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Troubled waters: Water availability drives human-baboon encounters in a protected, semi-arid landscape

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ABSTRACT

Most animal habitats are affected by humans. While some species tolerate and even benefit from these changes, others suffer. Understanding when and how human-altered landscapes affect animal behavior, health, reproduction, and survival is essential to species management in a human-dominated world. Here we use 27 years of data on human-baboon encounters in a protected, semi-arid ecosystem in Kenya to: (i) identify spatial, environmental, and group-level predictors of baboon encounters with pastoralists; (ii) test whether human-built water sources alter baboon ranging patterns; and (iii) test if human encounters are linked to baboon survival, reproduction, and health. We find that the primary driver of human-baboon encounters is water availability. During dry periods, pastoralists migrate into baboon rangelands, leading to frequent human-baboon encounters, especially near water wells. Further, the baboons shift their ranges to encompass newly built wells and move away from abandoned, dried-up wells. Since 2006, a third of adult baboon deaths were linked to violent encounters with humans or their dogs. Human encounters were also linked to high infant mortality and parasite diversity in females (but this effect could not be disentangled from seasonal confounds). For wild baboons, life in protected, pastoralist conservancies presents a double-edged sword: human-built wells enable the baboons to access water during dry periods, but these wells lead to encounters with humans, which have become a common source of baboon mortality. Together, our results serve as a comprehensive case study of anthropogenic effects on wild primates, highlighting the complex interactions between humans and wildlife in protected areas.

1. Introduction

Most animal rangelands are patchworks of human use. Some areas are relatively untouched, while others are heavily altered by people. As animals move through these landscapes, they increasingly encounter and interact with people, crops, garbage, and domesticated animals, leading to diverse outcomes—from increased disease risk and mortality (e.g., Estrada et al., 2017; Mbora et al., 2009; Meijaard et al., 2011), to access to new resources and release from predators and competitors (e.g., Pokharel et al., 2019; Purdon and van Aarde, 2017; Thatcher et al., 2019). The diversity of these outcomes is well-illustrated by nonhuman primates. On the one hand, anthropogenic effects on primates have created existential threats for most species: 75 % of primate populations are declining in size, and ~60 % of primate species are threatened with extinction (Estrada et al., 2017). On the other hand, some primates with generalist foraging strategies and ecological similarity to humans are occasionally successful at exploiting human-dominated landscapes (Hoffman and O'Riain, 2012; Sha and Hanya, 2013). Understanding primate-human encounters therefore requires holistic, long-term data on both the causes of these interactions and their multifaceted

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outcomes.

Here we use detailed data on the drivers and consequences of human encounters for baboons living in protected conservancies in the Amboseli ecosystem in Kenya. To date, most research on human-primate encounters, especially human-baboon encounters, has focused on agricultural or suburban settings (van Doorn and O'Riain, 2020; Walton et al., 2021; Warren et al., 2011). In these contexts, baboons commonly raid human-derived foods, including crops and garbage. While these resources bestow energetic advantages on baboons, they can lead to conflict with farmers and landowners, alter baboon ranging patterns, and change baboon social behavior (Alberts and Altmann, 2012; Altmann and Alberts, 2003; Altmann and Muruthi, 1988; Chowdhury et al., 2020; Hoffman and O'Riain, 2011a; van Doorn and O'Riain, 2020; Walton et al., 2021; Warren et al., 2011). In contrast, the Amboseli ecosystem is neither agricultural nor suburban; Amboseli is a semi-arid savannah where most human inhabitants make a living via pastoralism, and where water is limiting for both people and wildlife. This ecosystem provides an unusual opportunity to use water availability as a lens through which to view the drivers and consequences of human-primate encounters. In dryland ecosystems, baboons and other animals are often unintentional victims or beneficiaries of human activities to control water, and human-wildlife encounters over water are an important and understudied aspect of anthropogenic effects on arid habitats and wildlife (du Toit et al., 2017; Muntifering et al., 2019; Hoffman and O'Riain, 2011b).

Baboons in Amboseli encounter many types of people (e.g., researchers, wildlife managers, and tourists; Kiiru, 2012), but they commonly encounter members of the pastoralist Amboseli-Longido Maasai community. The Maasai people migrated into Amboseli in the 1800s, catalyzed by periods of drought in Tanzania (Githumbi et al., 2018). Maasai pastoralists provide year-round food and water for their livestock by shifting their grazing areas with the seasons and digging shallow, earthen wells when natural water sources run dry (Kimiti et al., 2018; Kioko and Okello, 2010). The sizes of these hand-dug wells differ widely from well to well and vary across seasons (Fig. S1). The smallest wells are a few meters across in the dry season and the largest expand to >20 m across in the wet season. In 1974, the Kenyan government gazetted a 390 km^2 area as Amboseli National Park (ANP), which protected land for wildlife, but excluded the Maasai from important dry season grazing areas and year-round water sources (Kiiru, 2012; Kioko and Okello, 2010). This exclusion led the Maasai to focus livestock grazing outside ANP and increase their reliance on hand-dug wells. The zone surrounding the park consists of protected areas designated by local communities as conservancies to protect wildlife. Local communities who use these conservancies experience financial incentives to tolerate wildlife, primarily in the form of revenue from tourism, but also through employment opportunities with tourism, conservation, and research groups (including the Amboseli Baboon Research Project, which employs scouts in the conservancies). The wildlife conservancies are essential to supporting the park's wildlife, but they lead to frequent interactions between wildlife and members of the Maasai community, as well as their livestock and dogs, sometimes with injurious consequences for baboons (Okello and Kioko, 2010).

Within this context, we leveraged long-term data from the Amboseli Baboon Research Project (ABRP; Alberts and Altmann, 2012) to accomplish three main objectives: (i) to identify environmental, spatial, and group-level predictors of human-baboon encounters; (ii) to test whether human-provided sources of water (i.e., hand-dug wells) affect baboon ranging; and (iii) to identify correlates of human-baboon encounters for baboon survival, reproduction, and health (Fig. 1). For our first objective, we hypothesized that climate and seasonal changes in human and livestock migrations would result in more human-baboon encounters during low-rainfall periods (Kimiti et al., 2016). We also expected that hand-dug wells would be hotspots of human-baboon encounters. For group-level factors, we expected that groups with the largest home ranges (which includes both the smallest and the largest groups in our population; Markham et al., 2015) would have the highest rates of human encounters because their movements cover more area. For our second objective, we hypothesized that the construction and abandonment of wells would alter baboon ranging patterns, leading baboons to move into areas with newly active wells and leave areas when these wells are no longer active. For our third objective, we hypothesized that human encounters are costly to baboons, leading to rising baboon deaths over time and negative effects on infant mortality, reproductive rates, glucocorticoid hormone levels, and helminth burdens. Specifically, if human encounters are unpredictable and energetically expensive, then they could represent a source of psychosocial and energetic stress, leading to immunosuppression and, perhaps, elevated parasite burdens (Akinyi et al., 2019; Defolie et al., 2019; Machado et al., 2011; Monello et al., 2010). We also considered the alternative that, because the baboons experience some protection in the conservancies and can, as a species, tolerate some human-dominated landscapes, human-baboon encounters may have few costs for baboons. Our results provide an unusually comprehensive case study for

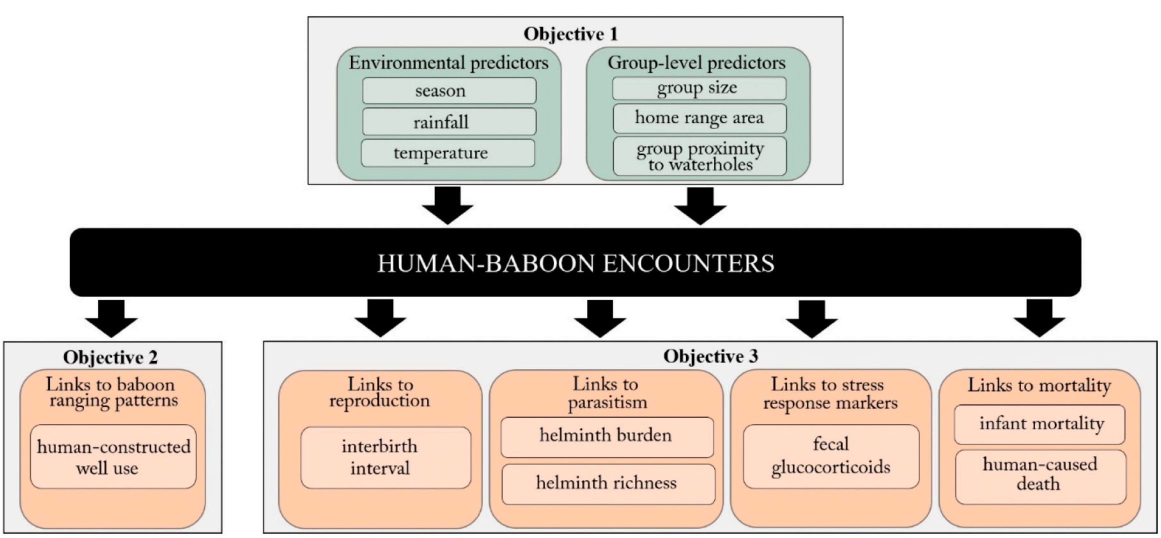

Fig. 1. Schematic illustrating the three main objectives of this paper: (1) to identify the environmental, spatial, and group-level predictors of human-baboon encounters in wildlife conservancies; (2) to test how wells in these conservancies affect baboon ranging patterns; and (3) to test the consequences of human-baboon encounters for baboon survival, reproduction, and health.

understanding how human presence is affecting the demography, resource use, survival, reproduction, and health of wildlife living in protected yet human-altered environments.

2. Methods

2.1. Study population

The Amboseli ecosystem is a semi-arid, short-grass savannah located in southern Kenya. Amboseli has strong wet-dry seasonality; each year has a 5-month long dry season from June to October, during which rainfall is negligible. From November to May, rainfall is temporally and spatially variable (mean annual rainfall = 355 mm, range = 140–757 mm; Alberts et al., 2005; https://amboselibaboons.nd.edu/downloads/). Multiple sequential low rainfall years can result in devastating droughts for people, livestock, and wildlife (Alberts et al., 2005; Western and Manzolillo Nightingale, 2003; Western et al., 2015).

Amboseli is home to a population of savannah baboons (primarily *Papio cynocephalus* with some admixture from *P. anubis*) that have been the subject of long-term study by the Amboseli Baboon Research Project (ABRP) since 1971 (Alberts and Altmann, 2012). At any given time, the ABRP monitors individually recognizable baboons living in four to six social groups (i.e., "study groups"), recording behavioral, environmental, reproductive, and demographic data during 5-h monitoring visits, two to four times a week per group. The data we use in this paper spans 16 study groups that were observed for different periods of time between 1993 and 2020 (147 group-years). This time span corresponds to the time after which the ABRP study groups had shifted their range out of the National Park (ANP) and into wildlife conservancies owned by the Maasai. The ABRP study groups moved their home ranges to areas largely outside of ANP in the early 1990s following long-term decline of the park's fever tree groves (*Vachellia xanthophloea*), which the baboons relied on for sleeping and food. The conservancies they entered provided the baboons with large, new groves, but it lacked natural, year-round sources of water; human-built wells constructed for livestock filled this need, enabling the baboons to persist in the conservancies (Alberts et al., 2005).

All data collection procedures adhere to the regulations of the Institutional Animal Care and Use Committees of Duke, Princeton, and Notre Dame universities, and to the laws of Kenya.

2.2. Measuring human-baboon encounters

Whenever a baboon group encountered humans during their daily movements, ABRP observers recorded: (i) the date and time of the encounter, (ii) the identity of the study group, (iii) whether the people were accompanied by livestock and/or dogs, (iv) whether the encounter involved people chasing the baboons from garbage, and (v) the baboons' response to the encounter, including producing alarm calls and/or fleeing from the people.

To understand spatial patterns, we also required GPS locations for human-baboon encounters. Because ABRP observers do not normally record GPS point locations when the baboons encounter people, we inferred the locations of these encounters using GPS points collected continuously every 30 min when they are with the group and whenever the baboons drink from a water source. Specifically, we assigned each human encounter to the closest GPS location in time, excluding observations that were recorded >15 min from any GPS point. While we analyzed data on human-baboon encounters beginning in 1993, we only analyzed locations for these encounters starting in 2004, corresponding to the first year ABRP observers recorded GPS points electronically using digital waypoints.

2.3. Measuring predictors of human-baboon encounters

Our first objective was to identify the environmental, spatial, and group-level predictors of human-baboon encounters. This objective required data on variables that may predict the frequency with which baboons encounter humans, including the hydrological year and season during which the encounter occurred, rainfall, spatial proximity to nearby water wells, social group size, and home range size. Information on how these variables were measured is in the Supplementary Materials.

2.4. Measuring range shifts in response to human-constructed water sources

Our second objective was to test whether baboons shift their ranges to encompass newly active wells or move away from wells when they become inactive. For these analyses, we identified instances when a well transitioned from "active" to "inactive" or vice versa. Aside from temporary pools created by the rains of the wet season, the baboons get nearly all of their water from human-provided wells. However, the wells require human maintenance to prevent them from filling with soil (e.g., Fig. S1F). When they fill in, they are no longer usable by people, livestock, or wildlife. These changes provide natural experiments to test whether the baboons shift their ranges to encompass usable wells or move away from unmaintained, non-usable wells.

We identified usable, "active" wells as those that ABRP observers directly observed one or more of the baboon study groups using at least two times in each of two consecutive years, while inactive wells were used less often. This definition is a good proxy for the usability of the well from the baboons' perspective, because water is in such high demand in Amboseli that if a well contains potable water, it will be discovered and used by at least one baboon group, allowing us to characterize well activity/inactivity by baboons' usage. We grouped spatially clustered wells that could not be analyzed independently; these clusters were treated as single wells in our analyses (e.g., wells PHABC, PHDE, and SH123 in Fig. S2).

2.5. Measuring survival, reproductive, and health-related correlates of human-baboon encounters

Our third objective was to understand the consequences of human encounters for baboon survival, reproduction, and health. We began by estimating both (i) the percentage of human encounters that resulted in the baboons fleeing from people, and (ii) the percentage of baboon deaths attributable to human encounters. In Amboseli, people or their dogs sometimes accidentally or intentionally kill baboons, for instance when the baboons encounter domestic dogs that are accompanying herders, or when people retaliate against baboons for killing newborn goats. However, the baboons die for many other reasons (e.g., predators, pathologies, or accidents), and establishing the cause of death, especially human responsibility, in each case is difficult and prone to biases. However, we had corroborating or circumstantial evidence to support a given cause of death for 34.8 % of observed deaths (225 of 646 deaths) between 1993 and 2020, and we categorized these deaths into 6 basic categories: accidents (e.g., falling out of a tree), conspecific-caused deaths (e.g., killed by a group member during infanticide or kidnapping), pathologies (including apparent infectious and non-infectious diseases), predation (e.g., by lions, leopards, eagles, or hyenas), interruption of maternal care (e.g., infants whose mothers died), and deaths due to interactions with humans or their dogs. The remaining deaths (65.2 %; 421 of 646 deaths) were categorized as unknown.

In addition to investigating potential causes of death, we also tested how the frequency of human encounters predicted five outcome variables relevant to baboon reproduction, health, and survival: the survival of females' infants, female interbirth intervals, individual helminth burdens, individual helminth richness, and individual fecal glucocorticoid (fGC) levels. See the Supplementary Materials for details on how these variables and relevant covariates were measured and Tables S1-S7 for a complete list of covariates in each model.

2.6. Statistical analyses

2.6.1. Objective 1: modeling predictors of human-baboon encounters

To test which environmental and group-level factors explained the frequency of human-baboon encounters, we used a linear mixed model with a Gaussian error distribution via *lme4* in R (Bates et al., 2015). Our response variable was the frequency of human-baboon encounters for each group in each season (dry or wet) and hydrological year ($n = 264$ group-seasons), calculated as the number of days each study group encountered humans, divided by the number of monitoring visits observers made to each group. To minimize non-independent encounters, the maximum number of encounters for a given group and day was one, even if multiple encounters were observed.

Our fixed and random effects are listed in Table S1 (see Supplementary Methods for how each variable was measured). Briefly, our fixed effects were the hydrological year and season over which the encounter frequency was calculated, total rainfall across the season (in mm), the average daily maximum temperature across the season (in °C), average adult group size, the quadratic of group size across the season, and an interaction effect between season and year. We modeled baboon social group identity as a random effect. To test whether the group home range sizes predict human encounter frequencies, we ran a sub-analysis on data spanning 2004 to 2020 (the timespan of digital GPS data), which included all the variables above, and additionally included home range size in m^2 and home range size squared. All continuous variables were centered and standardized.

For all analyses, we report the "complete" model, which included all variables, and the "best" model, which was the model with the lowest AIC (Akaike information criterion); if multiple models were within 2 AIC units of the best model, we reported the model with the fewest degrees of freedom. Best models were identified using the dredge function from the package *MuMIn* (Barton, 2020). Following best statistical practices, we only considered variables retained in the best model to be important predictors of the outcome, and we only report *p*-values for complete models (Harrell, 2016).

To test whether a group's proximity to a well predicted the incidence of human encounters, we used a different model structure (Table S2). The units of analysis were 111,376 GPS observations collected at 30-min intervals on each visit to every study group, with a binomial response variable indicating whether each GPS point was taken within 15 min of the time a human encounter was recorded. The fixed effects include the distance in meters between the GPS point in question and the nearest active well, season, rainfall and average of daily maximum temperature in the month before the GPS point was taken (in mm and °C, respectively), and hydrological year. Social group identity was modeled as a random effect. Our model selection process was the same as that described above.

2.6.2. Objective 2: modeling baboon home range shifts in response to well creation and loss

To test whether baboon groups shift their ranges to encompass newly active wells, or away from wells that no longer had water, we identified 9 instances when 6 wells transitioned from "active" to "inactive" or vice versa between 2004 and 2020. For each transition, we identified baboon groups we expected to be affected by the well's transition and used linear mixed models to test whether the ranges of these groups moved towards a well when it became active, or away from a well when it became inactive. These data spanned 7 baboon groups and 9 well transitions over 67 total group-years (13 distinct group-well pairs). To be included in the analysis, a group-well pair needed to meet the following criteria: (i) the group must have been studied by the ABRP for 1 to 3 years before and after the well transitioned; (ii) the group must have included the well in its home range in the year before the well became inactive (confirming the group was using the well before it became inactive); (iii) the group's 95 % kernel density home range must not have included the well in the year before the well became active (confirming the group was not already using the land around the well); and (iv) the edge of the group's 95 % kernel density home range must have been <2 km from the well in the year before the well became active (because annual range edge shifts of >2 km are unusual in our population).

The response variable in our linear mixed model was the shortest straight-line distance between the edge of the focal group's 95 % kernel density home range and the focal well, calculated for each of the 67 group-years. A positive distance indicated that the well was outside the group's home range; a negative distance indicated that the well was inside the group's range. Distances were calculated using the *raster* package and the spDistsN1 function in the *sp* package in R (Bivand et al., 2013; Hijmans, 2019; Pebesma and Bivand, 2005). The model structure and all fixed effects are in Table S3.

2.6.3. Objective 3: modeling baboon reproductive and health consequences of human encounters

To understand the consequences of human-baboon encounters for baboon survival, reproduction, and health, we calculated the percentage of observed human encounters ($n = 4660$ encounters) that resulted in the baboons fleeing from people, and we plotted the percentage of baboon deaths over time attributable to humans or their dogs and other causes for three baboon age classes: infants <70 weeks, juveniles between 70 weeks and 5 years of age, and individuals >5 years old ($n = 646$ total deaths; 283 infant deaths; 149 juvenile deaths; 214 deaths in animals >5 years).

To identify reproductive and health-related outcomes linked to human-baboon encounters, we built separate mixed models for each of the five outcome variables: (1) the survival of individual infants (coded as a binary variable; $n = 872$ infants born between 1993 and 2020); (2) log-transformed interbirth interval (IBI) durations in days ($n = 590$ IBIs from 181 females); (3) log-transformed whipworm egg counts ($n = 908$ fecal samples from 147 females; 423 samples from 51 males); (4) helminth parasite richness (n = 908 samples from 147 females; 423 samples from 51 males); and (5) log-transformed fGC concentrations ($n = 14{,}404$ fecal samples from 236 females; 8442 samples from 221 males). For measures of parasitism and fGCs, we modeled each sex separately based on prior research (Akinyi et al., 2019; Habig et al., 2019; Levy et al., 2020), leading to eight total models. The structure of each model, including all fixed and random effects are in Tables S4-S7. For each of these models, we checked for multicollinearity using variance inflation factors (VIF; no combination of variables was found to have VIF >4). As above, we report both the "complete" and "best" models, which were identified using the dredge function from the package *MuMIn* (Barton, 2020). The best model had the lowest AIC; if multiple models were within 2 AIC units of the best model, we chose the model with the fewest degrees of freedom.

3. Results

3.1. General patterns of human-baboon encounters

Between 1993 and 2020, we observed 4660 encounters between humans and ABRP study groups. Study groups encountered humans on 19.4 % of group-days (3299 of 17,024 group-days across the study). Annual human encounter rates fluctuated over time, with especially high rates (>40 % of group-days) in several seasons and years (Fig. 2A). The most common type of encounter involved humans and their livestock (48.2 % of encounters; blue area and points on Fig. 2A and D), followed by humans unaccompanied by animals (37.6 %; purple area and points on Fig. 2A and C), humans accompanied by dogs or dogs and livestock (9.9 %; teal area and points on Fig. 2A and E), and interactions in which humans chased the baboons from garbage at tour camps or human settlements (0.5 %; black area and points on Fig. 2A and F; for the remaining 3.8 % of encounters, the type was not specified).

Human-baboon encounters were distributed widely across the baboons' habitat (red points; Fig. 2B). There were few obvious spatial

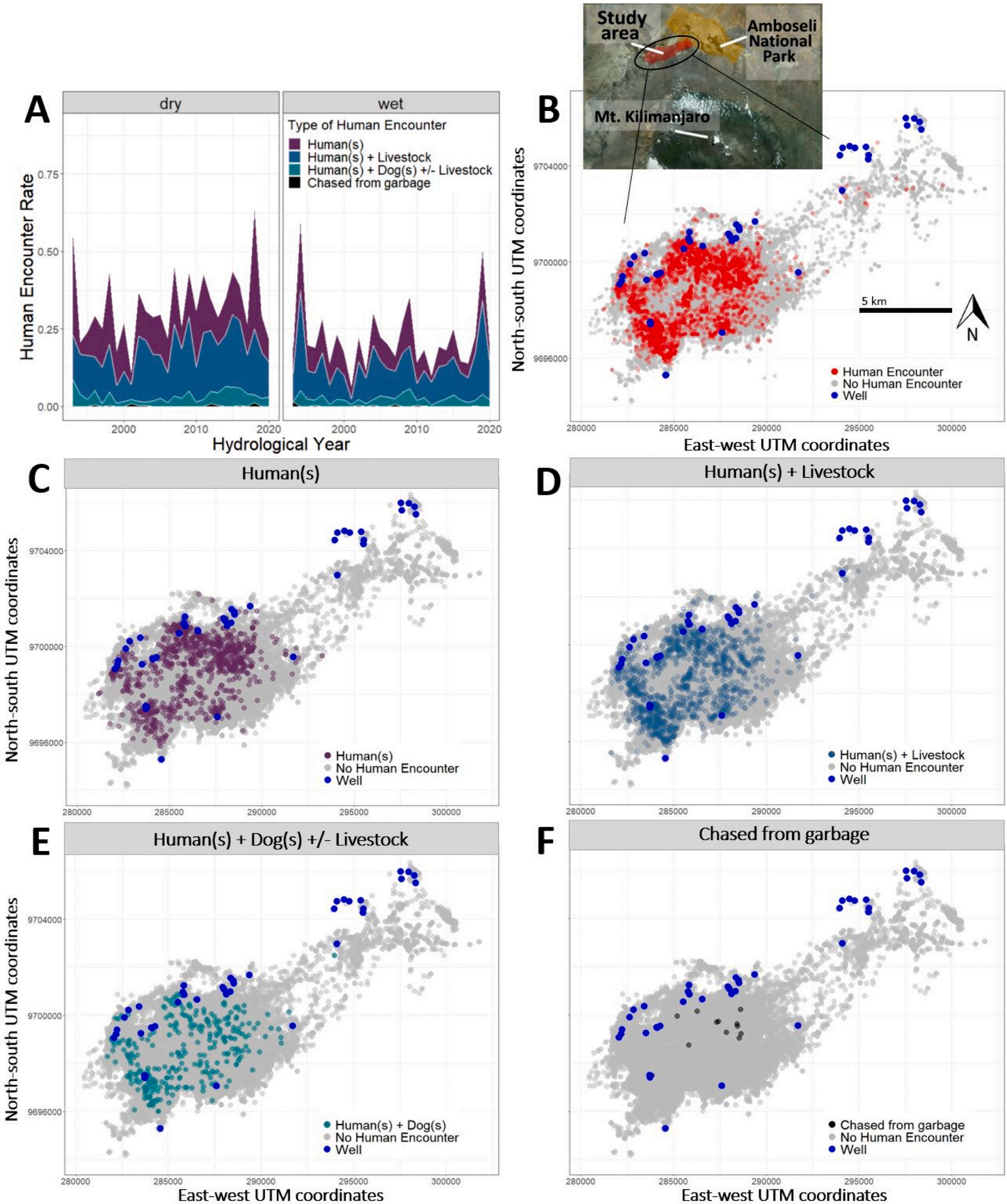

Fig. 2. Human-baboon encounters through space and time. Panel (A) shows the daily rate of human-baboon encounters across all groups in the dry (left) and wet seasons (right) in each year. Panel (B) shows 111,376 GPS point locations (as universal transverse mercator (UTM) coordinates) collected on ABRP study groups between 2004 and 2020. Red points show the locations of 3,148 human-baboon encounters; grey points show GPS observations with no human-baboon encounter. Blue points represent the location of human-constructed wells. The inset aerial photo shows the location of the study area. Panels C-F show the same GPS points as in panel B, partitioned into encounters with (C) humans only (purple points), (D) humans and livestock (blue points), (E) humans and dogs +/− livestock (teal points), and (F) involving human garbage (black points). As in panel B, the larger, bright blue points in panels C-F represent the location of human-constructed wells.

patterns to the different types of encounters as baboons could encounter humans, and their dogs and livestock, across all parts of the study area (Fig. 2C-E). Interactions involving garbage were sparse and located close to sites of known temporary tourist camps (Fig. 2F).

3.2. Objective 1: baboons encounter humans most often during dry periods and when close to wells.

As expected, human-baboon encounters were most frequent during dry periods (Fig. 3A; Table S8; effect of rainfall: b = −0.043). Indeed, when rainfall in a given season decreased from the 75th percentile (331 mm) to the 25th percentile (9 mm), human encounter frequency rose by 7.7 % (Table S8; Fig. 3A). Season did not explain significant variation in human encounter frequencies controlling for rainfall, indicating that rainfall was a stronger predictor of human-baboon encounters than season per se (Table S8).

Human-baboon encounter rates have changed little over time. While hydrological year was significant in the "complete" model that included all factors, the best-supported model only included the total rainfall across the season (Table S8), and the inclusion of hydrological year, or a year by season interaction did not improve model fit (AIC for the "best" model: −508.76, compared to the same model including hydrological year = −504.44; or the same model including a hydrological year by season interaction = −488.46). We also found no evidence that maximum temperature, group size, or home range size influenced the frequency that the baboons encountered humans (Tables S8, S9).

In support of the idea that baboons may compete with people and livestock for water, proximity to a well predicted the likelihood of a human encounter (Table S10; b = −0.273). Controlling for hydrological year and climatic variables, when groups were closer to wells, they were more likely to encounter people (Table S10; Fig. 3B). Indeed, baboons were nearly twice as likely to encounter people when they were within 250 m of a water source, compared to when they were >1 km from water.

3.3. Objective 2: baboon groups shift their home ranges to include human-constructed wells

Because water is limiting in Amboseli, we expected baboon groups to shift their ranges to encompass newly active wells. To test this idea, we identified 9 instances when 6 wells transitioned from "inactive" to "active" or vice versa between 2004 and 2020 (red triangles in Fig. 4A). We used these transitions to test whether 7 baboon groups changed their ranging patterns in the years before and after these wells transitioned (13 group-well pairs; 67 group-years). In support, we found that, controlling for home range size and nearby active wells, the edges of groups' home ranges shifted by nearly 0.5 km (435.18 m) to be closer to and usually encompass wells in group-years when the well was active, compared to group-years when the well was inactive (b = 435.18; $p <$ 0.001; Table 1; Fig. 4B). Fig. 4C shows one example shift for one study group in 2007. In group-years when wells were active, they were almost always located within the focal group's 95 % kernel density home range, reflected in the negative distances between the edge of group ranges and the focal well (Fig. 4B).

3.4. Objective 3: baboons are killed by humans and their dogs, and baboons experience some reproductive and health-related costs of human encounters

Encounters with humans have some negative consequences for baboons. In support, the baboons were observed fleeing from humans in 93.0 % of observed encounters. Moreover, we estimate that, since 2006, the percentage of deaths of baboons >5 years old that we attributed to violent encounters with humans has varied from 6.3 % to 35.7 % (Fig. 5C; red bars). For infants and juveniles, human-caused deaths have also been common since 2006, varying from 0 % to 17.4 % (Fig. 5A and B; measured over three-year intervals, red bars). These percentages likely underestimate the true percentage; some of the deaths whose causes are unknown (Fig. 5; grey bars) may have been caused by humans, and infants who died due to the interruption of maternal care (Fig. 5A; light blue bars) may have lost their mother during a human interaction.

We also found other costs of human encounters for baboons. For instance, we observed a trend that infants living in groups that experienced elevated human encounter rates in the 180 days before their birth (i.e., pre-natal human encounters) were slightly more likely to die in the first 70 weeks of life (b = 0.191; Table S11, upper). However, the rate of human encounters in the 180 days before the infant died or survived to 70 weeks did not predict infant survival (human encounter frequency did not appear in the best model; Table S11, lower). For females only, the frequency of human encounters was included in the best model for the number of helminth species they were infected with (b = 0.105;

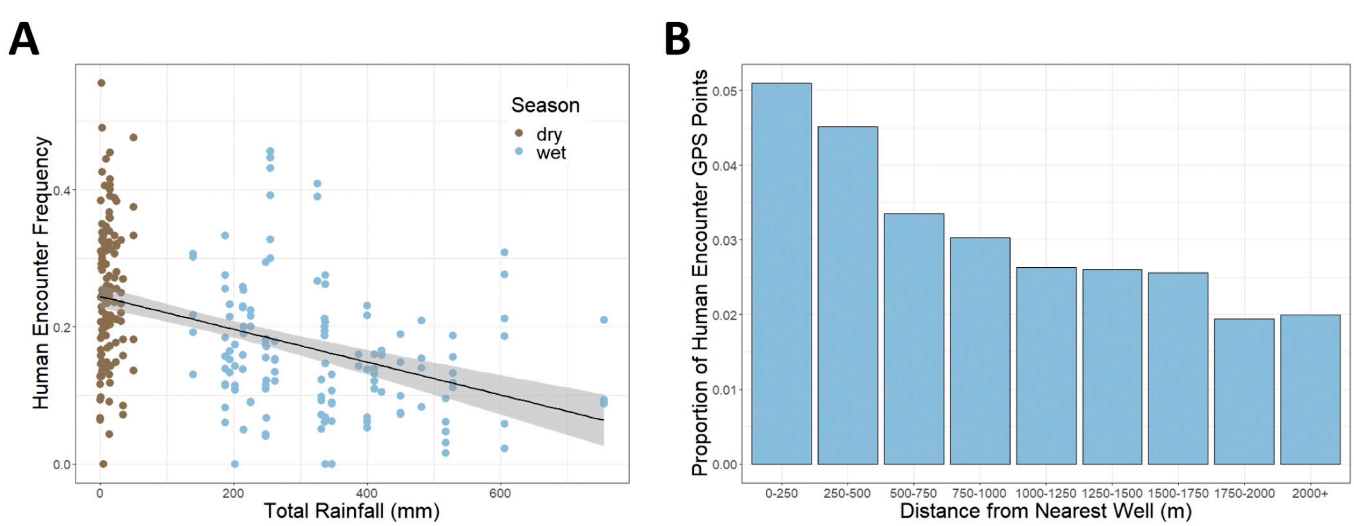

Fig. 3. Human encounters are most common during low rainfall periods and when the baboons are close to wells. Each point on panel (A) represents a human encounter frequency for a given baboon study group and season. Brown points are observations in the dry season (June to October); blue points are observations in the wet season (November to May). Panel (B) shows the relationship between the proportion of GPS points that are associated in time with a human encounter and the GPS point's distance in 250 m intervals from the nearest well. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

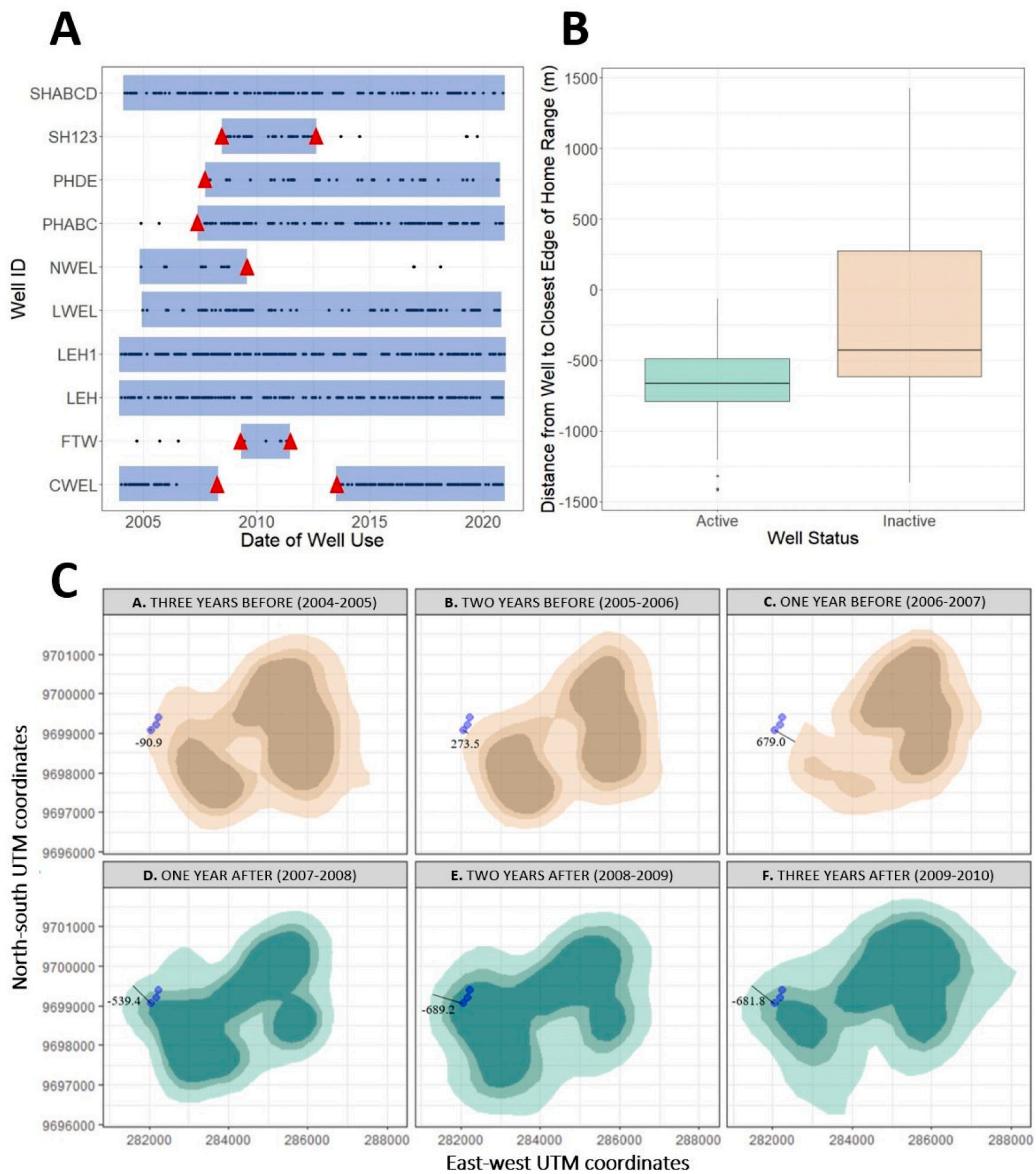

Fig. 4. Baboon social groups shift their home ranges to encompass "active" wells (see Methods for definition). Panel (A) shows changes in well activity from 2004 to 2020. The y-axis shows all wells that were active during the study period. Each dark point represents an observation of any baboon group drinking from the well. Active periods are shaded in blue, and transitions from active to inactive (or vice versa) are marked by red triangles. The wells included in our analyses had lifespans from 2 years to >17 years. Panel (B) shows the shortest straight-line distance between the edge of social group ranges and wells (y-axis) as a function of whether the well was active or inactive in a given year (x-axis; positive distances on the y-axis indicate wells outside the edge of the group's range; negative distances indicate wells within the group's range). The edges of group ranges typically encompassed wells in years when they were active (b = 435.181, $p = 1.11 \times 10^{-5}$). Panel (C) shows an example for one study group (Nyayo's group), which shifted their home range to include wells PHABC (Fig. S2), shown as blue points, which became active in 2007. This plot shows the 95 %, 80 %, and 65 % kernel density home ranges of Nyayo's group in the three years before (top row; brown ranges) and three years after (bottom row, green ranges) PHABC became active, plotted as a function of UTM coordinates on the x- and y- axes. Numbers near the wells are the shortest straight-line distance (in m) from the well PHABC to the edge of the 95 % kernel density home range. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table S12, upper). However, this effect size was small; when human encounter frequency increased from the 25th percentile to the 75th percentile, helminth richness increased by 0.14 parasite species. Furthermore, it was difficult to disentangle these effects from seasonal covariates (for the model of female helminth richness, the effect of human encounters was smaller and insignificant in the complete model that controlled for season; Table S12, upper; Akinyi et al., 2019; Habig et al., 2019). Human encounter frequency did not predict helminth richness in males, nor did it predict whipworm egg counts in either males or females (Tables S12, lower and S13). We found no relationship between human-baboon encounters and the duration of female inter-birth intervals or fecal glucocorticoid (fGC) levels in either females or males (Tables S14 and S15). Note that human encounter frequency was a significant predictor of male fGCs in the complete model, but this variable was not retained in the best-fitting model (see Methods: Statistical analyses).

Table 1
Predictors of the shortest straight-line distance between the edge of a given social group's range (as 95 % kernel densities) and wells before and after the well transitioned from inactive to active or vice versa. The "complete" model was also the best-supported model based on AIC Bold P values are <0.05.

Complete model ($n = 70$ group years)

Random effects	Variance	SD	N
Group identity	145,888	382.0	7
Well identity	357,068	597.6	6

Fixed effects	Estimate	SE	P	Interpretation
Well state (inactive)	435.181	94.009	**<0.001**	Inactive wells, ↑ Likelihood the well is outside the edge of the group's home range
Active neighboring well distance	106.637	179.293	0.563	
Home range area	−286.680	76.167	**<0.001**	↓ Range area, ↑ Likelihood the well is outside the edge of the group's home range

4. Discussion

Using 27 years of data on human-baboon encounters, we found that conservancies in Kenya present both favorable and unfavorable conditions for baboons. On the one hand, baboon ranging is enabled by water provided year-round by people for their livestock. On the other hand, low rainfall periods are linked to high rates of human-baboon interactions, and human-provided water serves as a hotspot for baboons to encounter people. These encounters can present considerable mortality risks to baboons: people or their dogs are implicated in a third of recent adult baboon deaths, and high rates of human encounters during the prenatal (but not the postnatal) period were weakly linked to higher infant mortality. Human encounters are not linked to female fertility or glucocorticoid hormone levels. Overall, our results highlight the complexity of human-nonhuman primate relationships in protected conservancies: conservancies offer resources and protections to wildlife, but increasing pressures on dryland ecosystems may also increase human violence towards animals they view as threats to their livelihoods.

4.1. Water sources shape human-baboon encounters and baboon ranging patterns

Most research on human-baboon interactions centers on conflict over human crops and garbage, but water limitation is a distinctive driver of human-baboon encounters in arid ecosystems. In Amboseli, during dry periods, people migrate into the baboons' range to take advantage of existing wells, or dig new wells, to provide water for their livestock. Wildlife, including baboons, rely on these water sources, making drought and proximity to water the dominant predictors of human encounters. Indeed, group proximity to wells was the only significant group-level predictor of human-baboon encounters, with no impact of group size or group home range size. One explanation for these patterns is the non-random spatial distribution of humans and baboons throughout the Amboseli ecosystem. Both the baboons and Maasai livestock need to drink water every day to survive, meaning they structure their movements around guaranteed daily access to water. Thus, avoiding humans and getting enough water during the dry season is likely not an option for the baboons.

Previous research has shown that wildlife sometimes benefit from human-provided resources, including food, habitats, and predator release, and may change their ranging patterns accordingly (Selier et al., 2015; Thatcher et al., 2019). However, evidence that water sources for livestock, managed by pastoralists, can also affect wildlife ranging behavior is limited. While prior studies have found that wildlife populations shift their ranges based on seasonal water availability—for instance, that human-constructed wells or waterholes can serve as vital water sources for wildlife populations such as elephants and red-fronted lemurs (Amoroso et al., 2020; Purdon and van Aarde, 2017)—all of these studies focused on artificial or experimental waterholes built purely for the support of wildlife populations. Our findings support the idea that human wells are important resources for wildlife populations in semi-arid and arid ecosystems. The finding that baboon social groups shift their ranging patterns to encompass wells emphasizes the control that humans have on water availability for wildlife in Amboseli. Human-constructed wells have obvious benefits for both the humans and baboons, yet wells are also sites of frequent human-baboon encounters.

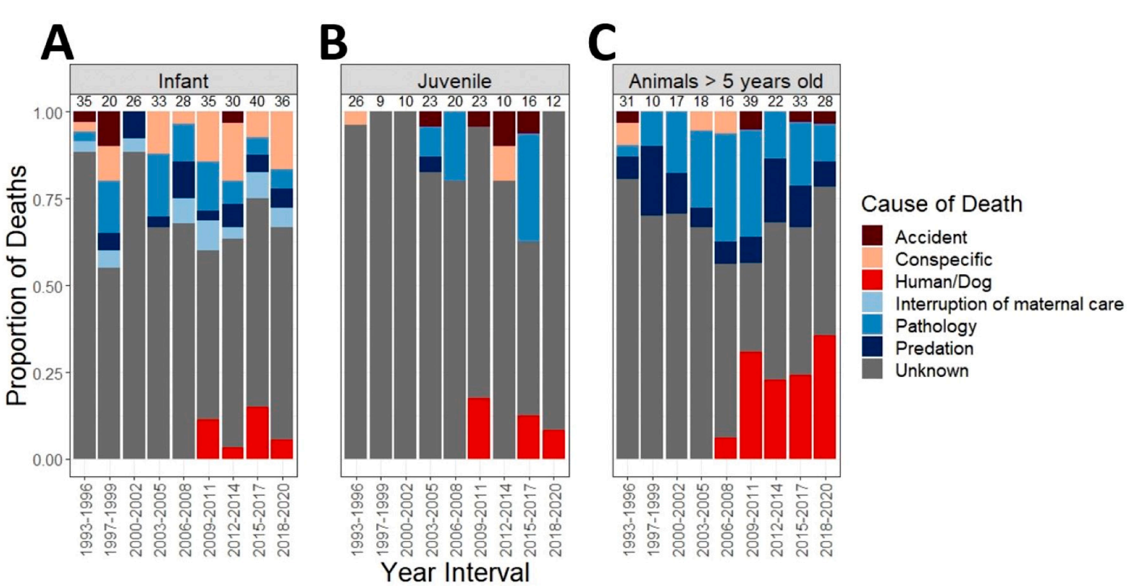

Fig. 5. Baboons are frequently killed by humans and/or their dogs. Bar plots show the percentage of baboon deaths observed between 1993 and 2020 (in 3-year intervals) that are attributable to the six main causes of death or have unknown causes. Each panel shows these patterns for a baboon age class: (A) infants <70 weeks of age, (B) juveniles between 70 weeks and 5 years of age, and (C) animals older than 5 years of age. The numbers at the top of each bar are the total number of animals who died of any cause in each 3-year interval.

4.2. Human population growth, human encounters, and consequences for baboons

The benefits of human-provided water and the protection offered by conservancies raise the question of whether human-baboon co-existence in conservancies is overall positive or negative for baboons. In many ecosystems, human population growth leads to increased interactions between humans and wildlife (Estrada et al., 2017; Schell et al., 2021). Human populations are also increasing around Amboseli National Park, although precise estimates of growth are hard to find (Kimiti et al., 2016). The consequences of this growth for baboons are complex; while we found no systematic rise in the overall rate of human-baboon encounters between 1993 and 2020, there has been a marked recent increase in baboon deaths attributable to humans, especially since 2009. Notably, during the 2008/2009 hydrological year, Amboseli experienced the worst known drought in at least 50 years (Carabine et al., 2014; Lee et al., 2021; Okello et al., 2016). Tensions during the drought led to human-wildlife conflict, including one instance where at least twelve baboons were killed by people in one day. Since this drought, human- or dog-related interactions have become common causes of deaths for baboons.

One reason for this rise in violent human-baboon encounters may be that retaliatory killings are an increasingly acceptable way for people to cope with the frustration and unpredictability of living in an arid habitat with high environmental stress. In semi-arid savannahs like Amboseli, grazing likely has a ceiling beyond which the grasslands are rendered unusable for livestock (Western et al., 2009). In Amboseli conservancies, considerable pressure on the ecosystem is bringing us closer to this ceiling. To help mitigate these pressures, the conservancies have policies and laws to discourage negative encounters between wildlife and people (Kiiru, 2012). The ABRP also employs a team of game scouts who live in nearby Maasai settlements and work to inform their community about baboons and ABRP research, and to help mitigate conflicts. As a result, human-caused deaths may be less common in Amboseli than they are in towns, agricultural areas, and other conservancies where there are fewer protections and concessions to wildlife.

The protections and mitigation efforts described above may be one reason why we found few other negative effects of human encounters on baboon reproduction, disease risk, or stress responses (aside from human-caused deaths). Indeed, the effects of human encounters on infant mortality were weak and restricted to prenatal exposure, and the effects on parasitism were restricted to females and difficult to disentangle from seasonal covariates. Further, we found no significant relationships between human encounters and baboon interbirth intervals, fGCs, or helminth burdens.

The lack of a relationship between human encounters and fGCs is interesting, given that the baboons fled from people in 93.0 % of observed encounters—a reaction that might be expected to provoke energetic or psychosocial stress responses and hence elevated fGCs. In support, previous studies have found that several animal species exposed to human activity (including chacma baboons) have elevated fGCs (Bhattacharjee et al., 2015; Chowdhury et al., 2020; Creel et al., 2002). However, human-baboon encounters occurred on average only once every 5 days for any given baboon group in Amboseli (see Results), and they typically lasted a relatively short time (often <15 min). Fecal GC concentrations reflect integrated measures of circulating glucocorticoids over a 12–24 h period, and one possibility is that the energetic and psychosocial costs of being chased may be too short-lived to be strongly reflected in fGCs (Christensen et al., 2022; Gesquiere et al., 2008; Khan et al., 2002; Lynch et al., 2003). Another possibility is that the effects of human encounters—which have a strong seasonal and rainfall component (Fig. 3; Table S9)—are partially reflected in the effects of season and rainfall in our models of predictors of fGCs, particularly for female baboons (Table S15, upper). The benefits of reliable access to water may also mitigate energetic stress, leading to few measurable effects on fGCs (Pokharel et al., 2019). Therefore, while encountering humans may lead to a seemingly negative behavioral response, this response may be predictable and outweighed by the stress of finding resources in the dry season and the necessity of using human-constructed wells to survive. At the same time, the lack of a relationship between human encounters and fGCs supports the idea that effects of human encounters on infant mortality are not directly caused by the energetic or psychosocial stress of human encounters. Instead, human encounters that occur during an individual's pre-natal period may affect pregnant females' foraging efficiency, with negative consequences for fetal development and infant survival (Foroughirad and Mann, 2013).

5. Conclusions

Our results serve as an unusually holistic case study examining the patterns, drivers, and consequences of encounters between pastoralists and baboons in a protected area. The findings of this study have global importance as wild animals across the planet traverse human-altered landscapes and compete with humans for resources, even in protected areas. Human-baboon encounters in Amboseli represent a balance between benefits to baboons (i.e., access to water) and liabilities (encounters with people and their domestic animals). High encounter rates between humans and baboons arise from water stress, and while the encounters can be fatal to baboons, the other reproductive and health consequences are small. While the recent rise in human-caused deaths is concerning, compared to unprotected lands, humans and baboons in Amboseli may have achieved a relatively stable relationship, serving as a case study for how pastoralists influence wildlife, and for how other ecologically flexible wild animals—like baboons—may thrive near humans in protected habitats. Understanding the movement and population centers of local people along with tourists and other sources of human activity is vital for understanding how and when wildlife populations are being most heavily impacted, especially at a time of heightened anthropogenic change for wild animals. A valuable direction for future research would be to evaluate the consequences of human encounters for wildlife in less protected areas, urbanized areas that are becoming large human population centers, or areas where the people have a more sedentary livelihood system in comparison to pastoralism.

Credit authorship contribution statement

ENP, CJW, VO, SCA, and EAA conceived the ideas and designed the study; DAJ, RSM, JKW, ILS, LRG, SCA, and EAA collected the data; ENP, CJW, and EAA analyzed the data; ENP, CJW, and EAA led the writing of the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

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

Data availability

All data reported in this paper have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.m63xsj45h). Additionally, code for data analysis and figures are available on GitHub (https://github.com/earchie/human-baboon_encounters).

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Statement on inclusion

Our study brings together authors from both the United States and Kenya, including the Amboseli field team and Kenya Wildlife Services. This study includes four authors based in the country where the study was carried out. We communicated with these authors from the onset of the study to ensure that the study included multiple perspectives and a thorough understanding of the pastoralist communities in the region.

Appendix A. Supplementary information

Supplementary information for this article can be found online at https://doi.org/10.1016/j.biocon.2022.109740.

References

Akinyi, M.Y., Jansen, D., Habig, B., Gesquiere, L.R., Alberts, S.C., Archie, E.A., 2019. Costs and drivers of helminth parasite infection in wild female baboons. J. Anim. Ecol. https://doi.org/10.1111/1365-2656.12994.

Alberts, S.C., Altmann, J., 2012. The Amboseli baboon research project: 40 years of continuity and change. In: Kappeler, P., Watts, D.P. (Eds.), Long-term Field Studies of Primates. Springer, pp. 261–287. https://doi.org/10.1007/978-3-642-22514-7_12.

Alberts, S.C., Hollister-Smith, J.A., Mututua, R.S., Sayialel, S.N., Warutere, J.K., Altmann, J., 2005. Seasonality and long term change in a savannah environment. In: Brockman, D.K., Van Schaik, C.P. (Eds.), Primate Seasonality: Implications for Human Evolution. Cambridge University Press.

Altmann, J., Alberts, S.C., 2003. Variability in reproductive success viewed from a life-history perspective in baboons. J. Hum. Biol 15, 401–409. https://doi.org/10.1002/ajhb.10157.

Altmann, J., Muruthi, P., 1988. Differences in daily life between semiprovisioned and wild-feeding baboons. Am. J. Primatol. 15 (3), 213–221. https://doi.org/10.1002/AJP.1350150304.

Amoroso, C.R., Kappeler, P.M., Fichtel, C., Nunn, C.L., 2020. Water availability impacts habitat use by red-fronted lemurs (Eulemur rufifrons): an experimental and observational study. Int. J. Primatol. https://doi.org/10.1007/s10764-020-00136-9.

Barton, K., 2020. MuMIn: Multi-model inference. R package version 1.43.17. https://cran.r-project.org/package=MuMIn.

Bates, D., Machler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48.

Bhattacharjee, S., Kumar, V., Chandrasekhar, M., Malviya, M., Ganswindt, A., Ramesh, K., Sankar, K., Umapathy, G., 2015. Glucocorticoid stress responses of reintroduced tigers in relation to anthropogenic disturbance in Sariska Tiger Reserve in India. PLoS ONE. https://doi.org/10.1371/journal.pone.0127626.

Bivand, R.S., Pebesma, E., Gomez-Rubio, V., 2013. Applied Spatial Data Analysis With R, Second edition http://www.asdar-book.org/.

Carabine, E.A., Wainwright, J., Twyman, C., 2014. In: Narratives of a Drought: Exploring Resilience in Kenya's Drylands. Advances in Intelligent Systems and Computing, 229. AISC, pp. 307–317. https://doi.org/10.1007/978-3-642-39829-2_27.

Chowdhury, S., Brown, J., Swedell, L., 2020. Anthropogenic effects on the physiology and behaviour of chacma baboons in the Cape Peninsula of South Africa. Conservation Physiology. https://doi.org/10.1093/conphys/coaa066.

Christensen, C., Bracken, A.M., O'Riain, J.M., Heistermann, M., King, A.J., Furtbauer, I., 2022. Simultaneous investigation of urinary and faecal glucocorticoid metabolite concentrations reveals short-versus long-term drivers of HPA-axis activity in a wild primate (Papio ursinus). Gen. Comp. Endocrinol. 318, 113985 https://doi.org/10.1016/j.ygcen.2022.113985.

Creel, S., Fox, J.E., Hardy, A., Sands, J., Garrott, B., Peterson, R.O., 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conserv. Biol. https://doi.org/10.1046/j.1523-1739.2002.00554.x.

Defolie, C., Merkling, T., Fichtel, C., 2019. Patterns and variation in the mammal parasite-glucocorticoid relationship. Biol. Rev. Camb. Philos. Soc. https://doi.org/10.1111/brv.12555.

van Doorn, A.C., O'Riain, M.J., 2020. Nonlethal management of baboons on the urban edge of a large metropole. Am. J. Primatol. https://doi.org/10.1002/ajp.23164.

Estrada, A., Garber, P.A., Rylands, A.B., Roos, C., Fernandez-Duque, E., Fiore, A.Di, Anne-Isola Nekaris, K., Nijman, V., Heymann, E.W., Lambert, J.E., Rovero, F., Barelli, C., Setchell, J.M., Gillespie, T.R., Mittermeier, R.A., Arregoitia, L.V., de Guinea, M., Gouveia, S., Dobrovolski, R., Li, B., 2017. Impending extinction crisis of the world's primates: why primates matter. Science Advances. https://doi.org/10.1126/sciadv.1600946.

Foroughirad, V., Mann, J., 2013. Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins. Biol. Conserv. 160, 242–249. https://doi.org/10.1016/j.biocon.2013.01.001.

Gesquiere, L.R., Khan, M., Shek, L., Wango, T.L., Wango, E.O., Alberts, S.C., Altmann, J., 2008. Coping with a challenging environment: effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons (Papio cynocephalus). Horm. Behav. 54, 410–416. https://doi.org/10.1016/j.yhbeh.2008.04.007.

Githumbi, E.N., Kariuki, R., Shoemaker, A., Courtney-Mustaphi, C.J., Chuhilla, M., Richer, S., Lane, P., Marchant, R., 2018. Pollen, people and place: multidisciplinary perspectives on ecosystem change at Amboseli, Kenya. Front. Earth Sci. https://doi.org/10.3389/feart.2017.00113.

Habig, B., Jansen, D.A.W.A.M., Akinyi, M.Y., Gesquiere, L.R., Alberts, S.C., Archie, E.A., 2019. Multi-scale predictors of parasite risk in wild male savanna baboons (Papio cynocephalus). Behav. Ecol. Sociobiol. https://doi.org/10.1007/s00265-019-2748-y.

Harrell, F.E., 2016. Regression Modeling Strategies. Springer International Publishing.

Hijmans, R.J., 2019. Geographic data analysis and modeling. R package version 3.0-7. https://cran.r-project.org/package=raster.

Hoffman, T.S., O'Riain, M.J., 2011a. The spatial ecology of chacma baboons (Papio ursinus) in a human-modified environment. Int. J. Primatol. 32 (2), 308–328. https://doi.org/10.1007/S10764-010-9467-6/FIGURES/5.

Hoffman, T.S., O'Riain, M.J., 2011b. The spatial ecology of chacma baboons (Papio ursinus) in a human-modified environment. Int. J. Primatol. 32 (2), 308–328. https://doi.org/10.1007/s10764-010-9467-6.

Hoffman, T.S., O'Riain, M.J., 2012. Landscape requirements of a primate population in a human-dominated environment. Front. Zool. https://doi.org/10.1186/1742-9994-9-1.

Khan, M.Z., Altmann, J., Isani, S.S., Yu, J., 2002. A matter of time: evaluating storage of fecal samples for steroid analysis. Gen. Comp. Endocrinol. 128, 57–64. https://doi.org/10.1016/S0016-6480(02)00063-1.

Kiiru, W., 2012. Understanding the Spatial, Temporal and Socio-economic Factors Affecting Human-elephant Conflict Around Amboseli National Park in Kenya.

Kimiti, K.S., Wasonga, O.V., Western, D., Mbau, J.S., 2016. Community perceptions on spatio-temporal land use changes in the Amboseli ecosystem, southern Kenya. Pastoralism. https://doi.org/10.1186/s13570-016-0070-0.

Kimiti, K.S., Western, D., Mbau, J.S., Wasonga, O.V., 2018. Impacts of long-term land-use changes on herd size and mobility among pastoral households in Amboseli ecosystem, Kenya. Ecological Processes. https://doi.org/10.1186/s13717-018-0115-y.

Kioko, J., Okello, M.M., 2010. Land use cover and environmental changes in a semi- arid rangeland, southern Kenya. J. Geogr. Region. Plann. 3, 322–326.

Lee, P.C., Moss, C.J., Njiraini, N., Poole, J.H., Sayialel, K., Fishlock, V.L., 2021. Cohort consequences of drought and family disruption for male and female african elephants. Behav. Ecol. https://doi.org/10.1093/BEHECO/ARAB148.

Levy, E.J., Gesquiere, L.R., McLean, E., Franz, M., Warutere, J.K., Sayialel, S.N., Mututua, R.S., Wango, T.L., Oudu, V.K., Altmann, J., Archie, E.A., Alberts, S.C., 2020. Higher dominance rank is associated with lower glucocorticoids in wild female baboons: a rank metric comparison. Horm. Behav. https://doi.org/10.1016/j.yhbeh.2020.104826.

Lynch, J.W., Khan, M.Z., Altmann, J., Njahira, M.N., Rubenstein, N., 2003. Concentrations of four fecal steroids in wild baboons: short-term storage conditions and consequences for data interpretation. Gen. Comp. Endocrinol. 132, 264–271. https://doi.org/10.1016/S0016-6480(03)00093-5.

Machado, E.R., Carlos, D., Sorgi, C.A., Ramos, S.G., Souza, D.I., Soares, E.G., Costa-Cruz, J.M., Ueta, M.T., Aronoff, D.M., Faccioli, L.H., 2011. Dexamethasone effects in the Strongyloides venezuelensis infection in a murine model. Am. J. Trop. Med. Hyg. 84 (6), 957–966. https://doi.org/10.4269/ajtmh.2011.10-0490.

Markham, A.C., Gesquiere, L.R., Alberts, S.C., Altmann, J., 2015. Optimal group size in a highly social mammal, 112. https://doi.org/10.1073/pnas.1517794112, 48.

Mbora, D.N.M., Wieczkowski, J., Munene, E., 2009. Links between habitat degradation, and social group size, ranging, fecundity, and parasite prevalence in the Tana River mangabey (Cercocebus galeritus). Am. J. Phys. Anthropol. https://doi.org/10.1002/ajpa.21113.

Meijaard, E., Buchori, D., Hadiprakarsa, Y., Utami-Atmoko, S.S., Nurcahyo, A., Tjiu, A., Prasetyo, D., Nardiyono, Christie, L., Ancrenaz, M., Abadi, F., Antoni, I.N.G., Armayadi, D., Dinato, A.E., Gumelar, P., Indrawan, T.P., Kussaritano, Munajat, C., Mengersen, K., 2011. Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia. PLoS ONE. https://doi.org/10.1371/journal.pone.0027491.

Monello, R.J., Millspaugh, J.J., Woods, R.J., Gomper, M.E., 2010. The influence of parasites on faecal glucocorticoid metabolite levels in raccoons: an experimental assessment in a natural setting. J. Zool. 282 (2), 100–108. https://doi.org/10.1111/j.1469-7998.2010.00717.x.

Muntifering, J.R., Ditmer, M.A., Stapleton, S., Naidoo, R., Harris, T.H., 2019. Hartmann's mountain zebra resource selection and movement behavior within a large unprotected landscape in Northwest Namibia. Endanger. Species Res. 38, 159–170. https://doi.org/10.3354/ESR00941.

Okello, M.M., Kioko, J.M., 2010. Contraction of wildlife dispersal area in Olgulului - Ololorashi group ranch around Amboseli National Park, Kenya. Open Conserv. Biol. J. https://doi.org/10.2174/1874839201004010034.

Okello, M.M., Kenana, L., Maliti, H., Kiringe, J.W., Kanga, E., Bakari, S., Ndambuki, S., Massawe, E., Sitati, N., Kimutai, D., Mwita, M., Gichohi, N., Muteti, D., Ngoru, B., Mwangi, P., 2016. Population Density of Elephants and Other Key Large Herbivores in the Amboseli Ecosystem of Kenya in Relation to Droughts. https://doi.org/10.1016/j.jaridenv.2016.08.012.

Pebesma, E.J., Bivand, R.S., 2005. Classes and methods for spatial data in R. R News 5 (2).

Pokharel, S.S., Singh, B., Seshagiri, P.B., Sukumar, R., 2019. Lower levels of glucocorticoids in crop-raiders: diet quality as a potential 'pacifier' against stress in free-ranging Asian elephants in a human-production habitat. Anim. Conserv. https://doi.org/10.1111/acv.12450.

Purdon, A., van Aarde, R.J., 2017. Water provisioning in kruger National Park alters elephant spatial utilisation patterns. J. Arid Environ. https://doi.org/10.1016/j.jaridenv.2017.01.014.

Schell, C.J., Stanton, L.A., Young, J.K., Angeloni, L.M., Lambert, J.E., Breck, S.W., Murray, M.H., 2021. The evolutionary consequences of human–wildlife conflict in cities. Evol. Appl. https://doi.org/10.1111/eva.13131.

Selier, J., Slotow, R., Di Minin, E., 2015. Large mammal distribution in a transfrontier landscape: trade-offs between resource availability and human disturbance. Biotropica. https://doi.org/10.1111/btp.12217.

Sha, J.C.M., Hanya, G., 2013. Diet, activity, habitat use, and ranging of two neighboring groups of food-enhanced long-tailed macaques (Macaca fascicularis). Am. J. Primatol. https://doi.org/10.1002/ajp.22137.

Thatcher, H.R., Downs, C.T., Koyama, N.F., 2019. Positive and negative interactions with humans concurrently affect vervet monkey (Chlorocebus pygerythrus) ranging behavior. Int. J. Primatol. https://doi.org/10.1007/s10764-019-00099-6.

du Toit, J.T., Cross, P.C., Valeix, M., 2017. In: Managing the Livestock–Wildlife Interface on Rangelands. Springer, Cham, pp. 395–425. https://doi.org/10.1007/978-3-319-46709-2_12.

Walton, B.J., Findlay, L.J., Hill, R.A., 2021. Insights into short- and long-term crop-foraging strategies in a chacma baboon (Papio ursinus) from GPS and accelerometer data. Ecol. Evol. https://doi.org/10.1002/ece3.7114.

Warren, Y., Higham, J.P., Maclarnon, A.M., Ross, C., 2011. Crop-raiding and commensalism in olive baboons: the costs and benefits of living with humans. In: Primates of Gashaka. https://doi.org/10.1007/978-1-4419-7403-7_8.

Western, D., Manzolillo Nightingale, D.L., 2003. Environmental change and the vulnerability of pastoralists to drought: a case study of the Maasai in Amboseli, Kenya. http://hdl.handle.net/1834/436.

Western, D., Groom, R., Worden, J., 2009. The impact of subdivision and sedentarization of pastoral lands on wildlife in an African savanna ecosystem. Biol. Conserv. 142 (11), 2538–2546. https://doi.org/10.1016/J.BIOCON.2009.05.025.

Western, D., Mose, V.N., Worden, J., Maitumo, D., 2015. Predicting extreme droughts in Savannah Africa: a comparison of proxy and direct measures in detecting biomass fluctuations, trends and their causes. PLoS ONE 10 (8), e0136516. https://doi.org/10.1371/JOURNAL.PONE.0136516.