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RESEARCH ARTICLE

Diurnal pastoralism does not reduce juvenile recruitment nor elevate allostatic load in spotted hyenas

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Abstract

1. Anthropogenic activity can have substantial effects on wildlife. These effects may vary according to the characteristics of the activity and the species involved. Although effects on behaviour are well studied, studies of effects on fitness and physiology are scarce, particularly for group-living species.
2. We exploited a natural experimental setup to investigate the effect of diurnal pastoralism on juvenile recruitment and allostatic load in a population of free-ranging spotted hyenas in the Ngorongoro Crater, Tanzania, over a 24-year period.
3. Pastoralism was restricted to the territories of two of the eight study clans, allowing us to compare juvenile recruitment in exposed and unexposed clans. We also compared faecal glucocorticoid metabolite concentrations (fGMC)—a biomarker of an organism's allostatic load—between exposed and unexposed clans using 975 faecal samples from 475 hyenas.
4. We found no detectable difference in juvenile recruitment nor fGMC between the exposed and unexposed clans, indicating that the pastoralism had no substantial deleterious effect on the spotted hyenas. The lack of a deleterious effect likely stems from the combined effect of the predictable and undisruptive nature of the pastoralism, the socio-ecology of spotted hyenas and the Ngorongoro Crater's consistently abundant prey.
5. Our findings demonstrate that exposure to anthropogenic activity may be compatible with the persistence of certain group-living species, especially if the overlap between the species' critical behaviours and the activity is limited. Our study thereby provides new perspectives for ecologists, conservation biologists and stakeholders who seek to assess human–wildlife conflicts and balance the needs of local human communities and wildlife.

1 | INTRODUCTION

Anthropogenic activity poses challenges for conservation because it can strongly affect wildlife (Beale, 2007) and has become more intense and widespread since the industrial revolution (Lewis & Maslin, 2015). The effects of anthropogenic activity on wildlife may vary greatly, depending on an interaction between its characteristics and the species involved (Tablado & Jenni, 2017). To promote human–wildlife coexistence, it is therefore important to identify which activities are sustainable by quantifying their effects on different species. This evidence-based approach is key for the effective management of protected areas (Watson et al., 2014).

The effects of anthropogenic activity on wildlife behaviour are well documented (Bond et al., 2021; Doherty et al., 2021; Gaynor et al., 2018). In contrast, its effects on fitness traits (e.g. reproductive performance and survivorship) are poorly understood, despite being more salient to population persistence and conservation (López-Bao et al., 2017; Ménard et al., 2014). Similarly, anthropogenic effects on wildlife physiology (e.g. allostatic load) are comparatively not well studied, but may have strong implications for health and survival (Gingery et al., 2021). Changes in behaviour are not always indicative of fitness or physiological effects (Sullivan et al., 2017). For example, exposure to human pedestrians substantially altered space use, but not pup survival, in eastern wolves *Canis lycaon* (Argue et al., 2008). Therefore, detectable changes in behaviour due to anthropogenic activity may not always be of conservation concern. More knowledge of how anthropogenic activity affects fitness and physiology is needed (Beehner & Bergman, 2017).

The effects of anthropogenic activity on fitness may depend on how unpredictable and disruptive of critical behaviours the activity is (Francis & Barber, 2013). If an activity is unpredictable, the ability of animals to habituate is reduced, and thus, fitness costs may increase (Frid & Dill, 2002). For example, bighorn sheep *Ovis canadensis* herds subject to intermittent hiking by humans produced fewer recruits than herds subject to predictable hiking (Wiedmann & Bleich, 2014). Highly disruptive activities are those that greatly impede critical behaviours, which are necessary for reproduction and/or survival (e.g. foraging and offspring care; Broekhuis, 2018). Animals exposed to highly disruptive activities may lose the ability to detect threats, acquire food and find mates; disruptions to these critical behaviours have been associated with fitness costs (Longcore & Rich, 2004). Therefore, the unpredictability and disruptiveness of an activity may determine how conducive it is to human–wildlife coexistence.

The disruptiveness of an anthropogenic activity can also differ between species, depending on the species' biology and social system (Berger-Tal & Saltz, 2016). An activity that takes place during the day is unlikely to be very disruptive to species that conduct critical behaviours at night (Rottstock et al., 2020). For example, diurnal, non-motorized human recreation did not greatly disrupt foraging by nocturnal carnivores (Reilly et al., 2017). In contrast, artificial lighting at night strongly disrupted foraging and migration in nocturnal bats and birds, which resulted in fitness costs (Stone et al., 2009; Winger et al., 2019). Another factor that may influence the disruptiveness of an activity is the social system, in particular the social organization (sensu Kappeler, 2019), that is, whether animals live in groups, in pairs, or solitarily (Rowell, 1993). Group-living, for example, may improve vigilance and defence of food and offspring in response to human presence, which may buffer animals from suffering fitness costs compared to pair-living or solitary counterparts (Gittleman, 2019). Yet, not all group-living species are necessarily affected by anthropogenic activity the same way, due to variations in other aspects of their social system, including their mating system, social structure and care system (sensu Kappeler, 2019). For example, group-living species that are obligate cooperative breeders—a system in which 'helpers' provide offspring care—may be particularly susceptible to extinction from anthropogenic activities if group size is reduced (Angulo et al., 2013; Clutton-Brock, 2021). Yet, these effects have rarely been tested. Scientists can seldom complete studies of multiple social groups, due to immense financial, logistical and temporal demands, which may limit the generalizability of findings (Moss et al., 2011). Furthermore, such studies on large-bodied, long-lived species such as large carnivores are critically lacking. Large carnivores not only provide key ecosystem services, but are often implicated in human–wildlife conflict (Dheer et al., 2021; Nyhus, 2016), so understanding how they can coexist with humans is particularly important.

We used a natural experiment to study the effect of pastoralism—a globally widespread anthropogenic activity—on a population of free-ranging spotted hyenas *Crocuta crocuta* (henceforth 'hyenas') resident on the floor of the Ngorongoro Crater, Tanzania. The population has been the subject of a long-term study since 1996 (Höner et al., 2022). Hyenas are apex predators, crucial components of ecological communities across sub-Saharan Africa, and live in non-cooperative breeding, hierarchical (i.e. ranked) social groups called 'clans' (Davis et al., 2022; Frank, 1986). Critical behaviours (e.g. foraging and suckling) in hyenas mostly occur at night or dawn and dusk (Holekamp et al., 1997; Kruuk, 1972), although very young cubs are also regularly suckled during the day (Hofer et al., 2016; Wachter et al., 2002). Hyenas are behaviourally flexible; previous research suggests that they can greatly adjust their behaviour—for example, shifting den attendance and suckling bouts to nighttime—in response to diurnal pastoralism (Boydston, Kapheim, Szykman, et al., 2003; Kolowski et al., 2007). Yet, whether diurnal pastoralism affected fitness-related traits or physiology remains unknown.

The pastoralism we studied occurred from 1996 to 2016 (Melubo & Lovelock, 2019). It was restricted to the territories of two of the eight Crater clans (Figure 1), creating a natural experiment that allowed us to compare 'exposed' and 'unexposed' clans over an extended period of time. We assessed the effect of pastoralism on juvenile recruitment—estimated by the survival of cubs to 12 months—for an integrative comparison of fitness (Chesson, 2003). Our long-term data collection allowed us to quantify the effect of pastoralism while accounting for natural variations in recruitment through space and time. To disentangle the effects of pastoralism from those of other socio-ecological parameters, we accounted for disease outbreaks, the number of adult females in a clan, pressure from the main interspecific competitor (sightings of lions; *Panthera leo*), and prey availability (number of preferred prey animals) in the given clan territory. Previous research has associated these covariates with fitness-related traits in hyenas (Höner et al., 2005, 2006; Trinkel et al., 2004; Watts & Holekamp, 2008).

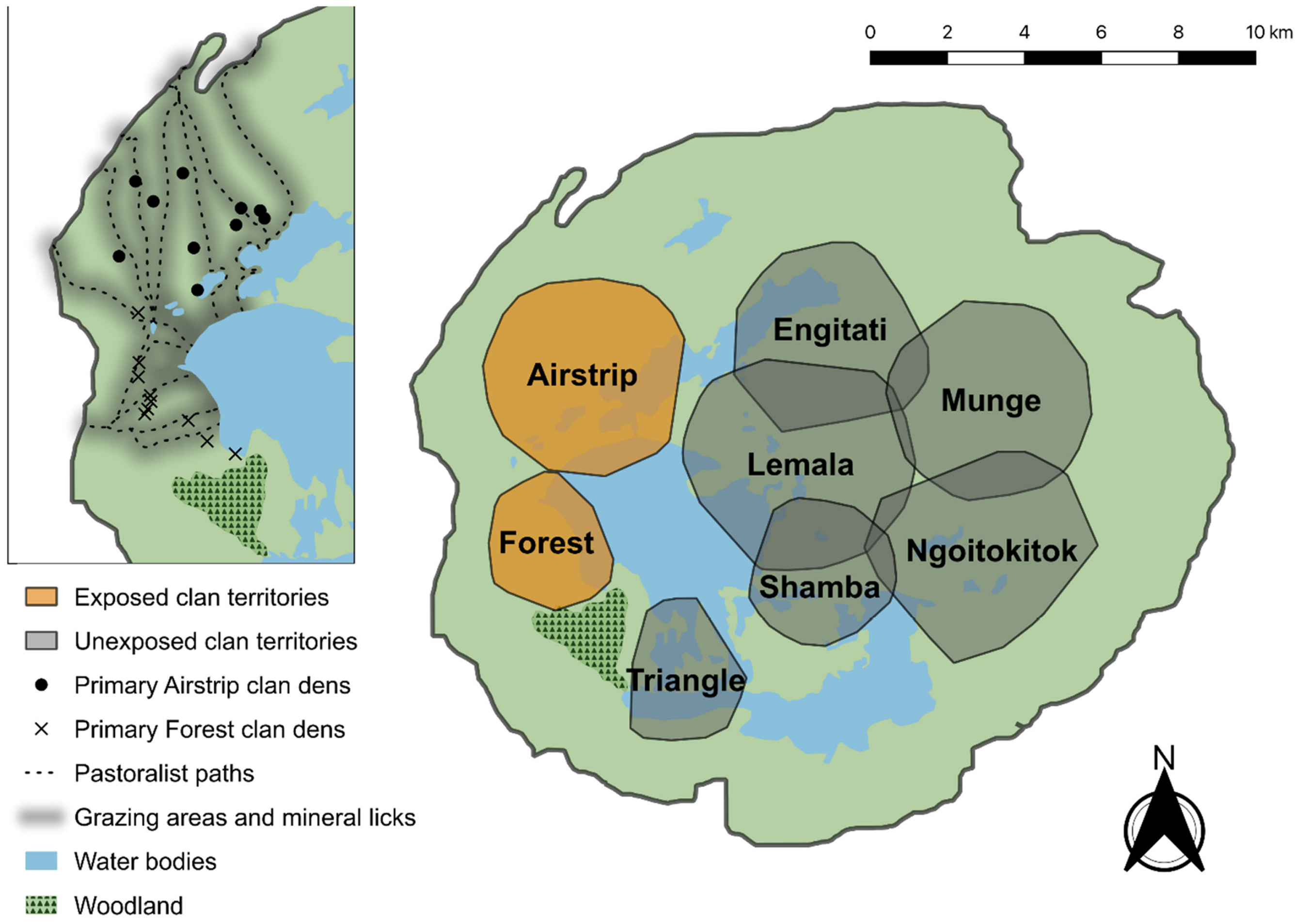

FIGURE 1 Hyena clan territories, primary clan dens, pastoralist paths, grazing areas and mineral licks in the Ngorongoro Crater. Territory boundaries are based on 85% minimum convex polygons (MCPs) of adult female hyena sightings from 1996 to 2019 for each clan. MCPs of 85% were chosen to accurately represent the locations of clan territories across the study period. Clan territories are colour coded based on whether or not they were exposed to pastoralism from 1996 to 2016. Territories are labelled with corresponding clan names. The inset depicts the primary dens ($n = 20$) that the exposed clans used from 1996 to 2016 and the major paths, grazing areas and mineral licks that Maasai and their livestock used from 1996 to 2016

Because the pastoralism we studied was diurnal, it was unlikely to affect foraging, but likely led to more nocturnal den attendance and suckling of young cubs (Kolowski et al., 2007). Such changes may also have increased the risk of hyenas being killed by lions, which are nocturnal (Cozzi et al., 2012). Thus, we predicted that exposed clans would produce fewer juvenile recruits than unexposed clans would.

Furthermore, to assess the effect of pastoralism on allostatic load, we compared the concentration of faecal glucocorticoid metabolite concentrations (fGMC) in hyenas from exposed and unexposed clans. Glucocorticoids are mediators of endocrine mechanisms that regulate essential biological functions (McEwen & Wingfield, 2003). Chronically elevated fGMC can occur as a response to repeated exposure to challenges, which may prevent an individual from adequately responding to subsequent challenges (Bonier et al., 2009). Thus, we predicted that if pastoralism led to chronically elevated allostatic load, then hyenas from exposed clans would have higher fGMC than those from unexposed clans.

2 | MATERIALS AND METHODS

2.1 | Study area and population

This study took place in the Ngorongoro Crater (3°11′S, 35°34′E), a volcanic caldera located in the wider Ngorongoro Conservation Area (NCA), Tanzania, part of the greater Serengeti ecosystem. The NCA is a multi-use protected area that was established in 1959 and is a United Nations Educational, Scientific, and Cultural Organization (UNESCO) World Heritage Site with a mandate to protect the interests of wildlife and local human communities (Charnley, 2005). The NCA is inhabited by the Maasai tribe, a semi-nomadic, pastoralist ethnic group traditionally ranging from central Kenya to southern Tanzania (Fratkin, 2001). The Maasai and their livestock resided in the Crater until 1974, when they were evicted and required to live in other parts of the NCA (Moehlman et al., 2020). They were still allowed to enter the Crater to conduct diurnal pastoralism until it was banned at the end of 2016 (Melubo & Lovelock, 2019).

In our study, diurnal pastoralism overlapped with the territories of two of the Crater's eight resident hyena clans from 1996 to 2016 (Figure 1). The pastoralism involved Maasai community members accompanying their livestock—primarily cattle—on designated paths in and out of the Crater. They were required to enter after sunrise and depart before sundown (Musiba & Mabulla, 2010). We tested for fitness and physiological effects of pastoralism by comparing exposed (Airstrip and Forest clans from 1996–2016) and unexposed clans (Engitati, Lemala, Munge, Ngoitokitok, Shamba, and Triangle clans from 1996 to 2016, and all eight clans from 2017 to 2019). Over the same period, the cattle population in the NCA grew from under 120,000 to over 240,000 and the human population from under 43,000 to over 100,000 (Manzano & Yamat, 2018).

2.2 | Data collection

Collection of demographic, behavioural and ecological data occurred between April 1996 and December 2019, on a near-daily basis between 06:00 and 19:00. We recognized individuals based on their pelage patterns, ear notches, scars and other traits. Ages were estimated based on pelage, body size, behaviour and locomotion of cubs, with an accuracy of ±7 days (Pournelle, 1965). For data filtering, cubs were defined as individuals <12 months old, juveniles as individuals 12 to <24 months old and adults as individuals ≥24 months old. The time period between the last sighting in our analyses (31 October 2019) and the last sighting in our database used to inform the analyses (09 July 2021) was 617 days. Individuals not sighted during this period were considered dead. The potential error resulting from this assumption is small because during our study period, only 2.5% of hyenas ($n = 53$ of 2096) were re-sighted after a 617-day absence. Sexes were identified through observation of external genitalia as described in Frank et al. (1990). Faecal samples were collected opportunistically, immediately after defecation by identified individuals. The study was conducted under research permits 2018-38-NA-90-48 and 2019-20-NA-90-45 issued by the Tanzania Commission for Science and Technology and did not require ethics approval.

2.3 | Juvenile recruitment

Juvenile recruitment in a given clan was defined as the number of cubs born into the clan within a given season (6-month period) that were still alive 12 months later. We chose a 12-month cut-off because mortality substantially decreases after 12 months (Hofer & East, 1995). Seasons were divided into 'dry' and 'wet' according to typical local rainfall patterns: dry seasons were the 6-month period from May 1st through October 31st of each calendar year and wet seasons were those from November 1st through April 30th of the following year (Brandell et al., 2021). We used the sequence of the seasons to test for temporal autocorrelation.

2.4 | Social rank

Individual social rank is an important determinant of various behavioural, reproductive and physiological traits in hyenas (Hofer & East, 2003; Höner et al., 2010). Ordinal ranks were determined based on the history of recorded agonistic interactions and our knowledge of rank inheritance and social queuing (for details, see Davidian et al., 2021). We converted the ordinal rank ($OrdRank_i$) of an individual (i) into a proportional rank ($PropRank_i$) bounded between −1 (bottom rank) and 1 (top rank), accounting for clan size N, using the following formula:

$$PropRank_i = \frac{N - OrdRank_i}{\frac{N-1}{2}} - 1.$$

2.5 | Disease outbreaks

Outbreaks of disease caused by pathogenic *Streptococcus* bacteria occurred multiple times over the course of the long-term study and have been significant sources of mortality in the Ngorongoro Crater hyena population (Höner et al., 2012). Therefore, seasons were categorized as being either outbreak or non-outbreak. The classification depended on whether there were observable clinical signs of *Streptococcus* infection in at least five individual hyenas during the season. Outbreak seasons ($n = 5$ seasons [3 dry and 2 wet], or 39 clan-seasons) were also associated with a mean 9% decline in total Crater hyena population compared to the preceding season, validating our criterion.

2.6 | Clan territories

We calculated clan territories based on minimum convex polygons (MCP) of adult female sightings. Each territory was characterized by fidelity to the focal clan of ≥90% (i.e. ≥90% of sightings of Crater clan adult females within a given territory were from adult female members of the focal clan). Thus, the percentages used for the MCP varied (Table S1) according to the largest area that still allowed for ≥90% fidelity to the focal clan. We contend this is a more biologically relevant approach than assigning a single MCP percentage for all clans, because it shows accurate variable space use and is rooted in observed behaviour. We divided clan territories into two temporal groups: period 1 (pre-2012) and period 2 (2012–2019), due to changes in prey per capita and clan territory sizes and locations in 2012 (Figures S1 and S2) that may have resulted from changes in vegetation due to a nearby volcanic eruption (De Schutter et al., 2015). A summary of the different MCP used for each clan in periods 1 and 2 is in Table S1. We did not split our territory calculations further because long periods of time were needed to have sufficient sample sizes to calculate accurate territories.

2.7 | Number of adult females

To account for the positive effect of the number of adult females on the total number of juvenile recruits in a given clan, we calculated the number of adult females for each clan-season combination. This was done by counting the maximum number of living adult female clan members at any point within the given 6-month season in the focal clan. For example, if a clan's maximum number of living adult female clan members during a given 6-month season was 20, they were allocated 20 adult females for that clan-season.

2.8 | Lion index

To estimate the competitive influence of lions *Panthera leo*, we created a lion index for each clan-season. We did so by attributing sightings of lions of any age and sex class to the clan territories using GPS coordinates (Garmin GPSMAP 64) and then dividing the obtained number of lion sightings by the corresponding number of adult female hyenas, from the given clan, seen in the clan territory during the given season. To avoid potential inaccuracies in the lion index caused by seasons with reduced observation effort, we only computed this index for seasons in which ≥50% of a clan's adult females were seen. For example, if only three adult females from a clan were seen during a given season, but we knew based on genetic data and sightings from subsequent seasons that the clan had 10 adult females during the given season, we deemed the lion index unreliable and excluded the entire clan-season from our analyses. Out of 384 clan-seasons, 45 had an observation effort of <50%, so we excluded them from our analyses.

2.9 | Prey per capita

We calculated prey per capita for each clan-season combination using data from the bi-annual Crater wildlife census, conducted by the Ngorongoro Conservation Area Authority (NCAA). Censuses fell within the defined seasons from our dataset. We summed counts of individuals from the five prey species most commonly eaten by hyenas in the Crater—blue wildebeest *Connochaetes taurinus*, plains zebra *Equus quagga*, African buffalo *Syncerus caffer*, Grant's gazelle *Nanger granti* and Thomson's gazelle *Eudorcas thomsonii* (Höner et al., 2002)—and divided the counts by the corresponding number of adult female hyenas in the clan during that season. Because the NCAA uses census blocks (Runyoro et al., 1995) that are not fully congruent with clan territories, we used the percentage overlap of census blocks with a given territory to allocate prey. For example, if a census block contained 100 prey animals, and 50% of the census block area overlapped with a clan's territory, then the clan was allocated 50 of the 100 prey animals. There were 10 seasons, that is, 80 clan-seasons, we could not calculate prey per capita for because the NCAA did not conduct censuses. Of those 80 clan-seasons, we had already removed seven from our analyses, because they did not meet our observation effort criterion for the lion index. Thus, we further removed 73 clan-seasons due to missing prey per capita. Our final juvenile recruitment data, therefore, consisted of 266 clan-seasons spread across 38 seasons.

2.10 | Immunoassay protocol

We assessed the physiological costs of pastoralism on hyenas using non-invasive measurements of fGMC. We collected 975 faecal samples from 475 (juvenile or adult) hyenas; 315 samples from 211 females and 660 samples from 264 males. Of these, 88 were from members of exposed clans and 887 from members of unexposed clans. Following collection, faeces were mechanically mixed, subsampled, stored in liquid nitrogen and then transported to the laboratory in Berlin, Germany, on dry ice where they were stored at −80°C until processed for analyses. Samples were freeze-dried before steroid extraction (see Benhaiem et al., 2012; Davidian et al., 2015 for the detailed extraction procedure). The fGMC were measured using an in-house, competitive Enzyme-Linked ImmunoSorbent Assay (ELISA) based on an antibody developed for cortisol-3-CMO previously validated analytically, physiologically and biologically for hyenas (Benhaiem et al., 2012). Measurements were performed in duplicates and deemed reliable when falling within the range of metabolite concentration for which the calibration curve is approximately linear (1.5–25 ng/g of dry faecal matter) and when their coefficient of variation (CV) was <5%.

Faecal extracts were assayed in two batches by the same technician. One batch was run in 2013 (n = 768 extracts, 23 plates) and another in 2020 (n = 207 extracts, 19 plates; Figure S3). Stability of ELISA accuracy and intra- and inter-assay precision were quantified using the CV of repeated measurements of faecal control pools with relatively low and high concentrations; for all pools, intra- and inter-assay CV met the <5% and <20% acceptance criteria (for more details, see Supporting Information). To ensure comparability of the fGMC between the two batches, we applied an established standardization method—as developed in Davidian et al. (2015)—and conducted a quality control assessment of key parameters of assay performance, such as parallelism, analytical precision and quantitative resolution (Table S2; Figure S4). We further exploited our setup to assess the possible deterioration and impact on fGMC of steroids in freeze-dried faecal samples and extracts that were stored at −80°C for 7 years (see Supporting Information and Figure S5).

2.11 | Statistical analyses

We conducted all statistical analyses in R software 4.2.0 (R Core Team, 2022). Data are presented as means ± *SD*, unless stated otherwise. The threshold for statistical significance was set to $\alpha = 0.05$. To test our predictions, we fitted two generalized linear mixed-effects models (GLMMs) using the 'fitme' function from package 'spaMM' (version 3.9; Rousset & Ferdy, 2014): one for juvenile recruitment and one for fGMC. *p*-values for each covariate were calculated using likelihood ratio tests for which the distribution of the test statistic under the null hypothesis was computed using 999 parametric bootstrap replicates. Model assumptions were evaluated and affirmed using package 'DHARMa' version 0.4.4 (Hartig, 2021).

We computed predictions associated 95% confidence intervals from the GLMM for each statistically significant independent variable and exposure category using the function 'pdep_effects' in 'spaMM'. For ease of interpretation, we calculated the percent change in the absolute value of juvenile recruitment and fGMC resulting from a one-unit change in the value of the focal predictor compared to its reference, calculated as [exp(coefficient) − 1]*100.

2.11.1 | Juvenile recruitment

We tested the effect of pastoralism (qualitative, two levels: exposed or unexposed), outbreaks (qualitative, two levels: yes or no), the number of adult females (quantitative), the lion index (quantitative) and prey per capita (quantitative) for each clan-season on the number of juvenile recruits per clan using a negative binomial GLMM fitted to the data. We chose the negative binomial family because the dependent variable was a non-negative integer and the goodness of fit for this model was better than that of a Poisson family on our data. These two distributions are the two main alternatives used to fit discrete quantitative data. We used the logarithm as the link function. We also applied a natural log transformation to the number of adult females for improved goodness of fit. The clan identity ($n = 8$) and the season ($n = 38$) were treated as random effects. We modelled possible temporal autocorrelation in the models by allowing for covariation between the successive realizations of the random effect 'season' (AR1 structure). We also performed likelihood ratio tests comparing model fits, considering either the presence or absence of interactions between exposure and all other covariates. We retained the model without interactions following the principle of parsimony, because there was no detectable improvement in likelihood after considering interactions ($\chi^2 = 2.02$, $df = 4$, $p = 0.72$; Table S3).

2.11.2 | fGMC

We tested the effect of pastoralism, age (quantitative, continuous number in years), clan size (quantitative, total number of hyenas in the clan, inclusive of all sexes, ages and ranks), and proportional rank (quantitative, range from −1 to 1), on natural log-transformed fGMC using a gamma GLMM fitted to the data. We chose the gamma family because the dependent variable was non-negative and continuous. We used the logarithm as the link function. The hyena's identity ($n = 475$) and the season ($n = 41$) were treated as random effects. We used 41 of the possible 48 seasons because faecal samples were not collected during 7 seasons. All covariates were accurate to the day of sample collection, for example, the proportional rank associated with a given fGMC was the defecating hyena's proportional rank on the day of sample collection. We modelled the possible temporal autocorrelation as previously described. As with recruitment, we performed likelihood ratio tests comparing model fits considering either the presence or absence of interactions between the exposure predictor and all other covariates. We again retained the model without interactions, because there was no detectable difference in likelihood after considering interactions ($\chi^2 = 0.28$, $df = 3$, $p = 0.98$; Table S4).

3 | RESULTS

3.1 | Effects of pastoralism and ecological covariates on juvenile recruitment

Exposed clans produced more juvenile recruits per season (4.46 ± 3.85 juveniles, $n = 56$ seasons) than unexposed clans did (3.50 ± 3.11 juveniles, $n = 210$ seasons), though the difference was not detectable (Mann–Whitney *U* test; $U = 6798.5$, $p = 0.071$; Figure 2a). A GLMM confirmed that there was no detectable difference in predicted juvenile recruitment between exposed (4.27 juveniles; CI 95% = 2.68–6.83) and unexposed clans (3.50 juveniles, CI 95% = 2.35–5.23; Figure 3a) when controlling for other covariates (see Table 1 for detailed model coefficients). There were detectable effects of outbreaks (negative), number of adult females (positive) and lion index (positive) on juvenile recruitment (Table 1). The predicted number of juvenile recruits produced by clans during outbreak seasons was 2.59 (CI 95% = 1.61–4.18); during non-outbreak seasons, it was 3.86 (CI95% = 2.63–5.68; Figure 3b). A one-unit increase in the number of adult females on the natural log scale (=32.03 real females for one log unit above the average number of adult females, 18.64 ± 10.52) led to a predicted 136.3% increase in the number of juvenile recruits (Figure 3c). A one-unit increase in the lion index (i.e. one additional lion sighting per adult female hyena seen) led to a predicted 6.5% increase in the number of juvenile recruits (Figure 3d). The effect of prey per capita was small and not detectable (Table 1).

There was no detectable difference in the number of adult females between exposed (mean = 19.75 ± 10.37, $n = 56$) and unexposed (18.35 ± 10.56, $n = 210$, $U = 6425.5$, $p = 0.29$; Figure S6) clans. The lion index was lower in exposed clan territories (mean = 1.00 ± 1.50, $n = 56$) than in unexposed clan territories (1.70 ± 2.13, $n = 210$; $U = 4586$, $p = 0.011$; Figure 2b), representing a difference of 0.70 lion sightings per adult female hyena seen. In contrast, prey per capita was higher in exposed (102.79 ± 86.11, $n = 56$) than unexposed clan territories (84.07 ± 87.81, $n = 210$; $U = 7294$, $p = 0.006$; Figure 2c).

3.2 | Effects of pastoralism and socio-ecological covariates on fGMC

There was a biologically small but near-detectable difference in observed fGMC between exposed clans (mean = 50.98 ± 63.56 ng/g,

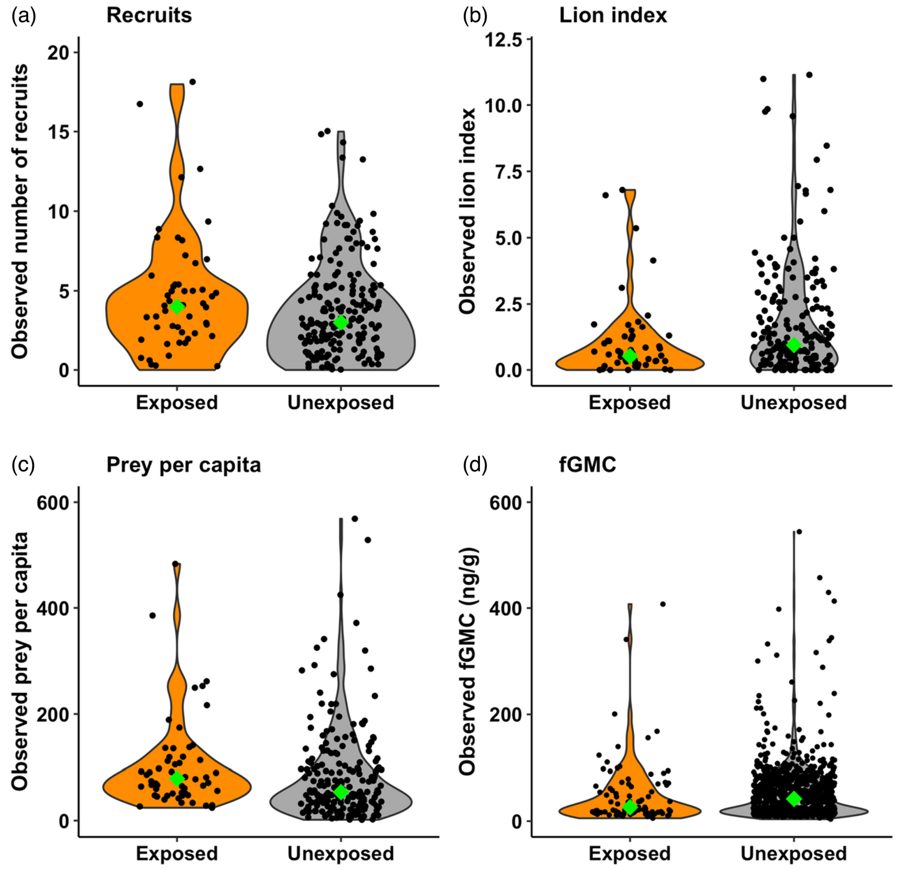

FIGURE 2 Observed ecological data pertaining to hyena clans. (a) Number of juvenile recruits, (b) lion index, (c) prey per capita, and (d) faecal glucocorticoid metabolite concentration (fGMC). Each violin plot displays the distribution of data for the respective clan category (exposed or unexposed to pastoralism). Exposed clans (orange) were subject to pastoralism while unexposed clans (grey) were not. Black dots represent observed data after horizontal jittering was applied for ease of visualization. Green diamonds represent sample medians

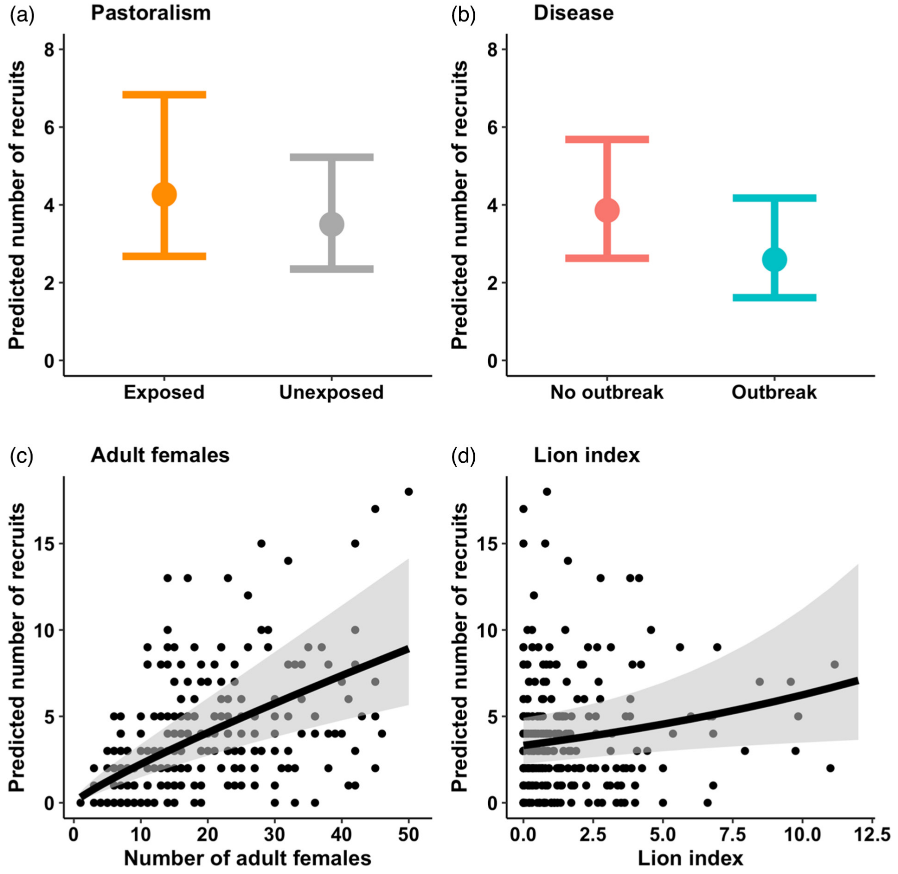

FIGURE 3 Effect of anthropogenic activity and ecological covariates on the predicted number of juvenile recruits in hyena clans. (a) Pastoralism, (b) disease, (c) number of adult females, and (d) lion index. Black dots represent observed data points. Plotted predictions show changes in the response variable given changes in a focal (fixed-effect) variable, computed as the average of predicted values (on the response scale) over the empirical distribution of all other fixed-effect variables and of inferred random effects. This method allows for the visualization of the effect of the given fixed-effect variable while avoiding any effects caused by association between the focal variable and other predictor variables

TABLE 1 Effects of anthropogenic activity and ecological covariates on the number of juvenile recruits in hyena clans. Covariates consist of anthropogenic activity (pastoralism), disease outbreaks, number of adult females, lion index and prey per capita on the number of juvenile recruits produced by hyena clans in the Ngorongoro Crater, Tanzania. The intercept for the model corresponds to the exposed category of hyena clans (subject to pastoralism) and no disease outbreak, with the number of adult females, lion index and prey per capita held at 0. The column 'S.E.' provides standard errors on parameter estimates. The column '% change' gives the percent change in the absolute value of the response variable resulting from a one-unit change in the value of the focal predictor compared to its reference. The column 'L.R.' and '*p*' give, respectively, the likelihood ratio statistics and the *p*-value associated with the likelihood ratio test. Data in bold were deemed statistically significant. Results are based on a negative binomial generalized linear mixed-effects model (GLMM; *p*-values based on a likelihood ratio test using 999 parametric bootstrap replicates). Random variances were estimated for time- ($n = 38$ seasons) and clan-level ($n = 8$ clans) at 0.03. The coefficient for the temporal autocorrelation (AR1 structure) between consecutive seasons was estimated to 0.58

	Estimate	S.E.	% change	L.R.	*p*
Intercept	−1.20	0.36			
Unexposed	−0.20	0.17	−18.0	0.92	0.35
Outbreak	**−0.40**	**0.17**	**−32.8**	**4.07**	**0.043**
Adult females	**0.86**	**0.11**	**136.3**	**28.87**	**0.001**
Lion index	**0.06**	**0.03**	**6.5**	**4.42**	**0.036**
Prey per capita	0.00	0.00	0.1	1.43	0.25

TABLE 2 Effects of anthropogenic activity and socio-ecological covariates on faecal glucocorticoid metabolite concentration (fGMC) in hyenas. Covariates consist of anthropogenic activity (pastoralism), age, clan size and proportional rank on the natural log of the fGMC of hyenas in the Ngorongoro Crater, Tanzania. The intercept for the model corresponds to the exposed category of hyena clans (subject to pastoralism), with age, clan size and proportional rank held at 0. Data in bold were deemed significant. Results are based on a gamma generalized linear mixed-effects model (GLMM; *p*-values based on a likelihood ratio test using 999 parametric bootstrap replicates). Random variances were estimated for time- ($n = 41$ seasons) and individual-level ($n = 475$ hyenas) at 0.003 and 0.005, respectively. The coefficient for the temporal autocorrelation (AR1 structure) between consecutive seasons was estimated to 0.55. See Table 1 legend for details on column names

	Estimate	S.E.	% change	L.R.	*p*
Intercept	1.15	0.04			
Unexposed	0.01	0.03	0.5	0.04	0.85
Age	**0.02**	**0.00**	**1.5**	**37.56**	**0.001**
Clan size	0.00	0.00	0.0	0.11	0.74
Rank	0.01	0.01	1.3	0.83	0.34

$n = 88$ faeces) and unexposed clans (55.09 ± 62.61 ng/g, $n = 887$ faeces; $U = 34{,}167$; $p = 0.054$; Figure 2d). A GLMM revealed no detectable difference in predicted fGMC between exposed and unexposed clans after controlling for other covariates (Table 2). The predicted fGMC for hyenas in exposed clans was 36.32 ng/g (CI 95% = 22.94–61.57 ng/g) and in unexposed 37.01 ng/g (CI 95% = 24.01–60.59 ng/g). The GLMM also revealed that age had a weak, positive effect on fGMC (Table 2); a 1-year increase in age led to the predicted fGMC (i.e. ng/g) increasing by 1.5%. Clan size and rank had small, non-detectable effects on predicted fGMC (Table 2).

4 | DISCUSSION

In this study, we investigated how diurnal pastoralism affected juvenile recruitment and allostatic load in free-ranging hyenas. We used a natural experiment to compare hyena clans exposed and unexposed to pastoralism over the course of 24 years. Exposure to pastoralism did not substantially reduce juvenile recruitment nor elevate fGMC in the hyenas. Three main, non-mutually exclusive scenarios may explain our results.

First, the pastoralism may not have been unpredictable or disruptive enough to reduce juvenile recruitment. Pastoralism occurred predictably, on the same designated paths in and out of the Crater. Its consistency may have allowed hyenas in exposed clans to habituate. The fact that the pastoralism was diurnal may also have made it largely undisruptive to critical behaviours such as foraging and suckling. Hyenas that undertake most of their foraging at night, dawn and dusk (Kruuk, 1972) would have limited overlap with pastoralism. The suckling of young cubs may take place during the day, but previous research showed that hyenas can shift suckling to nighttime to reduce overlap with diurnal pastoralism (Kolowski et al., 2007). Additionally, hyenas readily shift dens following disturbances (Périquet et al., 2015), which allows young cubs to safely suckle. This spatial separation may not have been an option for hyenas in our study, though, due to the small Crater clan territories and the large extent of the pastoralist paths. Our study suggests that spatiotemporal adjustments are not costly enough to reduce juvenile recruitment. Additionally, they indicate that behavioural plasticity may allow hyenas to persist in areas with diurnal anthropogenic activity (Frank & Woodroffe, 2001). Behavioural plasticity may also partly explain why fGMC did not greatly differ between exposed and unexposed clans. Previous research has suggested that hyenas may adjust their behaviour to minimize exposure to social challenges and downregulate their fGMC (Davidian et al., 2021). Thus, hyenas in exposed clans could have made behavioural adjustments, thereby levelling their fGMC to those of hyenas in unexposed clans. Altogether, our results support those of other studies which suggested that predictable, undisruptive activities are conducive to human–wildlife coexistence.

Second, the hyena social system may have buffered exposed clans from the potential negative effects of pastoralism. Hyena clans are hierarchical and have rank-related reproductive skew: low-ranking females have lower reproductive success than high-ranking ones do (Hofer & East, 2003; Holekamp et al., 1996).

Thus, even if the reproductive performance of low-ranking females is greatly reduced, the clan itself may persist. Low-ranking hyenas also have less access to preferred dens and resting areas (e.g. those further away from pastoralist paths) than high-ranking hyenas do (Boydston, Kapheim, Watts, et al., 2003). Accordingly, low-ranking hyenas in exposed clans therefore may have experienced more direct and stronger effects of pastoralism than their high-ranking counterparts did. But because low-ranking females produce fewer recruits a priori, the early loss of few low-ranking cubs may not be noticeable at the group level, allowing the clan to persist. Additional studies conducted at the individual level may detect if low-ranking females indeed buffer the negative effects of anthropogenic activity.

Third, the Crater's consistently high prey abundance (Moehlman et al., 2020) may have buffered any negative effects of pastoralism. Prey-rich environments such as the Crater allow female hyenas to produce sufficient milk for daily suckling and provide favourable early-life conditions (Wachter et al., 2002), which may facilitate juvenile recruitment. In exposed clans, even if pastoralism forced critical behaviours such as suckling to become more nocturnal, the relative ease of acquiring food may have reduced the cost of such adjustments. Furthermore, over the course of our study, the hyena population was recovering from a major decline (Höner et al., 2005) and therefore likely experienced little competition for prey. Consistently abundant prey may also explain why there was no detectable effect of prey per capita on juvenile recruitment, in stark contrast to other studies (Broekhuis et al., 2021; Mills & Harris, 2020). Even if prey per capita within a clan territory declined greatly, there would be plentiful prey in other clan territories that hyenas could access by intruding (Höner et al., 2005). Thus, the Crater's consistently abundant prey may have allowed for coexistence between pastoralism and hyenas.

Among the other covariates in this study, the lion index and the number of adult females had positive effects and outbreaks a negative effect on juvenile recruitment. One explanation for the effect of the lion index is that it may indicate favourable ecological conditions for hyenas, as the two species occupy very similar niches (Davidson et al., 2019; Périquet et al., 2015). Thus, clan-seasons with high lion indices may have had conditions that facilitated juvenile recruitment. A second explanation is that food provisioning by lions for hyenas may have boosted juvenile recruitment. A previous study in the Crater found that dominance between the two species at carcasses is relatively balanced, depending on the hyena-to-lion ratio and the presence of male lions (Höner et al., 2002). The study also found that klepto-parasitism and scavenging by hyenas increased when lion abundance increased. Clans may thus have enjoyed greater access to food (and subsequently, higher juvenile recruitment) when there was a high lion index. The detectable effects of the number of adult females and outbreaks on juvenile recruitment are consistent with previous findings (Green et al., 2019; Höner et al., 2012). Similarly, the detectable positive effect of age on fGMC supports the results from previous studies of hyenas and other mammals (Davidian et al., 2021; Hämäläinen et al., 2015). Evidently, other socio-ecological parameters in our study influenced juvenile recruitment and fGMC much more strongly than pastoralism did. This again suggests that pastoralism had no substantial deleterious effect on the Ngorongoro Crater hyena population.

Although anthropogenic activity is often considered inherently bad for wildlife, its effects may vary according to the type of activity occurring, the focal species' biology and social system, and food availability. Our findings demonstrate that exposure to anthropogenic activity may be compatible with the persistence of certain group-living species, especially if overlap between the species' critical behaviours and the activity is small. This result provides important insights for stakeholders and conservation biologists who seek to balance the needs of local human communities and wildlife. Our study also illustrates that changes in anthropogenic activity represent natural experiments that can be exploited to assess the effects of humans on wildlife. To best distinguish the effect of localized anthropogenic activity from that of larger environmental patterns, such changes in anthropogenic activity must be restricted to specific time periods and locations within a broader monitored area, as is the case in this study. More studies that collectively span a variety of anthropogenic activities, species and social systems—and that quantify anthropogenic effects on fitness and physiology—are needed for effective evidence-based conservation. With a growing number of such studies, it will soon be possible to perform comparative analyses to generate the knowledge needed optimize human–wildlife coexistence.

AUTHOR CONTRIBUTIONS

Arjun Dheer, Eve Davidian, Alexandre Courtiol, Liam D. Bailey and Oliver P. Höner conceived the ideas and designed the methodology; Arjun Dheer, Eve Davidian, Jella Wauters, Philemon Naman, Victoria Shayo and Oliver P. Höner collected the data; Arjun Dheer, Alexandre Courtiol and Jella Wauters analysed the data; Arjun Dheer 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

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.dv41ns226 (Dheer et al., 2022).

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SUPPORTING INFORMATION

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

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