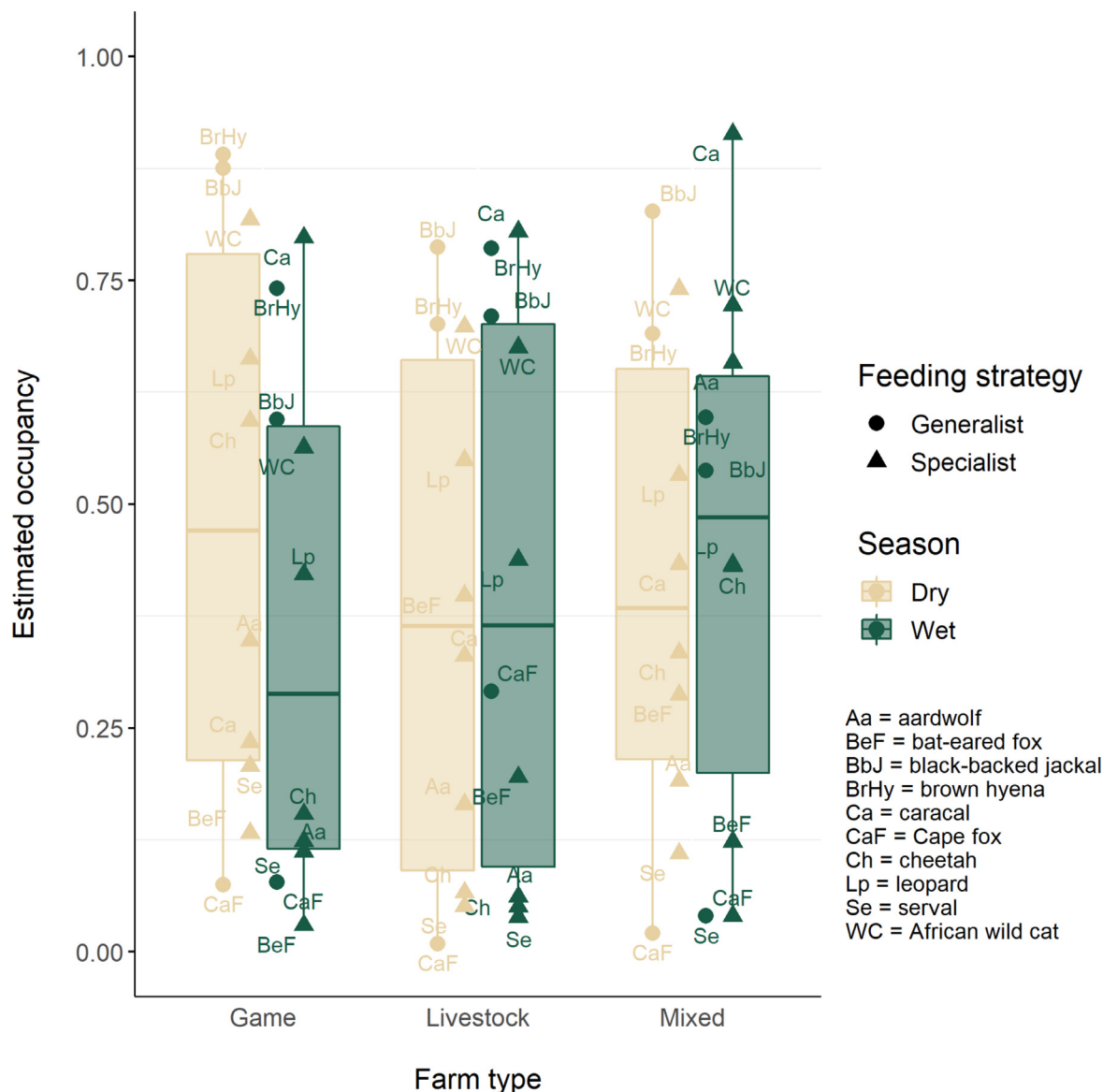
Figure 3. Mean seasonal carnivore occupancy estimates per farm type.

The encounter rates of cattle had a positive effect on the probability of occupancy of leopards (dry season) and a negative effect on the probability of occupancy of brown hyena (see Fig. 5).

Discussion

General patterns

In line with earlier studies, we found that rangelands can support relatively diverse carnivore communities (Kinnaird and O'Brien 2012; Msuha et al. 2012; Kiffner et al. 2015; Drouilly et al. 2018a), with estimates of occupancy and diversity comparable with PAs (Rich et al. 2017a). In fact, most species of the southern African carnivore guild were well represented in our study area, with the exception of the largest and/or group-living species (i.e., lion, spotted hyena, and African wild dog). The generalized patterns of diversity and occupancy across different farm types suggest that the structure of this free-ranging carnivore community tends to be homogeneous. In contrast to landscapes where clear segregation in land use practice exists (Kinnaird and O'Brien 2012; Msuha et al.

2012; Schuette et al. 2013), our study showed that local-scale variation in farm types did not limit carnivore distributions. This variation may, however, be essential for the persistence of the carnivore guild, which may be explained by source-sink dynamics at the metacommunity scale (Mouquet and Loreau 2003; Curveira-Santos et al. 2021) and the large home ranges of individual carnivores crossing multiple farm types (Marker et al. 2008). Namibian multiple-use rangeland may function as a viable socioecological landscape and act as an important link between PAs to benefit carnivore conservation on a national level.

At the spatial scale of the study area, our estimates for carnivore diversity, occupancy, and mean local abundance were largely similar across seasons, contrasting with our predictions that these parameters would be higher during the wet season due to increased resource availability. In semiarid grazing areas, long-term dynamics of ungulate populations are restricted by availability of key resources during the dry season (Illius and O'Connor 2000). Bottom-up control of prey populations directly affects carnivore communities (Burkepile et al. 2013; Gigliotti et al. 2020), which may explain the similarities in carnivore diversity and occupancy

Table 2

Summary of estimated coefficients for covariates with a robust effect (95% credible intervals [CI] did not include zero) or that are considered informative (80% credible intervals did not include zero). Values in bold show a robust effect.

| Covariate	Season	Species	β	95% CI	80% CI
Shrub cover	Dry	Bat-eared fox	**−0.34**	**(−0.69, −0.03)**	**(−0.54, −0.14)**
		Cape fox	0.93	(−0.21, 2.11)	(0.17, 1.69)
		Caracal	**0.43**	**(0.12, 0.75)**	**(0.23, 0.63)**
	Wet	Cape fox	0.84	(−0.05, 1.8)	(0.24, 1.44)
		Caracal	0.34	(−0.07, 0.77)	(0.07, 0.61)
		Cheetah	−1.2	(−2.93, 0.67)	(−2.39, −0.01)
		Serval	**−1.96**	**(−3.75, −0.03)**	**(−3.15, −0.77)**
Tree cover	Dry	Aardwolf	**−0.62**	**(−1.13, −0.13)**	**(−0.95, −0.29)**
		Bat-eared fox	**−0.56**	**(−0.96, −0.18)**	**(−0.82, −0.3)**
		Black-backed jackal	**−0.41**	**(−0.59, −0.24)**	**(−0.53, −0.29)**
		Caracal	**−0.44**	**(−0.8, −0.09)**	**(−0.67, −0.21)**
	Wet	Black-backed jackal	**−0.4**	**(−0.67, −0.13)**	**(−0.58, −0.22)**
Prey availability	Dry	Black-backed jackal	0.13	(−0.05, 0.3)	(0.01, 0.25)
		Caracal	−0.31	(−0.78, 0.09)	(−0.59, −0.03)
	Wet	African wild cat	−0.35	(−0.75, 0.01)	(−0.59, −0.11)
		Black-backed jackal	0.15	(−0.06, 0.34)	(0.02, 0.28)
		Brown hyena	**0.33**	**(0.16, 0.49)**	**(0.23, 0.43)**
		Leopard	0.26	(−0.01, 0.5)	(0.09, 0.43)
Larger competitors	Dry	Bat-eared fox	**0.46**	**(0.12, 0.77)**	**(0.26, 0.66)**
		Cape fox	**−2.68**	**(−6.05, −0.17)**	**(−4.65, −0.71)**
	Wet	African wild cat	−0.36	(−0.94, 0.1)	(−0.69, −0.03)
Similar-sized competitors	Dry	Black-backed jackal	**−0.22**	**(−0.43, −0.02)**	**(−0.36, −0.08)**
		Caracal	**−0.95**	**(−1.73, −0.27)**	**(−1.42, −0.48)**
		Leopard	−0.43	(−1.01, 0.03)	(−0.78, −0.08)
	Wet	Leopard	0.21	(−0.03, 0.42)	(0.07, 0.35)
		Serval	1.75	(−0.68, 3.84)	(0.25, 3.25)
Distance to urban built-up area	Dry	African wild cat	−0.24	(−0.53, 0.04)	(−0.43, −0.05)
		Bat-eared fox	**−1.02**	**(−1.6, −0.5)**	**(−1.38, −0.66)**
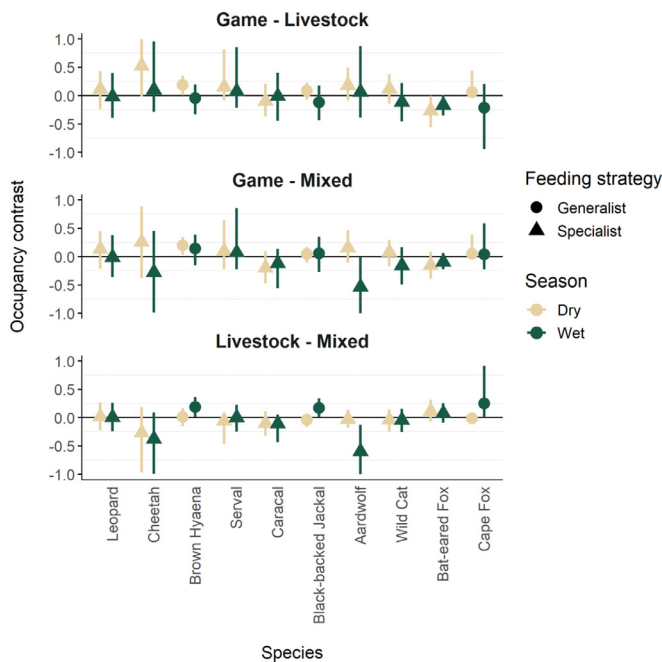
Figure 4. Species-specific occupancy contrasts between different farm types for 10 carnivore species on freehold farmland in north-central Namibia. Occupancy contrasts are derived by pairwise subtracting species-specific occupancy estimates between the different farm types. Error bars indicate 95% credible intervals.

across seasons. However, at the smaller spatial scale, we found seasonally contrasting covariate associations, which may suggest that carnivores select seasonally rewarding patches within their home ranges.

Carnivore occupancy during the dry season tended to be higher on game farms, which may indicate that these farms could act as refuges during periods of resource scarcity. Yet more detailed analysis of movement patterns would be required to confirm this hypothesis. In addition, game farms may not necessarily be safe havens as human persecution may occur across farm types (Marker et al. 2003; Schumann et al. 2008). Carnivores also get trapped and killed on game farms, where they may predate on highly prized game species (Marker et al. 2003). Improving tolerance toward carnivores across the landscape is important for human-carnivore coexistence and could be facilitated through conservancy membership (i.e., when land owners participate in collaborative land management to conserve biodiversity) (Schumann et al. 2008; Lindsey et al. 2009).

Throughout the study area, generalist species were relatively common, while specialist species were more restricted in space use, arguably because of their specific ecological requirements (Fedriani et al. 2001; Chubaty et al. 2014). Still, the probability of occupancy of leopard, African wild cat, and caracal (wet season) was relatively high, suggesting some variability within generalist/specialist feeding strategies as we defined them (Chubaty et al. 2014; Balme et al. 2020). It also highlights the ability of these species to survive well within this human-dominated matrix when compared with other specialists. In fact, despite being classified as specialists according to Jones et al. (2009) criteria, these species are well known to consume a wide range of prey within the same feeding category, which likely allows them to fulfill their ecological requirements under a broad spectrum of conditions (Palmer and Fairall 1988; Hayward et al. 2006; Drouilly et al. 2018b; Balme et al. 2020).

Cape fox, serval, and cheetah were rare in our study system, with estimated occupancy probabilities around 0.3 and lower. Despite being considered a generalist, the low Cape fox abundance in our study area could be related to the combined effect of the study areas' location at the northern edge of Cape fox's range (Hoffmann 2014), human persecution, and interspecific competition with black-backed jackals (Kamler and MacDonald 2014).
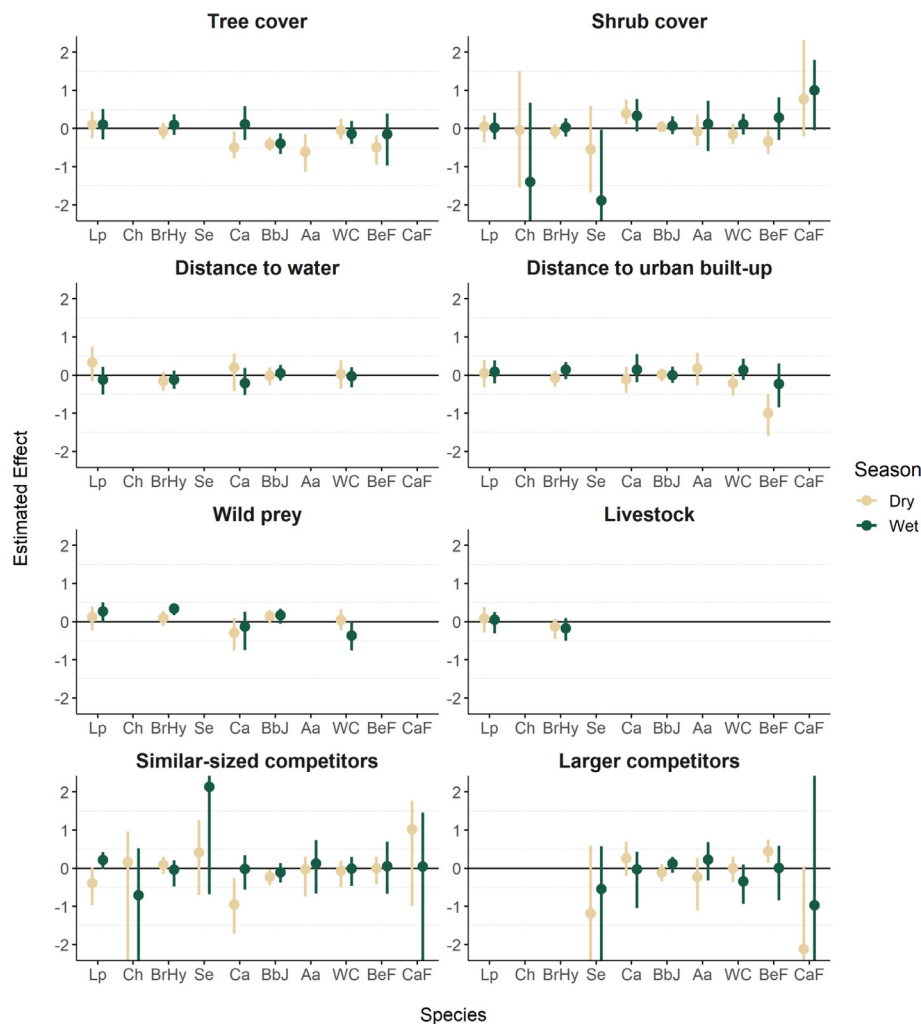
Figure 5. Predicted seasonal associations of carnivore occupancy for 10 species with six occupancy covariates on freehold farmland in north-central Namibia. Error bars indicate 95% credible intervals; Lp, leopard; Ch, cheetah; BrHy, brown hyena; Se, serval; Ca, caracal; BbJ, black-backed jackal; Aa, aardwolf; WC, African wild cat; BeF, bat-eared fox; CaF, Cape fox.

Namibia hosts a low-density (0.63−1.28 serval/100 km²), geographically limited population of servals (Edwards et al. 2018), while cheetahs have a more extended range, although similar and stable densities (1.94 cheetah/100 km²) are found in our study area (Fabiano et al. 2020). Targeted camera trap placement may be needed to increase detection of these rarer species in our study system (Brassine and Parker 2015; Cusack et al. 2015), yet the low detection of cheetah may be of concern as the study area is located within their regional stronghold (Weise et al. 2017).

Overall, detection probability was higher on two-tire track dirt roads compared with game trails. This suggests frequent use of roads by carnivores, which may facilitate communication, foraging, and moving (Hill et al. 2020; Rafiq et al. 2020). In contrast, road mortality may have significant impacts on carnivore populations (Forman and Alexander 1998), but the roads in our study area were mostly private roads with infrequent vehicle traffic and therefore assumed to have limited impact.

Covariate associations

The species-specific correlations with different covariates revealed interesting aspects of carnivore dependency on natural resources, their complex interactions with intraguild members, and seasonally contrasting associations with anthropogenic activities.

While the overall estimates of carnivore occupancy across the study area were similar across seasons, resource scarcity during the dry season appeared to have a predominant influence on the strength and direction of the covariate associations.

The different associations of carnivore occupancy with habitat covariates largely aligned with our a priori hypotheses of species-specific preferences. Carnivores that showed weak associations with habitat covariates are those considered habitat generalists (Rosenzweig 1981), while season-specific associations may be determined by reproductive or foraging strategies (Nielsen et al. 2010; Davidson et al. 2012). Carnivores that showed a positive association with availability of shrub cover are known to cope well with bush encroachment across Namibian rangelands (Kauffman et al. 2007). However, mean fractional cover of shrubs around the camera trap locations was mostly below 50%, which prevents us from extending our inference about the patterns of carnivore occupancy to highly shrub-encroached areas. Furthermore, bush encroachment reduces landscape heterogeneity, which is essential for intraguild carnivore coexistence (Pereira et al. 2012). Therefore, the importance of habitat structure in human-altered landscapes must not be neglected during landscape design (Manlick et al. 2020).

We found a tendency for carnivore occupancy to be independent of permanent sources of surface water during the dry season, contrasting with our initial hypothesis and previous studies

performed elsewhere (Pettorelli et al. 2010; Valeix et al. 2010; Schuette et al., 2013; Abade et al. 2014). We suggest that this could relate to our incapacity to account for many artificial and mobile waterpoints provided by farmers, which could mask the patterns of this valuable resource, particularly during the dry season (Edwards et al. 2015; Rich et al. 2017b). In arid and semiarid areas, many herbivore species aggregate around scarce water sources (Thrash et al. 1995; Redfern et al. 2003). Therefore, prey availability may be an indirect measure of water availability. We acknowledge that certain prey species (e.g., springbok and gemsbok) may occur independently of surface water availability as they balance most of their hydric needs from dietary water (Nagy and Knight 1994; Boyers et al. 2020).

In general, carnivore occupancy was positively related to availability of their preferred wild prey, as is the general trend found in other carnivore occurrence studies (Fuller & Sievert 2001; Rich et al. 2017a; Carbone & Gittleman 2002). However, our measure of prey availability may not have provided a good representation of caracal and African wild cat dietary preferences. These carnivores are known to consume a high proportion of prey smaller than those captured by camera-trapping protocols (Palmer and Fairall 1988; Rich et al. 2017b; Drouilly et al. 2018b). Hence, camera trap-based encounter rates may have provided a skewed estimate of the true site-specific prey availability for these smaller cats. One of the main threats to carnivores is prey depletion, so maintaining and restoring healthy populations of wild prey is important for the broader conservation of carnivore communities and overall biodiversity (Wolf and Ripple 2016; Rich et al. 2017a).

Our results did not support our initial spatial segregation hypothesis for competitor species with asymmetrical body mass ratios, which was supported by equivalent studies elsewhere (Palomares and Caro 1999; Edwards et al. 2015; Davis et al. 2018; Monterroso et al. 2020). Carnivore associations with larger competitor species on Namibian multiple-use rangelands revealed complex intraguild interactions, with season- and species-specific associations to the intensity of site-use by dominant carnivores. Positive associations with dominant carnivores were identified for the carnivore community in northern Botswana (Rich et al. 2017b) and may be attributed to carnivore densities being below the threshold at which avoidance begins shaping community structure (Palomares and Caro 1999; Caro and Stoner 2003). Furthermore, when resources are scarce, options for spatial partitioning with larger carnivores may be limited so that intraguild coexistence is facilitated through temporal resource partitioning (Hayward and Slotow 2009; Schuette et al. 2013; Edwards et al. 2015), body mass effects (Wilson et al. 2015), and food provisioning at kills (Yarnell et al. 2013; Bashant et al. 2020). Alternatively, fine-scale avoidance behavior may have not been captured by our level of analysis. This limitation is inherent to most protocols based on camera trapping, even when accounting for conditional co-occurrence probabilities (Cusack et al. 2017).

On the other hand, we found a relatively uniform pattern of avoidance between similar-sized competitors (i.e., dietary competitors), especially during the dry season and between intermediate-sized competitors. This suggests spatial niche partitioning between similar-sized competitors, which might be more intense when resources are scarce because of competition for similar prey (Palomares and Caro 1999; Linnell and Strand 2000; Donadio and Buskirk 2006). Our results contrast with earlier findings on the patterns of carnivore co-occurrence (Edwards et al. 2015; Davis et al. 2018; Monterroso et al. 2020), so we recommend further research on intraguild carnivore interactions in semiarid systems.

Anthropogenic disturbance did not result in explicit spatial avoidance for most of our target species. In fact, we found seasonally contrasting associations for certain carnivores with distance to urban built-up areas. During the dry season, carnivores may become more reliant on alternative resources, which are often of higher availability around farmhouses. Therefore, they may exhibit behavioural adjustments, such as changing diel activity patterns, to minimize the risks of encounters with humans in areas with high levels of human interference, rather than simply avoiding them (Schuette et al. 2013; Carter et al. 2015; Oriol-Cotterill et al. 2015). This strategy could allow many carnivore species to use rewarding areas in periods of resource scarcity with reduced risks for their survival and may explain the relative diversity of carnivores across the study area.

Livestock availability had limited impact on the distributions of larger carnivores, which were more strongly determined by availability of wild prey. This stresses the importance of preserving and restoring wild prey populations, which may promote human-carnivore coexistence across rangelands (Khorozyan et al. 2015). Opportunistic hunters, such as leopards, may occasionally kill cattle as alternative prey source (Kolowski and Holekamp 2006; Kandel et al. 2020), which could explain the weak association between leopard occupancy and livestock availability during the dry season (Khorozyan et al. 2015). Well-considered livestock husbandry practices should be implemented to reduce opportunistic depredation incidents (Breitenmoser et al. 2005).

Management implications

Local-scale variation in land use practices may result in greater diversity and viability of carnivore communities on rangelands, compared with broad-scale, homogenous livestock farmland. Such landscape-level approaches may enable rangelands to maintain ecological integrity and thus require consideration during landscape planning of nonprotected areas. Furthermore, private lands are known to provide significant conservation benefits (Lindsey et al. 2013b; Stolton et al. 2014; Clements et al. 2019; Shumba et al. 2020), where the presence of game farms may be important to reinforce the natural prey base. We encourage future research to investigate carnivore movements and mortality rates between different farm types as this could provide important insights into the functional landscape connectivity and source-sink dynamics in this study system.

Human-carnivore coexistence within semiarid rangelands is a complex issue that cannot be solved with one answer. Identifying and implementing conservation measures that are targeted at increasing the likelihood of carnivore persistence (e.g., local-scale variation in land use practices) is an important step to ensure the long-term viability of carnivore assemblages on semiarid rangelands in Africa. In addition, maintaining sufficient and suitably-sized natural prey in the landscape is important as it reduces the need for carnivores to seek alternative food sources, particularly during the dry season. Finally, preserving functional diversity will also be critical to maintain ecological resilience of semiarid rangelands as projections of climate change show that droughts are likely to become more frequent and more severe (Le Houérou 1996).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2021.07.007.

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