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RESEARCH ARTICLE

Droughts reshape apex predator space use and intraguild overlap

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Abstract

1. Droughts are increasing in frequency and severity globally due to climate change, leading to changes in resource availability that may have cascading effects on animal ecology. Resource availability is a key driver of animal space use, which in turn influences interspecific interactions like intraguild competition. Understanding how climate-induced changes in resource availability influence animal space use, and how species-specific responses scale up to affect intraguild dynamics, is necessary for predicting broader community-level responses to climatic changes.
2. Although several studies have demonstrated the ecological impacts of drought, the behavioural responses of individuals that scale up to these broader-scale effects are not well known, particularly among animals in top trophic levels like large carnivores. Furthermore, we currently lack understanding of how the impacts of climate variability on individual carnivore behaviour are linked to intraguild dynamics, in part because multi-species datasets collected at timescales relevant to climatic changes are rare.
3. Using 11 years of GPS data from four sympatric large carnivore species in southern Africa—lions (*Panthera leo*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*) and cheetahs (Acinonyx jubatus)—spanning 4 severe drought events, we test whether drought conditions impact (1) large carnivore space use, (2) broad-scale intraguild spatial overlap and (3) fine-scale intraguild interactions.
4. Drought conditions expanded space use across species, with carnivores increasing their monthly home range sizes by 35% (wild dogs) to 66% (leopards). Drought conditions increased the amount of spatial overlap between lions and subordinate felids (cheetahs and leopards) by up to 119%, but only lion-cheetah encounter rates were affected by these changes, declining in response to drought.

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5. Our findings reveal that drought has a clear signature on the space use of multiple sympatric large carnivore species, which can alter spatiotemporal partitioning between competing species. Our study thereby illuminates the links between environmental change, animal behaviour and intraguild dynamics. While fine-scale avoidance strategies may facilitate intraguild coexistence during periodic droughts, large carnivore conservation may require considerable expansion of protected areas or revised human-carnivore coexistence strategies to accommodate the likely long-term increased space demands of large carnivores under projected increases in drought intensity.

KEYWORDS

Acinonyx jubatus, climate change, intraguild competition, large carnivore ecology, *Lycaon pictus*, movement ecology, *Panthera leo*, *Panthera pardus*

1 | INTRODUCTION

Climatic extremes such as droughts are increasing in frequency and severity globally, with cascading effects on wildlife (Bailey & Pol, 2016; IPCC, 2021; Parmesan & Yohe, 2003). Water is a key resource for all living things, and water availability greatly impacts animal movement, distribution and behaviour (Gedir et al., 2020; McCluney et al., 2012). As such, both acute and long-term changes in resource availability induced by drought have important implications for ecological communities. Drought can confer acute reductions in surface water availability (Inbar & Bruins, 2004; Lake, 2003; Leblanc et al., 2009), large-scale vegetation die-offs (Kane et al., 2011) and reductions in availability and nutritional quality of vegetation, which in turn can cause prey body condition to decline and mortality to increase, potentially increasing predator access to prey (Knight, 1995). Drought can also have long-term impacts on resource availability, including reductions in broad-scale spatial heterogeneity (Pennington & Collins, 2007), changes in plant community composition (Pearson et al., 2017), and vertebrate population declines, genetic bottlenecks and extirpation (Abraham et al., 2019; Duncan et al., 2012; Knight, 1995).

Such drought-induced changes can have important impacts on wildlife community dynamics. For example, by changing the distribution of resources over space, droughts may alter the frequency of trophic interactions (Amundrud et al., 2019). However, although alterations in species interactions are an important link between environmental change and wildlife population declines (Cahill et al., 2013; Ockendon et al., 2014), the behavioural pathways through which environmental change alters species interactions are poorly understood. One mechanism by which this could occur is through changes in competitive dynamics between co-occurring species. As ecological niche theory predicts that species with similar requirements cannot coexist in resource-limited systems unless they use shared resources differently, we would expect dominant species to outcompete subordinate species (Gause, 1934). To avoid this competitive exclusion, animals frequently partition resource use in time and space. If environmental changes such as drought lead to resource scarcity, however, this coexistence may be jeopardized as animals compete for increasingly limited resources, resulting in elevated competition between species (Head et al., 2012; Prugh et al., 2018). Although numerous studies have demonstrated the impacts of drought at the population or community level (Duncan et al., 2012; Goldingay et al., 2023; Prugh et al., 2018), the behavioural responses of individuals that drive these broader-scale impacts are not well known.

Animal movement is a key behavioural process linking individual responses to resource availability with effects on competition and other species interactions (Nathan et al., 2008). Indeed, the space use of many species is strongly influenced by the spatiotemporal distribution of resources within their environment (Abrahms et al., 2021; Hayward et al., 2009; Mueller et al., 2011). Animal movement also fundamentally determines animal occurrence in space and time, which affects interaction patterns (Costa-Pereira et al., 2022). For example, in mammalian carnivores, interspecific variation in space use and habitat selection underpins patterns of spatiotemporal overlap between species, which in turn drive intraguild interactions (Jensen & Humphries, 2019). Thus, although movement responses occur at the individual level, they can scale up to impact community dynamics (Costa-Pereira et al., 2022; Jeltsch et al., 2013). Drought events are a valuable lens through which to examine this phenomenon, as reduced access to resources such as food and water may lead to increased competition among consumers, or, conversely, may cause competitive release (Belant et al., 2010; Pickett et al., 2018). Understanding how climate-induced resource variability impacts animal movement, and how species-specific behavioural responses scale up to impact community dynamics, is critical for predicting community-level responses to climate extremes like droughts.

Top predators remain among the most understudied taxa regarding the ecological impacts of climate variability (Abrahms et al., 2022; Cahill et al., 2013; Ockendon et al., 2014; Prugh et al., 2018), and yet understanding the forces shaping the behavioural and community responses of top predators to climate extremes is critical given that upper trophic levels have cascading top-down ecological consequences on ecosystems. Large carnivores, in particular, are keystone species that contribute substantially both to maintaining healthy ecosystems and to a range of services that benefit people (Ripple et al., 2014). For example, large carnivores contribute to a multi-billion-dollar global ecotourism industry (Esposito et al., 2020) and they reduce fatal vehicle collisions and zoonotic disease transmission by suppressing herbivore populations (Gilbert et al., 2017; Packer et al., 2003). In addition, large carnivore species are vulnerable to environmental extremes, which may threaten their viability under climate change (Rabaiotti et al., 2023). However, the effects of climate variability on behaviour and ecology in free-living large carnivore guilds is particularly challenging to identify, as their large home ranges, low population densities and cryptic behaviours make long-term observations over a range of climatic conditions difficult to obtain (Smith et al., 2017). The behavioural responses of large carnivores to drought events are therefore a key area for further study to uncover the potential impacts of increasingly common climatic extremes on carnivore persistence. Furthermore, we currently lack understanding of how the impacts of climate variability on individual carnivore behaviour are linked to broader ecological changes, such as intraguild dynamics.

Here, we examine the effects of drought on the spatial behaviour of four sympatric large carnivore species in southern Africa—lions (*Panthera leo*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*)—to determine the extent to which climate-driven resource availability impacts carnivore space use and intraguild dynamics. Southern Africa is experiencing progressively frequent and severe drought events (Chivangulula et al., 2023) and is also home to a large carnivore guild that exhibits complex interspecific interactions as they compete for similar resources in a shared landscape (Vanak et al., 2013). Lions are the largest and most competitively dominant species within the guild. The space use of smaller predators such as African wild dogs and cheetahs is consequently strongly influenced by their avoidance of larger and more dominant competitors (Broekhuis et al., 2013; Mills & Gorman, 1997), whereas the space use of dominant predators is primarily dictated by prey distributions (Vanak et al., 2013). In addition, water availability can significantly influence the behaviour and distributions of some African large carnivore species, with unknown consequences for intraguild competition. For example, lions move seasonally in response to water conditions, seeking out surface water in dry conditions when wild prey are aggregated around waterholes (Valeix et al., 2010). Carnivores may have larger home ranges when resources like prey or water sources are more sparsely distributed (Moyer et al., 2007; Tuqa et al., 2014), or alternatively may have smaller home ranges due to greater concentration around patchy water sources (Edwards et al., 2013); either of these processes may alter spatial partitioning between competing species.

We specifically investigated the effects of drought on (1) large carnivore space use, (2) broad-scale intraguild spatial overlap and (3) fine-scale intraguild interactions. To evaluate the effects of drought on carnivore space use, we examined whether carnivore home range sizes change in response to drought conditions. We considered two sets of alternative hypotheses: (1a) Carnivores will exhibit larger home ranges during drought, for example by ranging over greater areas to locate scarce resources; or (1b) Carnivores will exhibit smaller home ranges during drought, for example due to concentrating their movements around predictable resources. Second, to evaluate the effects of drought on broad-scale competitive dynamics, we examined whether spatial overlap between carnivore species changes during drought conditions. We hypothesized that (2a) drought will exacerbate spatial competitive exclusion of subordinate species, leading to decreased spatial overlap between subordinate and dominant species. Alternatively, we hypothesized that (2b) drought will increase subordinate carnivores' risk tolerance, leading to increased spatial overlap between subordinate and dominant species. Finally, to evaluate the effects of any drought-induced spatial changes on finer-scale intraguild interactions, we examined whether drought conditions affect interspecific encounter rates. Analogous to (2a) and (2b), we considered the alternative hypotheses of (3a) increased competitive exclusion leading to reduced encounter rates during drought; or (3b) increased risk tolerance leading to increased encounter rates during drought.

2 | MATERIALS AND METHODS

2.1 | Study system and data collection

Our study area was located in northern Botswana's Okavango Delta (*c*. 2700 km^2; centred at 19°31′ S, 23°37′ E; elevation *c*. 950 m), which encompasses Moremi Game Reserve and its adjacent wildlife management areas. This region experiences strong seasonal climatic variation, with a wet season occurring between December and May and a dry season occurring between June and November (mean annual rainfall ~300–600 mm/year). Seasonal flooding in the Okavango Delta is primarily influenced by rainfall in the Angolan Highlands, with river discharge and flood extent in the Delta lagging about 6 months behind Angola's climatic conditions (Byakatonda et al., 2018). Our study region experienced several government-designated drought events over the course of the study period, 2011–2022, with drought years classified as either 'severe' or 'extreme' occurring in 2014/15, 2015/16, 2018/19 and 2022/2023 (Ministry of Local Government and Rural Development, 2023; Figure 1). In addition to reduced local precipitation during these periods, the Delta experienced generally low flooding levels, reflecting widespread drought conditions across southern Africa, including in the Angolan Highlands (Mfundisi et al., 2021). For example, the 2019 drought, one of the most severe in recent history, resulted in markedly reduced inundation extents in the Okavango Delta (Mfundisi et al., 2021). Thus, classified drought events in the study area are characterized by reduced surface water availability from both local rainfall and floodwater (Byakatonda et al., 2018; Moses et al., 2023).

Between 2011 and 2022, we collected GPS data from 31 African wild dogs, 14 lions, 8 leopards and 5 cheetahs across a range of

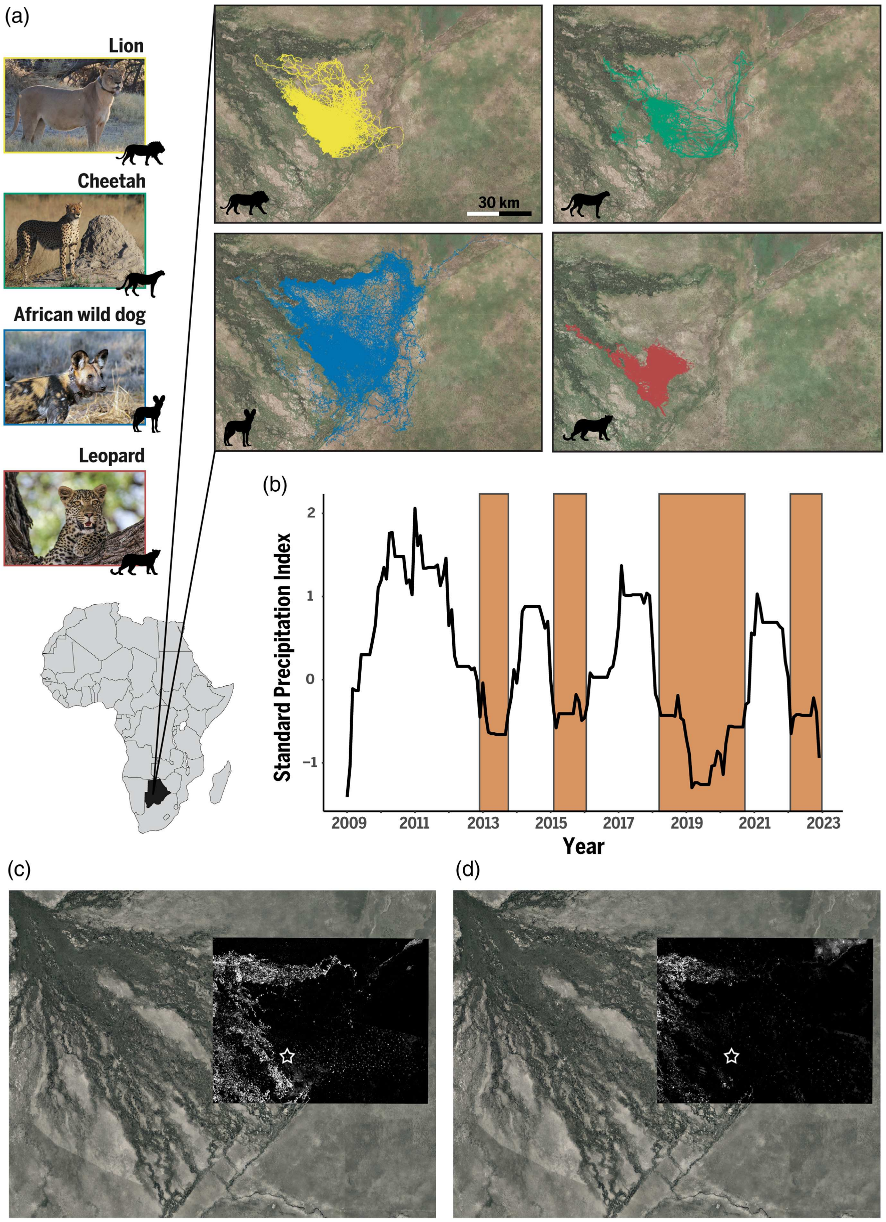

FIGURE 1 (a) Study area in northern Botswana's Okavango Delta, overlaid with GPS tracks from collared lions, cheetahs, African wild dogs and leopards. (b) Time series of 12-month lagged Standard Precipitation Index (SPI) values over the study period calculated from daily rainfall measurements at our field site, with government-designated severe-to-extreme drought events indicated with shaded boxes. (c, d) Satellite imagery of the Okavango Delta, overlaid with a raster of surface water extent in the study area during a wet period (c), the 2016–2017 wet season, and during a drought period (d), the 2018–2019 wet season, for demonstration. The star icon denotes the field site location. Satellite imagery was obtained from Google Earth.

climatic conditions (Figure 1, Table S1). Total days of data collected were 9497 days (median 210 days/individual) for wild dogs, 9302 days (median 349 days/individual) for lions, 3522 days (median 222 days/individual) for leopards and 3297 days (median 606 days/individual) for cheetahs (Table S1). Animals were captured across the study area based on a combination of spoor tracking, sightings and baited trap sites as part of a long-term carnivore monitoring program (Rafiq et al., 2023). For collars deployed between 2011 and 2018, GPS relocations were collected at 5-min fix intervals when animals were active, and at 1-h intervals when animals were resting (Hubel et al., 2016, 2018; Wilson et al., 2018). Collars deployed after 2018 collected relocations at 3-hour intervals. All capture and collaring was approved by the Royal Veterinary College Ethics and Welfare Committee, the University of Washington Animal Care and Use Committee (Protocol #4514-01) and the Botswana Department of Wildlife and National Parks.

2.2 | Drought index

To quantify drought severity, we used the Standard Precipitation Index (SPI), which is commonly used to describe drought conditions (Cancelliere et al., 2007; Tirivarombo et al., 2018) and is the metric used by the Republic of Botswana to designate drought events (Batisani, 2020). SPI compares the precipitation total within a specific time period with the historical average precipitation total during the same time of year (e.g. for a given location, it compares the precipitation total from January–March 2022 with the average January–March precipitation totals from all recorded years). In this way, SPI is indicative of precipitation anomalies within a specified time period at an inter-annual timescale, and is independent of intra-annual variation. Negative SPI values represent anomalously dry conditions, and positive SPI values represent anomalously wet conditions.

We generated monthly SPI values in our study area based on 32.7 years (January 1990–October 2022) of daily precipitation measurements collected from a rain gauge at our field site using the National Drought Mitigation Center's SPI Generator (National Drought Mitigation Center, 2018). Across the study period, the minimum SPI value recorded was −1.26 and the maximum SPI value recorded was 1.72; the 25th percentile of SPI values was −0.5 and the 75th percentile was 1.0. SPI values <−0.4 represented severe to extreme drought events based on the government drought classifications (Figure 1). We hypothesized that the ecological effects of drought, such as changes in resource availability, might occur at multiple temporal scales. For instance, acute resource shifts at the seasonal scale may represent environmental changes such as surface water availability or primary production, whereas shifts at the annual scale may represent potential longer-term ecological changes such as changes in prey abundance or distribution. We therefore tested lagged SPI values to reflect the effects of drought at both acute (previous 3 months' total precipitation) and longer-term (previous 12 months' total precipitation) timescales.

2.3 | Home range, spatial overlap and encounter estimation

To quantify carnivore home ranges, we fit Brownian Bridge Movement Models to GPS relocations (Horne et al., 2007) using the R package *adehabitatHR* (Calenge, 2023). All GPS relocations were first regularized to a 3-hour sampling rate to match the lowest resolution data collected. This resulted in a total of 57,759 fixes (median 1548 fixes/individual) for wild dogs, 54,771 fixes (median 2523 fixes/individual) for lions, 16,291 fixes (median 1782 fixes/individual) for leopards and 14,914 fixes (2213 fixes/individual) for cheetahs (Table S1). Using these data, we estimated monthly home range (95% utilization distribution) and core area (50% utilization distribution) sizes for each individual across the study period. Monthly estimates for some individuals were excluded from analyses based on reproductive status, which can affect female home range sizes in some species (Jhala et al., 2009; Maruping-Mzileni et al., 2020; Pomilia et al., 2015). Home ranges of individuals within the same social group were not included if they occurred in the same month to avoid pseudoreplication, leading to a final set of 22 wild dogs, 11 lions, 8 leopards and 5 cheetahs included in analyses. See Appendix S1 for details on exclusion criteria.

To examine the impact of drought conditions on spatiotemporal overlap between carnivore species, we evaluated whether monthly overlap between individuals of different species (referred to as dyads, e.g. overlap between ‘cheetah individual 1’ and ‘leopard individual 1’) was related to SPI. We calculated overlap for both home ranges and core areas in each month using Bhattacharyya's affinity metric, which represents overlap as a value between 0 (no overlap) and 1 (perfect overlap; Carroll et al., 2019).

To examine the impact of drought conditions on finer-scale interactions between carnivore species, we evaluated whether encounter rates between individual dyads were related to SPI. We restricted analysis to 5-min interval encounter data to capture fine-scale interactions (Table S1). We quantified encounter occurrences using the R package *wildlifeDI* (Long, 2023). Encounters were defined as occurring when simultaneous fixes from individual dyad members were within a specified distance threshold of one another (Broekhuis et al., 2013; Rafiq et al., 2019). Following Long (2023) and Rafiq et al. (2019), fixes were defined as simultaneous when occurring at half of the sampling frequency, that is within 2.5 min of one another. New encounter events could not occur until dyad members had vacated the distance threshold and had been separated for at least 4 hours since their last encounter, as this is a typical duration of African carnivore activity periods (Cozzi et al., 2012; Hayward & Slotow, 2009; Rafiq et al., 2023). We evaluated encounter rates at two biologically meaningful distance thresholds determined from field observations: 200 and 400 m, which are critical distance thresholds for interactions from previous studies on large carnivores (Elbroch & Quigley, 2017; Jordan et al., 2017; Rafiq et al., 2019, 2020).

2.4 | Statistical analysis

To evaluate the impact of drought conditions on carnivore home range size, overlap, and encounters, we built linear mixed effects models with SPI as a predictor in all models (R package *glmmTMB*; Brooks et al., 2023). Before fitting models, we tested data for temporal autocorrelation in monthly home range and overlap estimates using acf() function in R's *stats* package and found no significant autocorrelation. In all cases, we used bootstrapping to calculate 95% confidence intervals on model coefficients and predictions.

For home range size analyses, we fit species-specific models with a gamma distribution and a log link function, with all models including home range area as the response variable and SPI as a predictor variable. For wild dog data which only included one individual per pack, we included group ID as a random effect to account for repeated measures. For lions, we included individual ID nested within group ID as a random effect, whereas for solitary felids (cheetahs and leopards) only individual ID was included as a random effect. For lions and cheetahs, we also included sex as a predictor as it affects felid home range size (Loveridge et al., 2009; Welch et al., 2015). Sex was not included for leopards as all collared individuals were male.

For overlap analyses, in which the overlap coefficient between two individuals took values between 0 and 1, inclusive, we used a Bernoulli-beta mixture model to accommodate zero-inflation with SPI as a predictor in all models. First, we used a Bernoulli distribution with a logit link to evaluate whether SPI had an effect on a binary response of whether there was (1) or was not (0) overlap between two species (i.e. the *probability* of overlap). Second, we used a beta distribution with a logit link to investigate whether, for those species that had any overlap >0, SPI had an effect on the *amount* of overlap.

For all models, we included an interaction between SPI and species dyad (e.g. cheetah–leopard) to allow responses to vary at the species dyad level. To account for repeated measures, we included individual dyad ID (e.g. 'cheetah individual 1'–'leopard individual 1') as a random effect. Due to convergence issues from insufficient data, we excluded dyads with fewer than 10 observations distributed across 3 SPI values. This led to the exclusion of the cheetah-leopard species pair for the core area Bernoulli model, and cheetah-wild dog, cheetah-leopard, and wild dog-leopard species pairs for the core area beta model.

Finally, for encounter analyses, we used a zero-truncated Poisson distribution with a log link, as encounters were treated as a count variable and we only included dyads where the count was >0. In each encounter model, the number of encounters per month was the response variable, SPI was a predictor, and dyad ID was included as a random effect. As above, we included an interaction between SPI and species dyad (e.g. cheetah-leopard) to allow responses to vary at the species dyad level. All model formulas, analyses and sample sizes are summarized in Tables S2 and S3.

3 | RESULTS

3.1 | Home range size

In support of our first hypothesis (1a), we found a general pattern across species toward expanded space use as conditions became drier (Figure 2, Table S4). African wild dogs expanded their

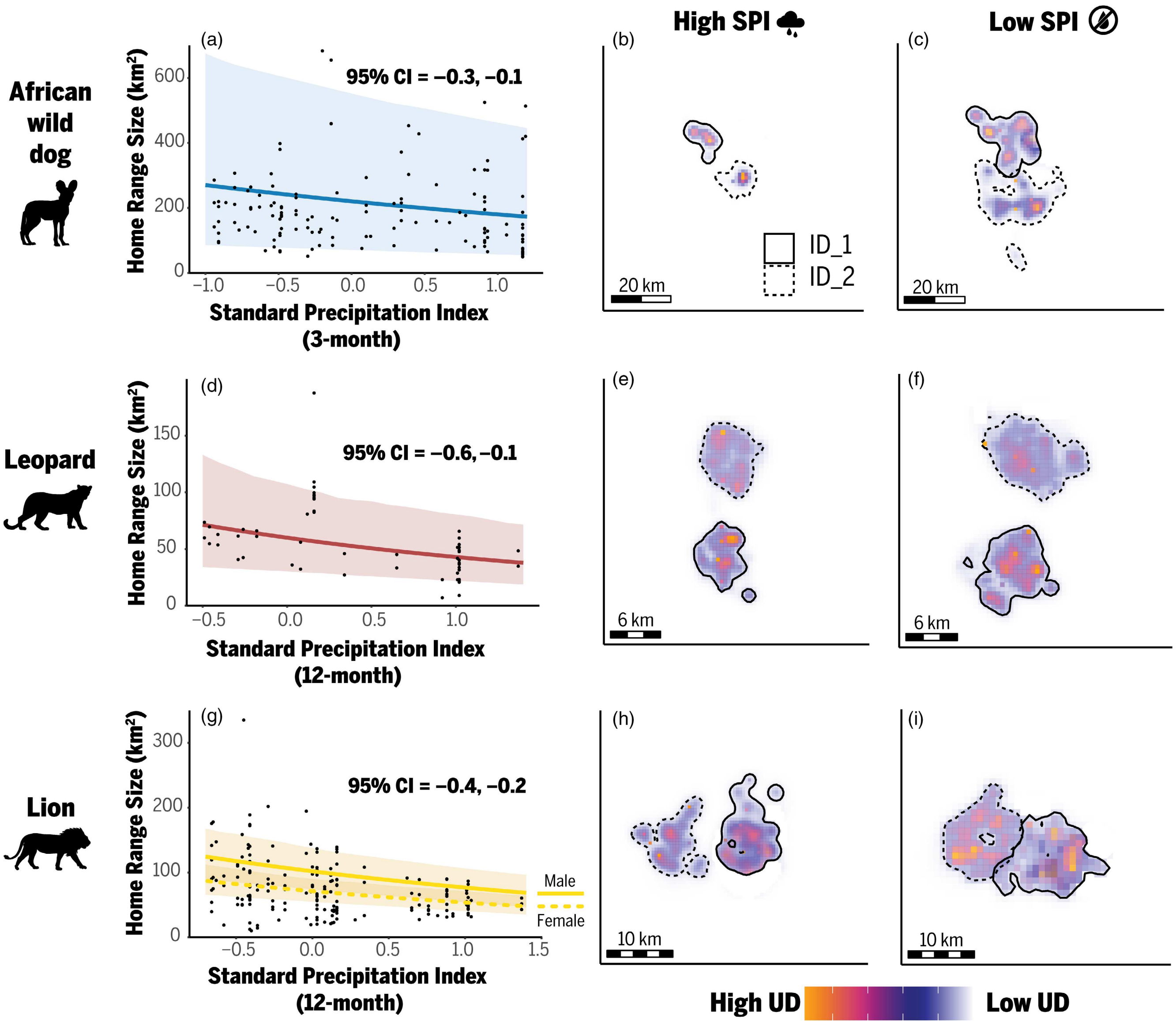

FIGURE 2 Observed data (points) and model predictions (lines, Table S7) for African wild dog (a), leopard (d) and lion (g) 95% home range size as a function of Standard Precipitation Index (SPI). Shaded regions represent bootstrapped 95% confidence intervals. For visual demonstration, maps show how two African wild dog (b, c), leopard (e, f) and lion (h, i) individuals' 95% monthly home ranges expand from a high (wet) SPI to a low (dry) SPI period.

home ranges in response to acute (i.e. 3-month) drought conditions, with 95% home range sizes increasing by 35% when in low (25th percentile) versus high (75th percentile) SPI conditions ($\beta_{95}=-0.21$, 95% CI = −0.30, −0.12). Similarly, wild dog core areas increased by 65% in low versus high SPI conditions ($\beta_{50}=-0.33$, 95% CI = −0.48, −0.18). We did not find evidence that wild dog space use responded to prolonged (i.e. 12-month) drought conditions ($\beta_{95}=0.002$, 95% CI = −0.1, 0.1; $\beta_{50}=0.03$, 95% CI = −0.2, 0.2). In contrast, both lion and leopard ranges expanded in response to prolonged drought conditions. Lion home range sizes increased by 53% when in low versus high SPI ($\beta_{95}=-0.28$, 95% CI = −0.42, −0.15). Lions exhibited a similar pattern of expanding their core areas under drier conditions ($\beta_{50}=-0.19$, 95% CI = −0.4, 0.02), however the smaller effect size in combination with a confidence interval that slightly crosses zero indicates that this effect is uncertain. Leopards increased their home ranges by 66% ($\beta_{95}=-0.33$, CI = −0.62, −0.05), and their core areas by a marked 228% ($\beta_{50}=-0.78$, 95% CI = −1.22, −0.34), in low versus high SPI conditions. Finally, cheetahs also demonstrated a tendency to expand their core areas under prolonged dry conditions, although as with lion core areas, this effect was uncertain ($\beta_{50}=-0.22$, 95% CI = −0.5, 0.03). These results suggest that there is a general trend toward carnivores increasing their space use in drier conditions, with the magnitude and certainty of these effects varying across species.

3.2 | Spatiotemporal overlap

We found moderate support for the hypothesis (2b) that drought conditions increase spatial overlap between dominant (namely, lion) and subordinate species, although the strength of this relationship varied by timescale and species dyad (Table S5). While the probability of any overlap between lion and cheetah home ranges decreased in response to prolonged (12-month) drought conditions ($\beta=4.14$, 95% CI = 1.18, 7.29), for lion-cheetah dyads with some home range overlap, the amount of overlap increased under prolonged drought conditions ($\beta=-0.65$, 95% CI = −1.29, 0.0; Figure 3). This translated to a 119% increase in the amount of spatial overlap between lions and cheetahs when experiencing low (25th percentile) versus high (75th percentile) SPI. Similarly, the amount of overlap between lion and leopard core ranges increased in response to prolonged drought ($\beta=-0.4166$, 95% CI = −0.79, −0.06), with overlap between lions and leopards increasing by 78% in low versus high SPI conditions. Although the magnitude of these observed changes in amount of overlap for the lion-cheetah and lion-leopard dyads suggests a substantial response to drought, the

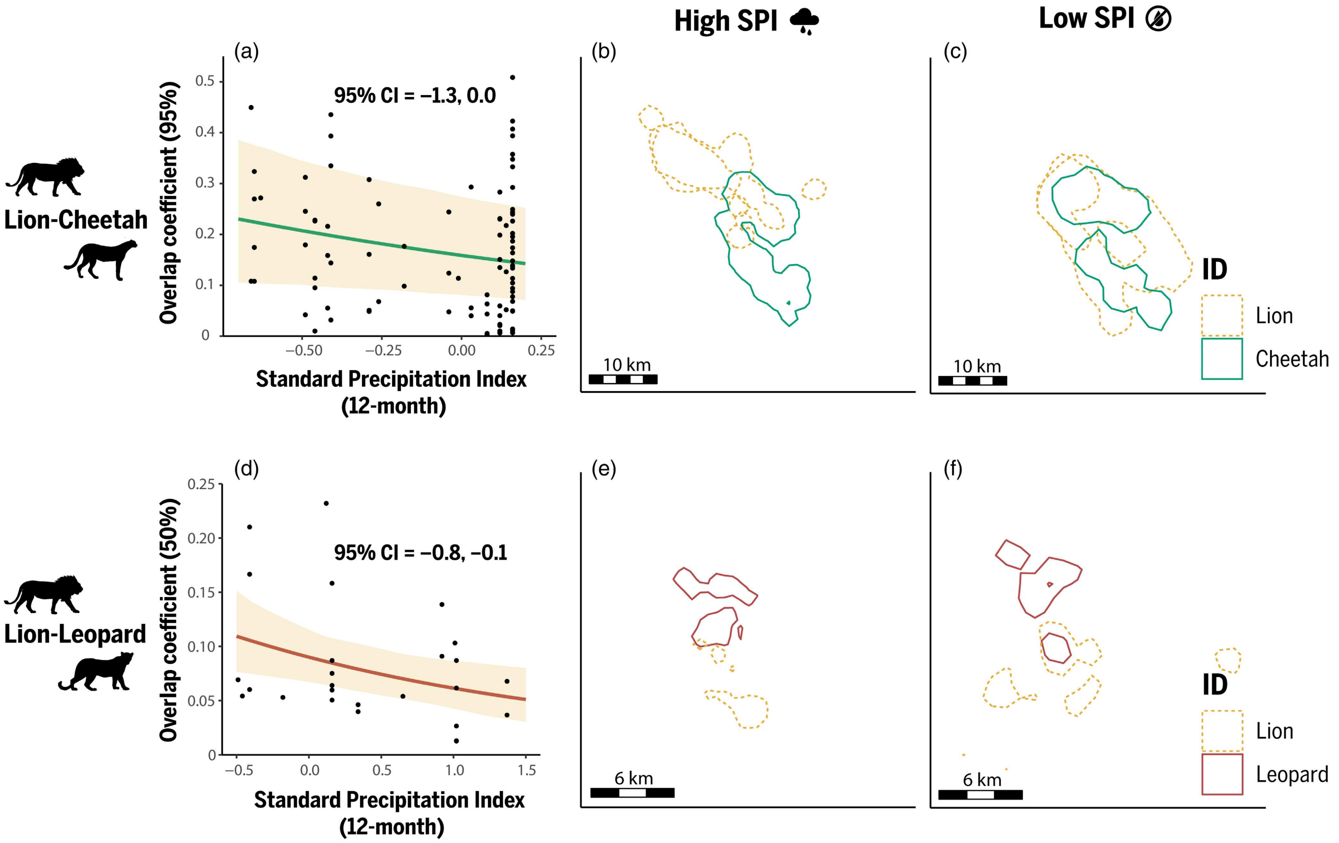

FIGURE 3 Observed data (points) and model predictions (lines, Table S8) for amount of home range overlap (beta model) as a function of Standard Precipitation Index (SPI) for (a) lion-cheetah dyads and (d) lion-leopard dyads, which showed evidence of a response to SPI. Shaded regions represent bootstrapped 95% confidence intervals. For visual demonstration, maps show how lion-cheetah (b, c) and lion-leopard (e, f) overlap increases from a high (wet) SPI to a low (dry) SPI period.

wide confidence intervals which come close to crossing zero indicate these effects should be interpreted cautiously. There was no effect of acute drought conditions on overlap with any lion dyads, although there was weak evidence that the probability of overlap between wild dog and leopard home ranges ($\beta = -0.9203$, 95% CI = −1.9, 0.09), and between wild dog and cheetah core areas ($\beta = -1.2761$, 95% CI = −4.2, 0.2), increased in response to acute drought.

3.3 | Encounters

Our encounter analysis led to 184 total encounters at the 200 m distance threshold: 26 for the lion-cheetah dyad, 48 for the leopard-wild dog dyad, 50 for the lion-leopard dyad and 60 for the lion-wild dog dyad. At the 400 m threshold, there were 287 total encounters: 62 for lion-cheetah, 52 for leopard-wild dog, 77 for lion-leopard and 96 for lion-wild dog.

Broad-scale changes in spatiotemporal overlap between species dyads generally did not translate into changes in fine-scale encounter rates (Table S6). The only detectable effect of SPI on encounter rates was a decrease in lion-cheetah encounters at the 400 m distance threshold in response to both acute ($\beta_{400} = 1.24$, 95% CI = 0.4, 3.2) and prolonged ($\beta_{400} = 3.28$, CI = 0.6, 19.8) drought conditions, despite increased overlap among lion-cheetah dyads whose home ranges intersected. Thus, the prediction that drought conditions would lead to reduced intraguild encounter rates (3a) was supported by one species dyad, but no effect was observed among the other dyads evaluated.

4 | DISCUSSION

Understanding how individual behavioural responses to environmental variability may affect higher-order ecological processes such as interspecific competition is a key challenge in ecology, particularly for wide-ranging and/or elusive species. Our study showcases how species-level responses to climatic variation and extreme events may scale up to community-level effects. Specifically, we found evidence that droughts further expand the already wide-ranging space use of multiple large carnivore species, leading to increased spatiotemporal overlap between competing guild members. The increased space requirements under drought conditions found here not only have likely consequences for the energetics and competitive dynamics of carnivore species, but also have important implications for conservation planning and human-wildlife interactions as long-term aridification and acute drought events increase into the future (Chivangulula et al., 2023).

Across species, we found that drought increased either home ranges or core areas, or both, supporting the hypothesis that droughts may necessitate wider-ranging movements among animals to find depleted or sparsely distributed resources. This was true even for classically subordinate species like African wild dogs, whose space use is primarily influenced by the presence of competitors rather than resource availability (Vanak et al., 2013). These results are congruent with general theory on home range formation, in which animal home ranges are expected to increase as resource availability decreases (Börger et al., 2008). Indeed, increases in home range size in response to drought conditions have been documented in multiple other mammalian taxa and systems (Stradiotto et al., 2009; Waterman & Fenton, 2000). For example, during a major drought event in the southern USA, when food resources dramatically declined black bears expanded their search for food over broader areas, leading to the largest bear home ranges recorded over a multi-year study (Moyer et al., 2007). The expansion of space use during droughts documented here and elsewhere may have underappreciated energetic consequences if carnivores are required to spend more energy to access water and/or prey during periods of resource scarcity; moreover, reduced access to water may exacerbate the concurrent climate impacts of higher temperatures by making it harder to thermoregulate, which negatively impacts survival and reproduction in African wild dogs (Abrahms et al., 2022; Woodroffe et al., 2017).

We additionally found that the spatial responses of carnivores were sensitive to the duration of drought conditions, with African wild dogs responding to acute or short-term drought conditions and felids to prolonged drought conditions, highlighting the importance of considering the ecological effects of climate events at multiple scales. As the smallest guild member, wild dogs may be more quickly excluded by dominant competitors from high-quality resource areas like waterholes as drought conditions develop (Davies et al., 2021; Vanak et al., 2013). Larger guild members might find adjusting their space use to these short-term variations in resource availability energetically inefficient, but eventually their movements will likely be affected by reduced resource availability as drought conditions persist. Similar patterns are found in lions in Kenya, where drought led to home ranges initially shrinking and then ultimately expanding in response to decreasing prey densities (Tuqa et al., 2014). While we did not have the data to assess drought effects on the availability of prey species (primarily zebra, *Equus quagga*, and impala, *Aepyceros melampus*) in our system, evidence from multiple ungulate species indicates that their distributions are strongly driven by the availability of surface water and/or primary production (Cain et al., 2008; Esmaeili et al., 2021), and reduced water availability can lead to more patchy and dispersed prey distributions over seasonal timescales (Tomaszewski et al., 2022). In addition to shifts in their distributions, in the short term drought may make prey species more accessible to predators, as poor body condition of prey during these periods can lead to higher hunting success (Mills, 1995). Over longer timescales, droughts can reduce prey availability to predators via increased mortality and population decline. For example, a major die-off of wildebeest (*Connochaetes taurinus*) in Botswana was causally linked to drought-induced food depletion, compounded by increased energy expenditure as animals moved long distances to find food and water (Williamson & Mbano, 1988). Thus, while identifying the specific mechanisms underlying carnivores' spatial responses to drought is beyond our scope, it is clear that a complex combination of ecological factors including intraguild competition and resource availability can drive species-specific responses at multiple timescales.

When considering carnivore responses to drought at varying scales, it is also important to consider the broader climatic context of our study region. Although our study defines drought events based on local rainfall, they are largely driven by larger-scale climatic phenomena like ENSO (El Niño-Southern Oscillation), which influence rainfall variability over much of southern Africa (Driver & Reason, 2017; Moses et al., 2023; Richard et al., 2000), and, by extension, flood extent and vegetation availability in the Delta (Moses et al., 2021). As reduced rainfall across Botswana and Angola leads to diminished river discharge with a 6- to 12-month lag (Byakatonda et al., 2018; Moses et al., 2023), the 12-month SPI lag employed in our analysis aims to capture these broad-scale ecological responses. Given that our study region is located on the outskirts of the Delta floodwaters, and that flood extent is correlated with broad-scale drought patterns in this area (Mfundisi et al., 2021), our findings reflect broad-scale spatial responses to reductions in both local rainfall and floodwater. However, future research is needed to investigate fine-scale behavioural responses of carnivores to both ephemeral water sources and delta fluctuation.

Consistent with the home range expansion following prolonged drought conditions observed among lions, leopards, and to a marginal extent cheetahs, we found that the amount of spatial overlap between the dominant predator, lions, and the other felids subsequently increased. Interestingly, the overall probability of any overlap between lions and cheetahs decreased during drought, but for the dyads whose home ranges did intersect, the amount of spatial overlap increased. We hypothesize that this may be because the benefits of accessing high-quality resource areas may outweigh the costs of lion encounter risk during drought. In other words, resource scarcity imposed by drought may lead subdominant competitors to make riskier space use decisions and select for areas of resource availability regardless of lion presence (i.e. use high-risk, high-reward locations). This aligns with theory on state-dependent risk-sensitive foraging, whereby animals use riskier patch selection strategies when faced with reduced energetic reserves (Caraco, 1980; Houston & Rosenström, 2023; Stephens, 1981). This has been demonstrated among several taxa in the context of animals shifting their prioritization of foraging opportunities versus predator or competitor risk avoidance based on their physical state (Balaban-Feld et al., 2019; Siegal et al., 2022): for instance, in pumas (*Puma concolor*), hungrier individuals engaged in more risky behaviour in relation to human settlements in order to meet their foraging needs (Blecha et al., 2018).

Increases in the spatiotemporal overlap between large carnivore species may amplify intraguild competition, with potential direct and indirect negative fitness impacts. As dominant competitors in this system, lions are a primary cause of mortality for wild dog and cheetah young, and they opportunistically steal kills from all guild members (Creel & Creel, 2002; Durant, 1998; Mills & Gorman, 1997). As a result, African wild dogs proactively adjust their space use to reduce overlap with lions (Davies et al., 2021; Vanak et al., 2013), and cheetahs and leopards reactively avoid lions to reduce direct encounters (Broekhuis et al., 2013; Vanak et al., 2013). In addition, lions monopolize prey-rich areas, particularly during periods of resource limitation such as dry seasons (Vanak et al., 2013). During droughts, therefore, lions may exclude subordinate competitors from high-quality resource areas, restricting their access to prey and/or water (Dröge et al., 2017; Swanson et al., 2014). This parallels observations in Central America, where jaguars (*Panthera onca*) displayed increased aggressive interactions and killing of smaller carnivores at a waterhole during a severe drought, which was attributed to the reduced ability of competing carnivore species to partition scarce resources during that period (Perera-Romero et al., 2021).

Across most species dyads, the observed changes in space use and spatiotemporal overlap during drought did not translate into changes in direct encounter rates. This is most likely due to the complex, fine-scale avoidance strategies these species employ to reduce direct intraguild encounters, particularly with lions (Broekhuis et al., 2013; Davies et al., 2021; Vanak et al., 2013). For example, Rafiq et al., 2020 hypothesized that leopards in our study region use scent marks to reduce exploitation competition, and in addition to exhibiting reactive spatial avoidance of lions (Broekhuis et al., 2013; Durant, 1998), cheetahs avoid temporal overlap with lions at a diurnal scale, particularly during peak lion hunting periods (Cornhill et al., 2023; Dröge et al., 2017; Durant, 1998). This complex avoidance behaviour likely explains our singular finding that encounters between cheetahs and lions decreased during drought even though dyads that overlapped in home ranges increased their shared space use at broad spatial scales. Indeed, broad-scale spatial overlap is an unreliable proxy for direct encounter rates, which are also influenced by the amount of temporal overlap between individuals, the detectability of individuals within their environment, fine-scale habitat selection strategies and other behavioural adaptations (Suraci et al., 2022). Future research could examine how similar extreme climate events affect the fine-scale behavioural strategies of competing large carnivore species, particularly in fenced reserves that are commonplace in southern Africa and where large carnivores may not be able to partition habitat to the same degree as in our relatively unbounded study area.

Beyond ecological insights, our study provides several important considerations for the conservation of threatened large carnivore species under climate change. As increases in drought frequency, duration, and severity are predicted across southern Africa (Chivangulula et al., 2023; IPCC, 2021), our finding that carnivores expand their ranges during droughts supports protecting larger reserve areas and movement corridors to enhance connectivity, as these management strategies promote ecosystem resilience to extreme events and provide climate refugia (Heller & Zavaleta, 2009; Ranius et al., 2023). This is particularly critical for African wild dogs, whose extensive spatial requirements heighten their vulnerability to population decline (Woodroffe & Ginsberg, 1999). Furthermore, increasing spatial requirements and reduced availability of natural resources during droughts may exacerbate human-carnivore conflicts in shared landscapes (Abrahms et al., 2023). Drought events are associated with increases in human-wildlife conflict among numerous taxa (Newsom et al., 2023; Pérez-Flores et al., 2021; Saberwal et al., 1994), and in our study region the 2018/2019 drought saw some of the highest incidences of livestock depredation by large carnivores on record (Ministry of Local Government and Rural Development, 2019). The wider-ranging movements of carnivores in response to drought found in our study point to a potential mechanism underlying these patterns. These insights are particularly useful given that upper trophic levels remain one of the most understudied taxa within the literature on the ecological impacts of climate variability (Abrahms et al., 2022; Cahill et al., 2013; Ockendon et al., 2014; Prugh et al., 2018). Altogether, our study shows that extreme climate conditions have a clear spatial signature on the behaviour of sympatric large carnivore species, shedding light on the links between climate variability, individual behavioural changes and potential consequences for community dynamics, and contributing to our understanding of how ecosystems may respond to projected water scarcity under ongoing climate change.

AUTHOR CONTRIBUTIONS

Our study includes authors from a number of different countries, including scientists based in the country where the study was carried out. Leigh West and Briana Abrahms conceived and designed the study; Leigh West, Briana Abrahms, Kasim Rafiq, Neil R. Jordan, Krystya A. Golabek, Alan M. Wilson and J. Weldon McNutt collected data; Leigh West performed analyses; Sarah J. Converse, Kasim Rafiq and Briana Abrahms assisted with analysis and interpretation of data; Leigh West and Briana Abrahms led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k98sf7mgm. (West et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Exclusion criteria for home range analyses.

Table S1. Summary information for GPS-collared carnivores.

Table S2. Summary of generalized linear mixed model structures.

Table S3. Sample sizes for each model.

Table S4. Summary of coefficients for Home Range analyses.

Table S5. Summary of coefficients for Overlap analyses.

Table S6. Summary of coefficients for Encounter analyses.

Table S7. Summary of predicted home range sizes from generalized linear mixed models and corresponding 95% bootstrap confidence intervals.

Table S8. Summary of predicted overlap coefficients from generalized linear mixed models and corresponding 95% bootstrap confidence intervals.

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