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ARTICLE

Climate change does not decouple interactions between a central-place-foraging predator and its migratory prey

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Abstract

Little is known about potential cascading effects of climate change on the ability of predators to exploit mobile aggregations of prey with a spatiotemporal distribution largely determined by climatic conditions. If predators employ central-place foraging when rearing offspring, the ability of parents to locate sufficient prey could be reduced by climate change. In the Serengeti National Park, Tanzania, migratory species dominate mammalian herbivore biomass. These migratory herds exploit nutrient-rich vegetation on the southern plains in the rainy season and surface water in the northwest in the dry season. Female spotted hyenas *Crocuta crocuta* breed throughout the year and use long-distance central-place-foraging "commuting trips" to migratory herds to fuel lactation for ≥12 months. Changes in rainfall patterns that alter prey movements may decrease the ability of mothers to locate profitable foraging areas and thus increase their overall commuting effort, particularly for high-ranking females that have priority of access to food resources within their clan territory and thus less commuting experience. In hyena clan territories, this may be reflected by a decrease in migratory herd presence and a decrease in the presence of lactating females, as maternal den presence represents the opposite of commuting effort. We investigated the strength of the relationship between rainfall volume, migratory herd presence in three hyena clan territories, and the responses of lactating females to this climate/prey relationship in terms of maternal den presence, using an observation-based dataset spanning three decades. The probability of migratory herd presence in hyena clan territories increased with the amount of rainfall 2 months earlier, and maternal den presence increased with migratory herd presence. Rainfall volume substantially increased over 30 years, whereas the presence of migratory herds in hyena clans and the strength of the relationship between rainfall and migratory herd presence decreased. Hyenas thus adjusted well to the climate change-induced decreased the presence of migratory herds in their territories, since maternal den presence did not decrease over 30 years and still matched periods of high prey abundance, irrespective of female social status. These results suggest a high plasticity in the response of this keystone predator to environmental variability.

KEYWORDS
climate change, herbivore migration, predator–prey interaction, rainfall, seasonality, Serengeti National Park, spatiotemporal trophic mismatch, spotted hyena

INTRODUCTION

Climate change influences the geographical range, morphology, behavior, and phenology of many animal species (Parmesan, 2006; Plard et al., 2014; Post & Forchhammer, 2008; Radchuk et al., 2019; Weeks et al., 2020). Changes in climatic factors such as temperature and precipitation may also induce phenological mismatches, which may affect trophic interactions (reviewed in Bellard et al., 2012 and Parmesan, 2006), with detrimental consequences for the survival and recruitment of predatory species (Durant et al., 2007). Relatively few studies have investigated phenological mismatches in mammals, and to our knowledge, all previously published ones consider seasonal breeders (e.g., Lane et al., 2012; Plard et al., 2014; Post et al., 2008; Réale et al., 2003). Little is known about potential effects of climate change in long-distance central-place-foraging systems, where predators have to regularly travel between a fixed location such as a roost, nest site, den or nursery beach, and distant foraging areas because the main prey is highly mobile (Boyd et al., 2017; Lai et al., 2017; Wakefield et al., 2014; Walton et al., 2001). As the distribution of highly mobile prey such as migratory herbivores changes in response to seasonal variation of resource quantity and/or quality (Fryxell & Sinclair, 1988; Riotte-Lambert & Matthiopoulos, 2020), which can be altered by changes in the timing, distribution, or amount of precipitation, climate change may ultimately influence the location of profitable feeding areas for central-place foragers.

Long-distance central-place foraging is used by seasonally breeding vertebrates including seabirds (Jakubas et al., 2020; Wakefield et al., 2014), bats (Calderón-Capote et al., 2020; Daniel et al., 2008), and marine or terrestrial carnivores (e.g., wolves *Canis lupus* Walton et al., 2001, jackals *Canis mesomelas* Jenner et al., 2011, sea-lions *Arctocephalus gazella* Jeanniard-du-Dot et al., 2017, or foxes *Vulpes lagopus* Lai et al., 2017) to fuel most of their offspring's growth. Theoretically, central-place foragers should use distant food resources when this provides more energy than would be acquired by foraging locally (Cuthill & Kacelnik, 1990). Yet, as the distance parents travel between their dependent young and feeding locations increases, parental provisioning rates of offspring often decline, which may decrease offspring growth, condition, and survival (Boyd et al., 2017; Burke & Montevecchi, 2009; Jeanniard-du-Dot et al., 2017). Unlike most species that use long-distance central-place foraging to fuel offspring growth, hyenas in the Serengeti National Park (NP) are not seasonal breeders but reproduce throughout the year (Hofer & East, 1995). In this species, cubs entirely depend on milk for their first 6 months of life and are weaned between 12 and 18 months of age (Hofer & East, 1995). Hyena milk has a very high fat content (Hofer et al., 2016), and in the Serengeti NP population, females fuel milk production by regularly commuting to feed on distant migratory herbivores and their main prey (Hofer & East, 1993a).

The Serengeti migration (see Figure 1) moves through an area of approximately 30,000 km^2 and includes one of the largest populations of migratory herbivores worldwide, with roughly over 1 million blue wildebeest *Connochaetes taurinus*, 200,000 plains zebras *Equus quagga*, and 400,000 Thomson's gazelles *Eudorcas nasalis* (Sinclair, 1995). At the start of the dry season (in approximately June) as the nutritious short-grass plains in the southeast of the ecosystem dry out, the migratory herds move to the wetter northwest of the ecosystem where they remain until the start of the rains in approximately October, which initiates their return to the southeast of the ecosystem in November. Hence, the Serengeti migration is a response to spatial gradients of rainfall with higher annual mean rainfall with 1200 mm in the northwest than the southeast with 400 mm (Boone et al., 2006; Holdo et al., 2009), and higher soil fertility and nutritional content of forage in the southeast than northwest (Fryxell & Sinclair, 1988; McNaughton, 1988, 1990; Pennycuick, 1975; Wilmshurst et al., 1999).

Hyenas in the Serengeti NP respond to periods of low prey density in their clan territory (~7.2 animals/km^2), which occur when migratory herbivores are absent, by commuting long distances (up to 140 km straight-line distance), between their cubs stationed at the communal den within the clan territory, and distant feeding areas containing large aggregations of migratory herbivores (Hofer & East, 1993b). During such periods, all animals in a clan regularly commute (Hofer & East, 1993b). Importantly, all lactating females regularly return from commuting trips to the communal den within the clan territory after one to several days to nurse their offspring

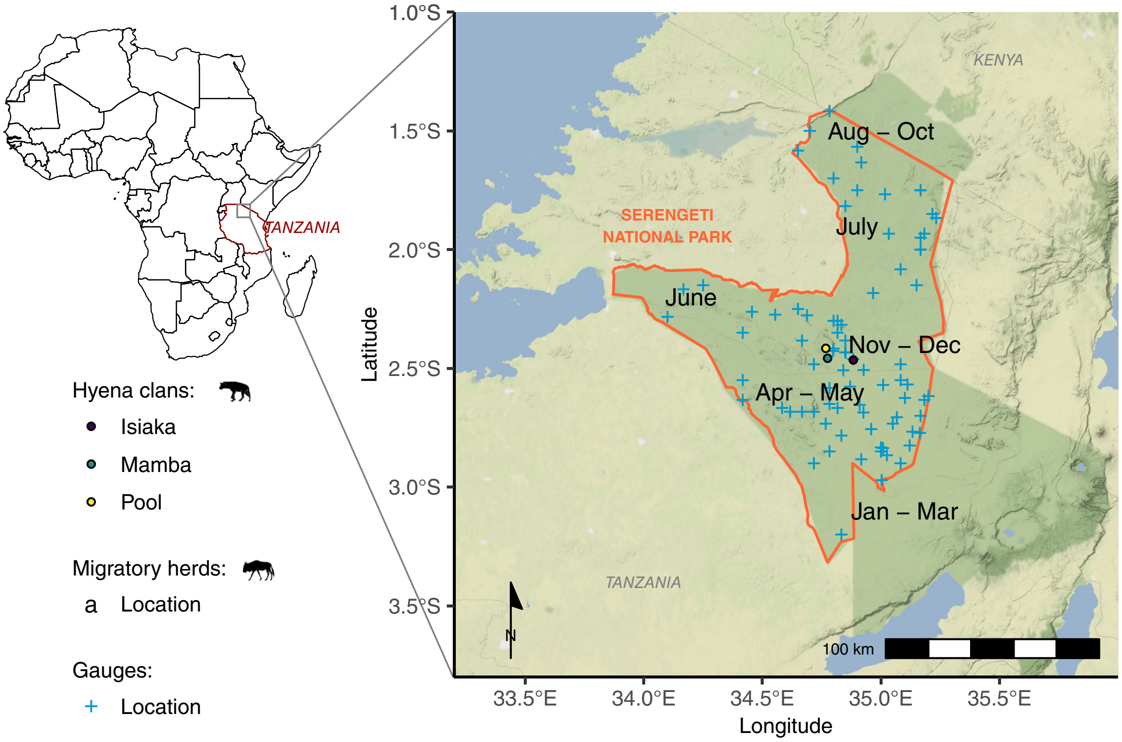

FIGURE 1 Exact locations of the studied spotted hyena clan territories (Isiaka, Mamba, and Pool; colored points) and of the rain gauges (blue crosses), and approximate locations of the migratory herds throughout the year (black text) in the Serengeti National Park, Tanzania. The borders of the park are in orange. The locations of the spotted hyena clan territories shown here are the centroid locations of each communal den over the entire study period (1990–2019)

there (Golla et al., 1999; Hofer & East, 1993a, 2008). When large aggregations of migratory prey occur in a clan territory (~238.5 animals/km^2), all lactating mothers feed inside the clan territory and therefore can nurse their cubs daily. This boosts the growth of milk-dependent cubs, which is associated with increased cub survival to adulthood (Hofer & East, 2003, 2008). Maternal den attendance at communal dens is therefore a key predictor of the provisioning rate at which offspring receive milk (Hofer et al., 2016; Hofer & East, 1993a, 1993b, 1993c, 2008) and of cub survival to adulthood (this study), and den attendance is substantially boosted by the presence of migratory prey in clan territories.

When migratory prey species are present in low numbers in a clan's territory (prey density ~31.0 prey/km^2), high-ranking females retain priority of access to remaining food resources, leading to low-ranking individuals commuting to feed on distant migratory herds. When only resident herbivores are present, even high-ranking females regularly commute long distances to feed (Hofer & East, 1993a, 1993b). As a consequence of these substantial and repeated changes in prey abundance within clan territories during the year, while all lactating females encounter periods when migratory herbivores are absent from their territories (Hofer & East, 2008), high-ranking females commute less often than low-ranking females (Hofer & East, 2003). As a result, high-ranking females nurse their offspring more frequently (Hofer et al., 2016; Hofer & East, 2008), their offspring are less likely to have low growth rates, which are associated with reduced survival to adulthood (Hofer & East, 2003), and are more likely to survive to adulthood following infection with virulent or energetically costly pathogens than those of low-ranking mothers (Ferreira et al., 2019; Hofer & East, 2003; Marescot et al., 2018).

Recent studies reported that annual rainfall pattern in the East Africa region is changing and volume is increasing, including in the Serengeti NP (Bartzke et al., 2018; Gebrechorkos et al., 2019; Hulme et al., 2001; Mahony et al., 2021). It is currently unclear whether and how changes in rainfall patterns would affect the movement patterns of migratory herds (Horns & Şekercioğlu, 2018; Ritchie, 2008) and thus the presence of migratory herds in hyena clan territories. Changes in the pattern of rainfall in the Serengeti NP might alter vegetation growth and hence the movements of migratory herds. Such changes in the movements of migratory prey may decrease the ability of hyenas to locate profitable foraging areas, thereby increasing their time spent searching for prey (i.e., increasing their commuting effort and thus the time spent away from the clan territory). Changes in patterns of rainfall might also alter the duration of the periods during a year when migratory herbivores are present in a clan territory, so alter the duration of the periods when females can boost the growth of their cubs.

Here, we used an observational long-term dataset spanning 30 years from three large hyena clans considered here as replicates of a single population in the center of the Serengeti NP to study a potential impact of climate change in terms of rainfall on the interactions between this central-place-foraging predator and its migratory prey. First, we assessed the overall strength of the relationship between rainfall patterns, migratory herd presence, and maternal den attendance of high- and low-ranking hyenas, tested whether maternal den attendance affected cub survival to adulthood, and described seasonal variation in rainfall, prey, and predator variables. We then investigated whether there were any changes in terms of the amount and pattern of rainfall, migratory herd presence, and maternal den attendance over the study period. We then asked whether (potential) changes in rainfall patterns within these territories over the last three decades reduced the strength of relationships between prey and predator variables. We predicted that the strength of the relationship between rainfall and migratory herd presence within hyena clan territories should decrease over time, as expected changes in rainfall patterns should alter the path or timing of herbivore migration, thus also potentially weakening the association between migratory herd presence and maternal den attendance. A decrease in this association could imply a decrease in the overall ability of hyenas to locate profitable foraging areas, resulting in an increase in the overall commuting effort when migratory prey are not present within the clan territory and hence a reduction in maternal den attendance. As high-ranking lactating females commute less often than low-ranking lactating females (Hofer & East, 2003), high-ranking lactating females may be generally less efficient at locating migratory herds. We thus predicted that they would experience a particularly strong reduction in maternal den attendance if climate change alters migratory herd movements.

METHODS

Data on spotted hyenas

Data were obtained in the context of a long-term project on three clans (Isiaka, Pool, and Mamba) that held territories in the center of the Serengeti National Park, roughly halfway between the northerly dry and southerly wet season ranges of the migratory herds (Figure 1). The three clans have been monitored continuously for 33 years (Isiaka: since May 1987), 31 years (Pool: since October 1989), and 30 years (Mamba: since August 1990). Individuals were recognized by their unique spot patterns, ear notches, and scars (Hofer & East, 1993b) and well habituated to the presence of observers in vehicles.

We defined a spotted hyena clan territory to occupy a circular area covering 55 km^2 with a radius of 4.2 km (Hofer & East, 1993c, 1995). We calculated a centroid den location using GPS locations of clan communal den sites used between 1990 and 2019 and set a radius of 4.2 km around the centroid den location for each clan (Figure 1).

During each field session (approximately 2–3 h at dawn or at dusk), in a given clan, we routinely scored the presence of all individuals present within a radius of 100 m of the communal den(s). Based on data from all-night watches and aerial tracking, we previously demonstrated that dawn and dusk observations at communal dens missed only a small proportion of clan members present in the territory (<5% of lactating females; Hofer & East, 1993c). For the purpose of this study, we used data on individually identified spotted hyenas from 1 January 1990 to 31 December 2019. Throughout the study period, the number of field sessions per study clan was roughly similar (Isiaka clan: 47% or 6202 days, Mamba: 39% or 5066 days, and Pool: 47% or 6457 days). We focused on the presence of lactating females with entirely milk-dependent offspring (less than 6 months old) because these females must regularly visit communal dens to nurse their offspring (Hofer & East, 1993a). The raw data included records from 346 lactating females (Isiaka: 118 females, Mamba: 116 females, and Pool: 112 females).

We determined the social status of lactating females using standard methods based on the observation of submissive acts in dyadic interactions recorded ad libitum and during focal observations. These dyadic interactions were used to construct an adult female linear dominance hierarchy updated daily for the entire study period (1990–2019). For the comparison of social status positions across clans, individuals within dominance hierarchies were assigned a standardized rank. This measure evenly distributed ranks from the highest (standardized rank: +1) to the lowest rank (standardized rank: −1), with the median rank being scored as 0 (details see, e.g., East et al., 2003; Goymann et al., 2001). For each lactating female with milk-dependent offspring, we calculated an average standardized rank between the cub's date of birth and (1) the cub's death date if the cub died before 6 months of age, or (2) the date when the cub reached 6 months of age. We then assigned lactating females to one of two main social status categories, with high-ranking females having an average standardized rank equal to or higher than 0, low-ranking ones an average standardized rank below 0.

As all our analyses are based on (hyena) population-level values aggregated at a monthly scale, we then calculated, for each month between 1 January 1990 and 31 December 2019, clan and social status category a variable termed "maternal den presence." This variable was defined as the number of observed lactating females (per month/clan/social status) at communal dens divided by the total number of known lactating females (per month/clan/social status).

Data on migratory herds

During each field session, in a given clan territory, we scored prey abundance during each field session (based on prey counts from ground transects, see Hofer & East, 1993a for further details). We denoted the absence or low number of migratory herds (Level 0) versus the presence of large migratory herds in each clan territory (Level 1). During Level 0 periods, only resident herbivore prey species were present (~7.2 prey/km^2), or migratory prey species were also present in low numbers (~31.0 prey/km^2). During Level 1 periods, in addition to resident prey species, large migratory herds were present (~238.5 prey/km^2; Hofer & East, 1993c, 2003, 2008). We then assigned for each month between 1 January 1990 and 31 December 2019 and for each clan a score of "migratory herd presence" as a binary variable scored as 1 if Level 1 periods (large migratory herds) were present for at least 1 day during a particular month, and 0 otherwise.

Data on rainfall

Rainfall estimate data were obtained from the long-term daily TAMSAT project (Tropical Applications of Meteorology using SATellite and ground-based observations; Maidment et al., 2014, 2017, Tarnavsky et al., 2014). These data provide satellite-derived daily rainfall estimates on a 0.0375° grid resolution (4 km^2) for Africa from 1983 to present. Rainfall estimates were based on high-resolution Meteosat thermal-infrared observations. We used version TAMSAT-3, which is based on a 5-day time-step, calibrated on cold cloud duration observations, for daily rainfall estimates. More information about the dataset and the TAMSAT rainfall estimation algorithm is provided in Maidment et al. (2014). We extracted daily rainfall estimates with the R package "raster" (version: 3.3; Hijmans, 2019). As hyena clan territories overlapped several grid cells unevenly, the proportion of grid cell surface covered by a territory was taken into account as a weight for the calculation of the mean rainfall volume per territory. We compiled total monthly volume of "rainfall estimates" within the entire Serengeti NP and within each clan territory from 1 January 1989 to 31 December 2019. We also compared TAMSAT total monthly rainfall volume estimate to total monthly rainfall volume obtained from rain gauges located across the entire Serengeti NP (Figure 1, Appendix S1: Table S1, Figure S1).

Statistical analyses

All statistical analyses were performed using R (version 4.0.1; R Core Team, 2020; RStudio Team, 2020). Results are presented as means and 95% confidence interval (95% CI).

Relationship between climate, prey, and predator variables

To identify the time lag that maximizes the association between rainfall estimate (a continuous variable) and migratory herd presence (a two-level categorical variable) within a clan territory, we used the sliding window analysis implemented in the package "climwin" (version 1.2.3; Bailey & van de Pol, 2016; van de Pol et al., 2016). This approach consists of fitting a set of models, which include all possible lags between response and predictor variables within a defined period, here set to 12 months. We included the clan ID as a spatial component that accounts for the different clans and consider them as replicates of a single population. The models with different time lags are then compared using Akaike's information criterion corrected for small sample size (AIC$_c$) to the intercept model. To overcome risks associated with multiple testing, we randomized the original data to remove any relationship between rainfall and migratory herd presence and then reran the sliding window analysis (van de Pol et al., 2016). We replicated this randomization procedure 100 times. We then compared our observed result to those 100 randomizations and determined the probability that our observed result could occur in a dataset where no relationship exists between rainfall and migratory herd presence. Once the best-fitting window was identified, we used the monthly rainfall values (automatically compiled by climwin) for the selected window and called this variable "lagged rainfall."

We then performed a path analysis to investigate the strength of the relationships between lagged rainfall, migratory herd presence, maternal den presence, and social status. We fitted the model using "piecewiseSEM" (version 2.1; Lefcheck, 2016) using confirmatory path analysis, which can include generalized linear, least-squared, and mixed-effects models. We specified the model used for each relationship; in our case, these were generalized linear models with binomial error distributions, since the response variables were either binary (migratory herd presence) or continuous (rainfall and maternal den presence).

Effect of maternal den attendance on cub survival

To assess whether maternal den attendance during the first 6 months of life significantly increases cub survival chance to adulthood, we used a generalized linear mixed-effects model with a binomial error distribution for the response variable cub survival to adulthood, the explanatory variable maternal den attendance during the first 6 months of cub development (the critical development period for which cubs entirely depend on maternal milk), and the mother identity as a random factor.

Climate change effects on prey and predator variables

First, to assess potential temporal changes in climate, prey, or predator variables over the three decades of the study period, we used linear regressions with year as an explanatory variable and rainfall estimates across our three clans, migratory herd presence, and maternal den presence of high- and low-ranking females inside hyena clan territories as response variables. We checked and confirmed that model assumptions were met.

Then, to assess whether potential temporal changes in rainfall patterns over the last three decades decreased migratory herd and maternal presence in hyena clan territories, we investigated whether the strength of the relationships between variables (as indicated by the beta coefficients) decreased over time. To do so, we used similar path analyses as described above and first considered the relationships between lagged rainfall in interaction with year, migratory herd presence, and maternal den presence of high- and low-ranking females and then between lagged rainfall, migratory herd presence in interaction with year, and maternal den presence of high- and low-ranking females.

RESULTS

Seasonal variation in rainfall, prey, and predator variables

As expected, total monthly rainfall across all study years in all hyena clan territories revealed a bimodal pattern (Figure 2a). The increase in rainfall between October and December corresponds to the short rains with a maximum monthly average of 107.5 mm (95% CI 99.3–115.7) in December. The increase in rainfall between March and April corresponds to the long rains with a maximum monthly average of 150.5 mm (95% CI 132.1–168.8) in April. In contrast, during the dry season from June to October, the maximum monthly average rainfall never exceeded 53.0 mm (Figure 2a). Migratory herd presence in hyena clan territories showed a similar but delayed pattern (Figure 2b). Migratory herd presence and maternal den presence both peaked in May–June, when migratory herds travel north to their dry season refuge, and to a smaller extent in October–November (Figure 2b,c)

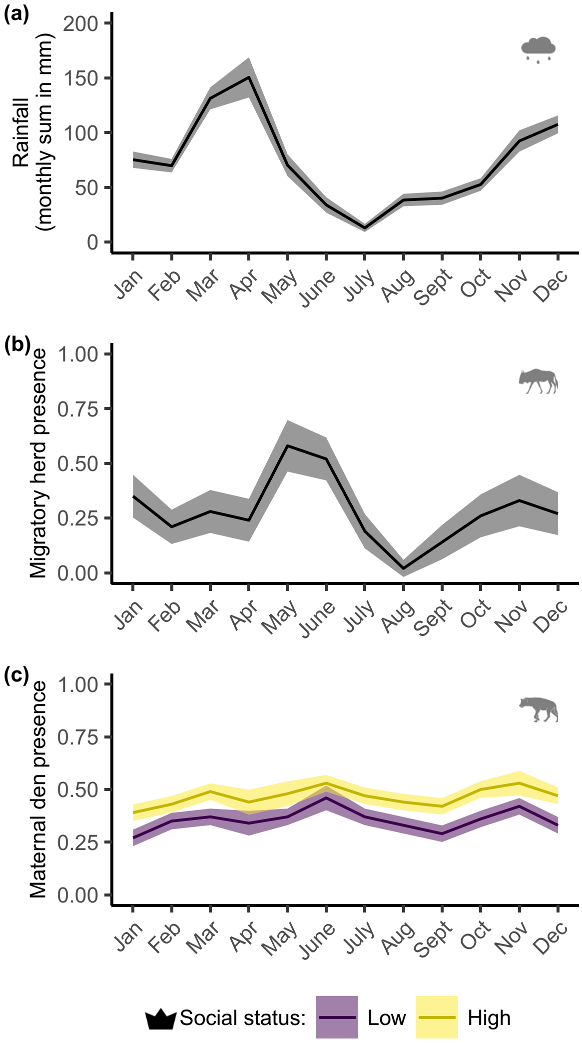

FIGURE 2 Averages of (a) total rainfall, (b) migratory herd presence, and (c) maternal den presence of high-ranking and low-ranking lactating females with milk-dependent offspring younger than 6 months at clan communal dens. The figure shows the monthly average (lines) and 95% confidence interval (ribbons) for the three spotted hyena clans together across years for the entire study period (1990–2019)

when migratory herbivores move south toward the short-grass plains. Throughout the year, high-ranking mothers were more often present at clan communal dens than low-ranking ones (Figure 2c).

Relationship between rainfall, prey, and predator variables

We identified a significant positive linear relationship between rainfall and migratory herd presence, characterized by a 2-month lag between both variables across all years of the study (Appendix S2: Table S1, Figure S1).

The path analysis model which considered the overall relationships between lagged rainfall, migratory herd presence, and maternal den presence fitted the data well (global goodness-of-fit Fisher's $C_4 = 0.53$, $p > 0.95$; Figure 3a). The relationship between migratory herd presence and lagged rainfall was positive and significant (Figure 3b, Appendix S2: Table S1). An increase of 100 mm of rainfall in a given month led to an increase in the probability of migratory herd presence within a hyena clan territory 2 months later by 10%. For a probability of migratory herd presence above 0.5, the total amount of rainfall 2 months before would thus have to be above 190 mm. The relationship

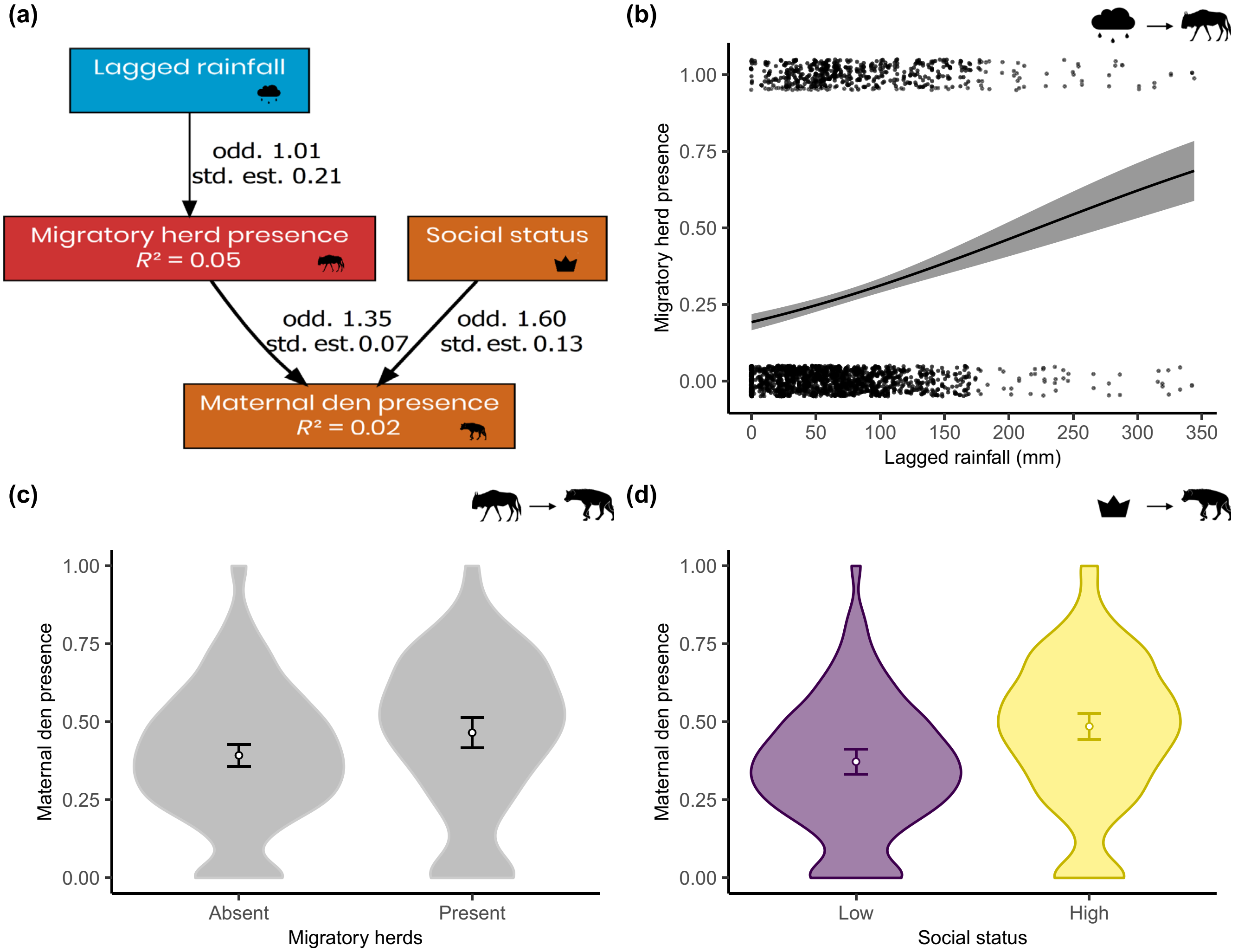

FIGURE 3 (a) Path analysis of the relationships between lagged rainfall, migratory herd presence, maternal den presence, and social status. All variables were aggregated at the monthly scale for the three spotted hyena clans together across years for the entire study period (1990–2019). Boxes represent measured variables. R^2 for response variables is given in their respective boxes, together with the odds ratio (odd.) and the standardized estimates for each relationship (std. est.). Solid arrows represent significant relationships. (b) Probability of migratory herd presence within clan territories in relation to lagged rainfall in millimeters; (c) proportion of lactating females with dependent cubs younger than 6 months present at the communal den (maternal den presence) in relation to the presence or absence of migratory herds within the clan territories; (d) maternal den presence in relation to maternal social status. The line (b) and open dots (c, d) represent the fitted values of the models with associated 95% confidence interval. Raw data are represented by small dots and by the violin diagrams

TABLE 1 Details of statistics for the path analysis presented in the main text

Response	Predictor	Estimate	SE	df	Crit. value	Std.est.	Odds ratio	p
Migratory herd presence	Lagged rainfall	0.006	0.001	1817	7.54	0.21	1.01	**<0.01**
Maternal den presence	Migratory herd presence	0.30	0.11	1816	2.85	0.07	1.35	**<0.01**
Maternal den presence	Social status	0.47	0.09	1816	4.85	0.12	1.59	**<0.01**

Note: Estimates obtained from the path analysis model were investigated for each relationship. Also shown are the associated standard errors (SE), df, and critical value (Crit. value). Standardized estimates (Std. est.) are useful to make comparisons about the relative strength of the predictors, where they represent the strength of the direct effect of the predictor on the response and odds ratios represent the effects of the predictors on the probability of the response.

between maternal den presence and migratory herd presence in the clan territory was also positive and significant (Figure 3c, Table 1). At migratory herd presence Level 0 (absence/low numbers), the probability of maternal den presence was 0.39 (95% CI 0.36–0.43), whereas when migratory herds were present (Level 1), the probability was 0.47 (95% CI 0.42–0.51). High-ranking females (0.49 [95% CI 0.44–0.53]) had a significantly higher probability of maternal den presence than low-ranking females (0.37 [95% CI 0.33–0.41]; Figure 3d).

The probability of cub survival to adulthood increased with maternal den presence during the first 6 months of life ($F_{1,1825} = 6.32$, $p = 0.01$; Figure 4).

Climate change effects on prey and predator variables

Total local rainfall per year substantially increased since approximately the year 2000 ($F_{2,27} = 18.61$, $p < 0.01$; Figure 5a), particularly because of an increase in rainfall during the wet season (Figure 5b, Appendix S3: Figure S1). Throughout the duration of the study period, migratory herd presence substantially decreased ($F_{1,28} = 6.42$, $p = 0.02$; Figure 5c). In contrast, there was no discernible trend for possible temporal changes in maternal den presence of both high- and low-ranking hyenas ($F_{1,57} = 0.44$, $p = 0.51$; power analysis: $u = 2$, $n = 57$, significance level $= 0.05$, power $= 0.99$; Figure 5d).

The annual coefficient values of the relationship between lagged rainfall and migratory herd presence decreased significantly between 1990 and 2019, indicating a decline in the strength of the relationship between both variables over time ($\chi^2{}_1 = 12.89$, $p < 0.01$; Figure 6a and c, Table 2). In contrast, the coefficients of the relationship between migratory herd presence and maternal den attendance did not show such a decrease, indicating a lack of change in the strength of the relationship between these variables over time ($\chi^2{}_1 = 1.21$, $p = 0.27$; Figure 6b and c, Table 2).

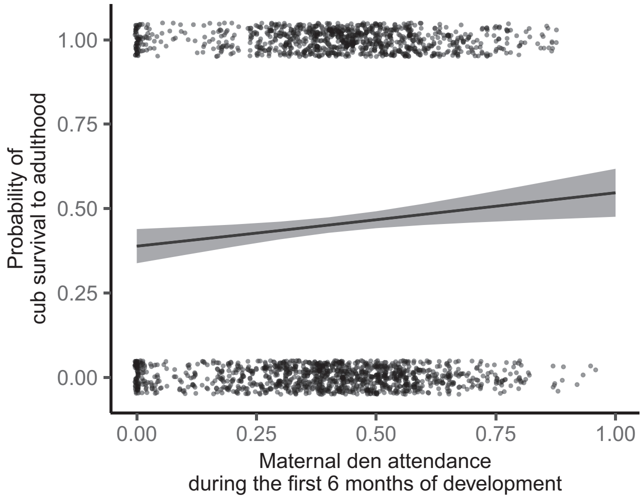

FIGURE 4 Probability of cub survival to adulthood (2 years, 730 days) in relation to maternal den attendance during the first 6 months of life (*N* cubs = 1825). The line represents the fitted values of the model with associated 95% confidence interval. Raw data are represented by small dots

DISCUSSION

Our results indicate that in the Serengeti NP, climatic, prey, and predator variables were globally well linked to each other. Nevertheless, the strength of the relationship between rainfall and migratory herd presence and the presence of migratory herds in clan territories decreased in 30 years. These results suggest a potential effect of climate change on movement patterns of migratory herds, inferred from our observations at the local scale of hyena clan territories in the center of the Serengeti NP. Hyenas seemed to adjust well to the decrease in migratory herd presence in their clan territories, as the presence of both high-ranking and low-ranking females matched periods of high prey abundance in clan territories and their commuting effort (i.e., absence from the clan territories) did not increase over time. Our results on maternal den presence of high-ranking and low-ranking females are also consistent with previous findings where high-ranking lactating females had shorter mean absence intervals

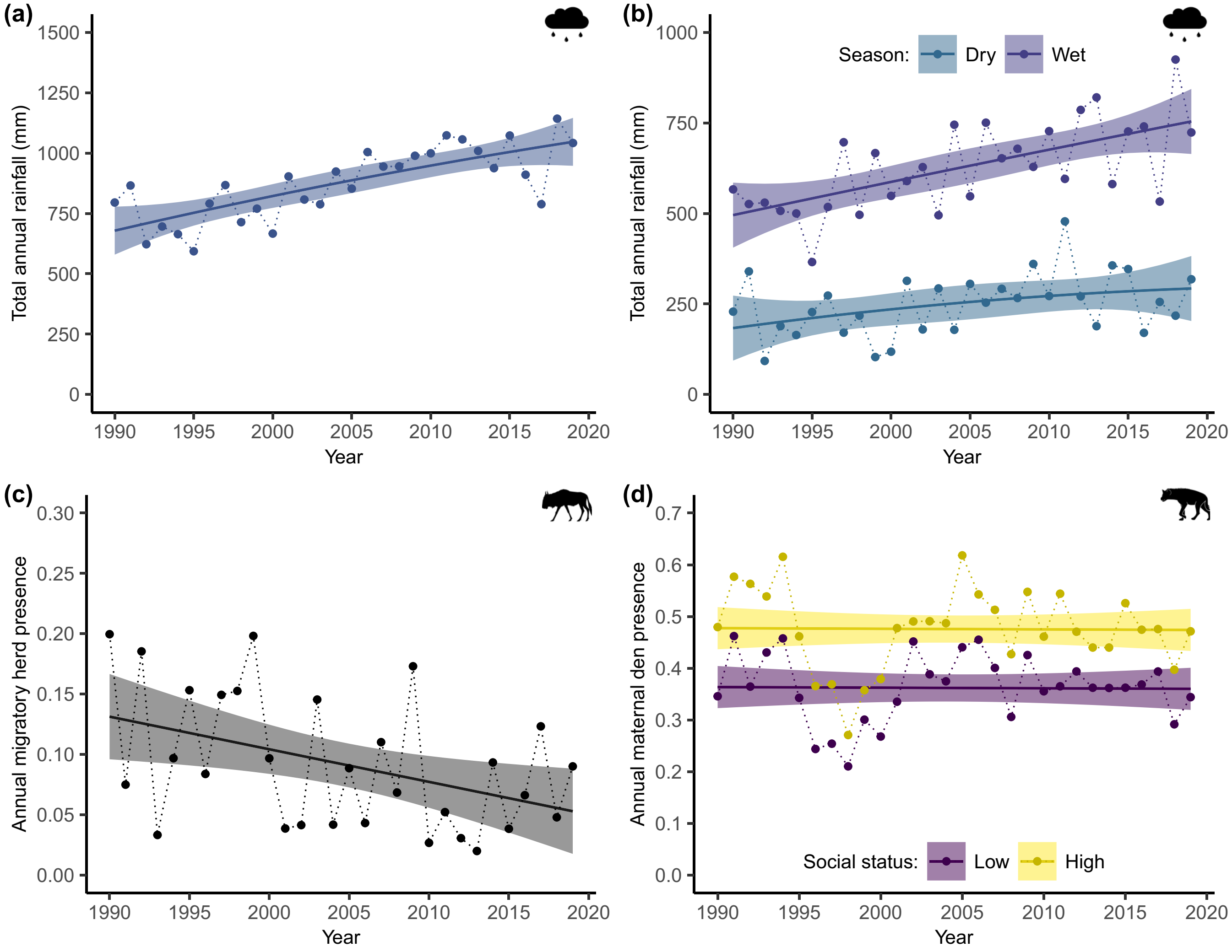

FIGURE 5 Temporal changes in (a, b) climate, (c) prey, and (d) predator variables throughout the study period. (a) Total annual rainfall, (b) total rainfall during the dry (June–October) and wet season (November–May) averaged for our three hyena clans, from 1990 to 2019 (see park borders in Figure 1), (c) annual average migratory herd presence within the three studied spotted hyena clan territories, and (d) annual average maternal den presence of high-ranking and low-ranking lactating females with milk-dependent offspring younger than 6 months at clan communal dens. Solid black lines indicate trends based on a weighted smoothing method, the ribbon with the associated 95% confidence interval

from communal dens and commute less often than low-ranking ones (Hofer & East, 1993a, 2003; Marescot et al., 2018) .

Despite some year-to-year variability in monthly rainfall volume, there were two clear seasonal rainfall peaks in March–April and November–December, corresponding to the long and short rains, respectively (Figure 2a). The main rainfall peak during the wet season in March–April preceded the arrival of migratory herds 2 months later in clan territories (Figures 2a,b and 4a,b, Appendix S2: Table S1, Figure S1). This finding is consistent with previous studies focusing on drivers of migratory herd movements in the Serengeti, which revealed the importance of the rainfall gradient (Holdo et al., 2009; McNaughton, 1988, 1990).

Serengeti hyenas may be able to predict, on the basis of past experience and possibly visual cues (e.g., rainfall volume), when large herds will pass through their territory and when they may need to commute and where to commute to locate profitable foraging areas. In line with this idea, the presence of lactating females in their clan territories matched migratory herd presence (Figures 2 and 4). The crucial aspect for hyenas is probably less about when migratory herds will be present or absent from their territory and more about successfully locating large herds of migratory herbivores in the Serengeti ecosystem. During the wet season, migratory herds are widely spread and move slowly (Hofer & East, 1993c; Sinclair et al., 2000), which probably facilitates their location by commuting hyenas. Locating migratory herds

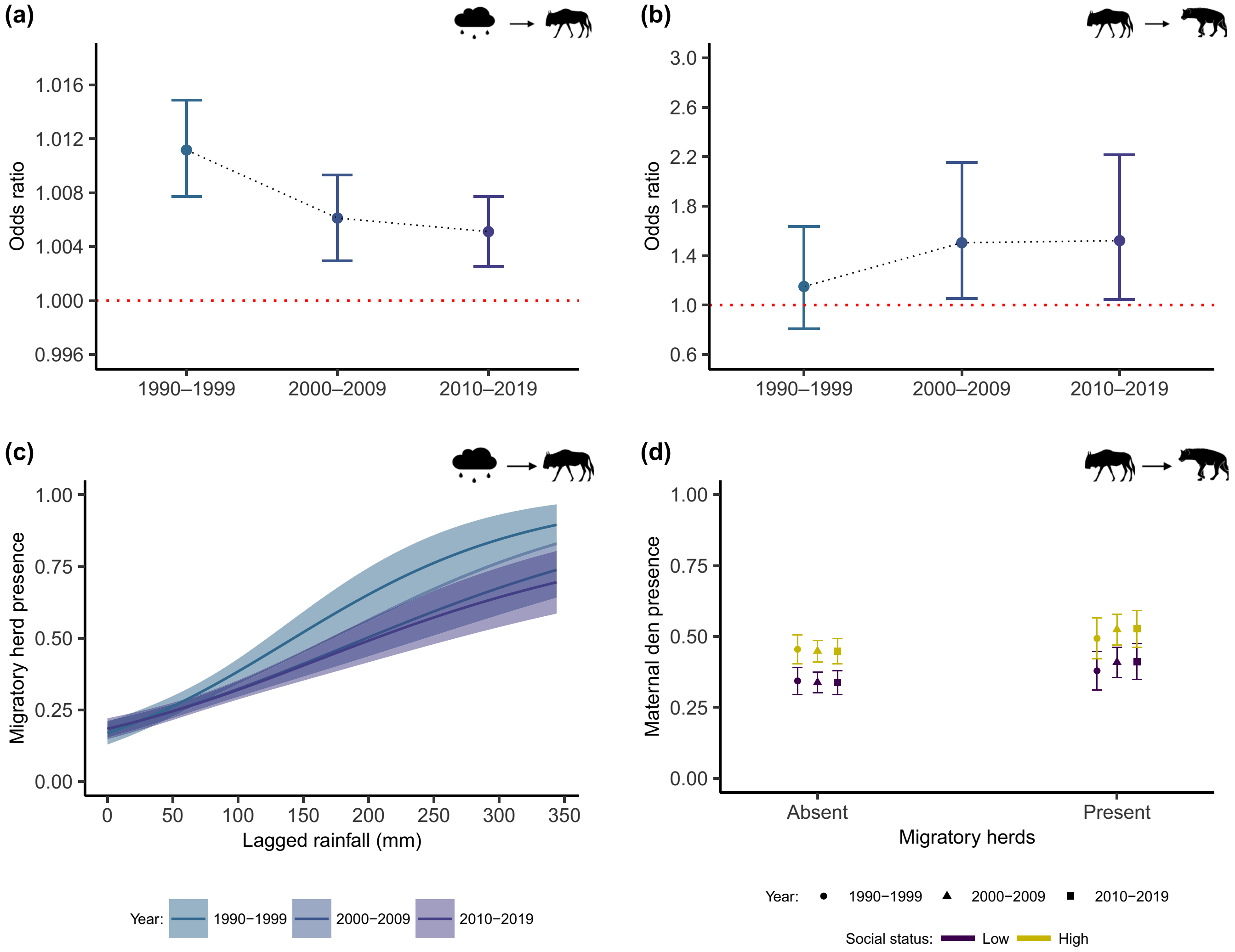

FIGURE 6 Climate change effects on (a, c) prey and (b, d) predator variables. Odds ratio for the three decades of the study period (1990–2019) for the effects of (a) monthly lagged rainfall on monthly migratory herd presence and (b) monthly migratory herd presence on monthly maternal den presence (error bars represent 95% confidence interval; the red dotted line indicates the odds ratio threshold, values above 1 indicate an increased occurrence of the event, and values below 1 indicate a decreased occurrence of an event); and (c) probability of migratory herd presence within clan territories in relation to lagged rainfall in millimeters and years; (d) proportion of high- and low-ranking lactating females with dependent cubs younger than 6 months present at the communal den (maternal den presence) in relation to the presence or the absence of migratory herds within the clan territories and years. The figure shows that years have an effect on the relationship between climate and prey but not on the relationship between prey and predator. These plots indicate that as the odds ratio decrease over time, particularly after the first decade of the study, the strength of the relationship between rainfall and migratory herd presence becomes less important. The line (c) and dots (d) represent the fitted values of the models with associated 95% confidence interval. Years were grouped into three decades to ease graphical interpretation

might be more difficult during the dry season, when herds travel west and north and are more clumped (Hofer & East, 1993c).

How did climate change affect the match between migratory herd presence in clan territories and maternal den presence? In accordance with previous findings for East Africa, we found that annual rainfall volume increased in recent years (Figure 5a; Bartzke et al., 2018; Gebrechorkos et al., 2019; Hulme et al., 2001; Mahony et al., 2021). This change in climate is likely responsible for the observed reduced strength of the link between rainfall and migratory herd presence in clan territories in recent years (Figure 6a–c, Appendix S4). Climate change could reduce restraints from vegetation productivity and thereby affect the timing of herbivore migration and/or the degree of aggregation of herds, and the different migratory herbivores species may have different responses based on if they rely on memory, social learning, or environmental cues (Bracis & Mueller, 2017; Jesmer et al., 2018). It would be very interesting to see

TABLE 2 Details of statistics for the path analysis with the variable "year" in interaction with other variables

Response	Predictor	Estimate	SE	df	Crit. value	Std.est.	Odds ratio	p
Migratory herd presence	Lagged rainfall	0.74	0.21	1815	3.49	23.44	2.08	**<0.01**
Migratory herd presence	Year	0.009	0.01	1815	0.90	0.04	1.01	0.37
Migratory herd presence	Lagged rainfall × year	−0.001	0.001	1815	−3.46	−23.24	0.99	**<0.01**
Maternal den presence	Social status	0.47	0.10	1814	4.85	0.13	1.59	**<0.01**
Maternal den presence	Migratory herd presence	−29.9	25.07	1814	−1.19	−7.34	0.00	0.23
Maternal den presence	Year	−0.003	0.007	1814	−0.37	−0.01	0.99	0.71
Maternal den presence	Migratory herd presence × year	0.02	0.01	1814	1.21	7.40	1.02	0.23

Note: Estimates obtained from the path analysis model were investigated for each relationship. Also shown are the associated standard errors (SE), degrees of freedom (df), and critical value (Crit. value). Standardized estimates (Std. est.) are useful to make comparisons about the relative strength of the predictors, where they represent the strength of the direct effect of the predictor on the response and odds ratio represents the effect of the predictor on the probability of the response. A visual presentation of their change over years is depicted in Figure 6a,b.

whether movement data on migratory herds corroborate our findings. Other known direct anthropogenic effects on the Serengeti NP include range reduction, habitat loss and/or degradation, disturbance, anthropogenic barriers, and poaching (Campbell & Hofer, 1995; Harris et al., 2009; Hofer et al., 1996, 2000; Msoffe et al., 2019). Little is known about climate change-induced effects on herbivore migrations worldwide, as most studies focus on other taxa (Seebacher & Post, 2015). Yet, some studies on migrating caribous identify a climate change-induced trophic mismatch between plant phenology and the usual migratory routes taken by caribous, with unknown consequences for their predators (Post et al., 2008; Post & Forchhammer, 2008).

Changes in movement paths or timing of the movements of migratory herds because of increased amounts of rainfall may decrease the time migratory herds spend in hyena clan territories, which may increase the time lactating females spend locating migratory herds, which would increase the length of commuting trips and decrease den presence. As maternal den presence did not decrease during the course of the study (Figure 5d) even though migratory herd presence decreased (Figure 5c, Appendix S4: Figure S1), time spent searching for migratory herds is unlikely to have increased over the years as a result of change in rainfall patterns. Similarly, the strength of the relationship between maternal den presence and migratory herd presence in clan territories did not decrease during three decades (Figure 6b–d). This finding suggests that lactating females may not so much rely on an expectation of where aggregations of migratory herds "should be," but rather employ other means of locating good foraging locations when commuting. The method by which Serengeti hyenas find such locations may be similar to the mechanism proposed by the "information center hypothesis" (Boyd et al., 2016; Sonerud et al., 2001; Ward & Zahavi, 1973) in that hyenas gain information through social learning (Bijleveld et al., 2010; Buckley, 1997) from other hyenas about the best direction to locate distant concentrations of migratory herbivores. A hyena at the communal den might obtain information on the best direction to set out on a commuting trip from the direction from which well-fed clan members return to the den, and/or the scent trail left by successful foragers. When commuting, hyenas use well-established "commuting routes," which cross many territories (Hofer & East, 1993c). The use of these tracks would allow hyenas to obtain information on the foraging success of hyenas from different clans they encounter on the way, which could help improve their efficiency in locating distant migratory herds (Hofer & East, 1993c).

There are several limitations to our study. Our data were collected at a local scale from hyena clan territories in the center of the Serengeti NP, approximately midway between the wet and dry season ranges of migratory herbivores, and the proportion of each year when migratory herds occurred in these territories was relatively low. By comparison, clans holding territories in the wet or dry season range of the migratory herds may contain migratory herds for a larger proportion of the year, which would have the benefit of increased maternal den attendance during these periods. However, the commuting distances of members of these clans may be more extreme when migratory herds are absent. For example, a lactating mother from a clan on the short-grass plains during the dry season would need to commute a longer distance northward to locate migratory herds than would lactating females from clans holding a territory in the center of the Serengeti NP. We tested relatively simple predictions for the effects of climate change on hyenas, despite the high variability and low predictability of the study ecosystem. Our data do not allow us to examine whether the movements of migratory herds and commuting hyenas changed during the past 30 years in response to increased rainfall volume in this ecosystem. Finally, our analysis is based on three clans only that we treated as a single population; including data on additional clans would have been valuable.

In conclusion, our results obtained with our data collected on a near-daily basis over 30 years suggest that hyenas appear to be well suited to cope with the change in the presence of migratory herds at their territories induced by climate change. The absence of change in the response of hyenas is in line with the high plasticity of the foraging behavior of hyenas and their use of anthropogenic landscapes (Green & Holekamp, 2019). Our study reveals that hyenas can adjust their foraging behavior to the shift in migratory herd presence in clan territories and the decline in prey presence. Although migratory herbivores in the Serengeti NP are the main prey of several large carnivore species when they occur in their territories (Craft et al., 2015), only hyenas regularly commute long distances outside their clan territory to feed on migratory herbivores (Hofer & East, 1993c). Even so, the impact of potential changes in migratory herbivore movements might affect other carnivores in this ecosystem. It is yet also possible that a potential temporal mismatch between migratory prey and predator movements caused by climate change may be of lower relevance to predators living close to the equator, as effects of climate change are more visible on high latitudes (Parmesan, 2006; Radchuk et al., 2019).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Gicquel et al., 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.17914031.

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