




RESEARCH ARTICLE

Interacting effects of surface water and temperature on wild and domestic large herbivore aggregations and contact rates

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Handling Editor: Marion Valeix**Abstract**

1. Earth's climate is rapidly changing, bringing forth questions of how domestic and wild animals will alter their behaviour in response to increasing temperatures and dryland expansion. Dwindling water availability will likely impact animal behaviour and water foraging, potentially increasing animal aggregations and interspecific contacts. These interspecific contacts are especially important for competition, predation and disease transmission among wildlife and domestic animals.
2. In this study, we analysed interspecific wildlife and cattle contacts using two years of camera trap data at an experimental water manipulation site at a conservancy in central Kenya.
3. We found that on average, the hourly probability of any interspecific contact was approximately 3.4 times higher at water sources versus drained water sources and 18 times higher than surrounding matrix areas, and that this relationship was amplified by dry and hot conditions.
4. Species-specific analyses revealed variation in the magnitude of responses across wildlife and domestic cattle, although all animals had approximately 2–3 times higher interspecific contact probability with other species at water in hot conditions versus other conditions. Notably, we observed the largest behavioural changes for relatively water-independent species, such as giraffe, which had 3.6 times higher interspecific contact probability at water sources in hot versus other conditions.
5. *Synthesis and applications.* These findings show how elevated temperatures that will become increasingly common with future climate changes can increase interspecific contacts around critical water resources. In mixed wildlife-livestock systems, maintaining wildlife-only water sources may be a practical management

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tool to mitigate human-wildlife conflict and disease transmission at this interface, especially during dry and hot conditions.

KEYWORDS

camera trap, climate change adaptation, ecological hotspot, interspecific disease transmission, temporal niche partitioning, waterhole, wildlife-livestock interface

1 | INTRODUCTION

Increasing temperatures, changing precipitation patterns and human adaptations to climate change are constantly reshaping the distribution of available surface water, resulting in net surface water losses globally (Donchyts et al., 2016). These recent changes are likely to intensify, and drylands are expected to cover more than 50% of Earth's land by the end of the century due largely to increasing aridity (Huang et al., 2016). In dryland systems, water sources form critical ecological hotspots where a broad range of animals forage for food and water (Ayeni, 1975; Western, 1975). In East African tropical savannas, a mammal biodiversity hotspot (Ceballos & Ehrlich, 2006), many large herbivores heavily depend on surface water (Kihwele et al., 2020). Indeed, in this region, irrigation, livestock and domestic drawdown of water by people have already reduced surface water availability (e.g. Mutiga et al., 2010), but the current and potential future effects of changing water supply on large herbivore water foraging behaviour and mixed species aggregations are unknown.

Increasing global temperatures will likely compound the effects of changing surface water for many herbivore species. Rising temperatures lead to increasing water evaporation, water scarcity and competition for water (Western, 1975). Rising temperatures also speed seasonal drying for plants, reducing water available to animals through food. Rising temperatures will also increase direct water losses, potentially causing animals to seek water more often and to congregate more heavily around water in drier areas and periods (Valeix, 2011). Surface water reductions may also affect migration timing or route, and may also prompt sedentary species to move. Prior research has demonstrated that the movements and migrations of several large herbivore species including elephants, zebra, and wildebeest depend on available surface water (Bennitt et al., 2022; Fryxell & Sinclair, 1988; Smit et al., 2007). Additional effects on herbivore behaviour include expanding home ranges as animals search for water over greater distances and shifting movements between herds (Owen-smith et al., 2020), mass mortality events that may have secondary disease transmission opportunities for scavengers (Ogada et al., 2012) and increased predation risk as fewer concentrated water points may attract higher carnivore densities (Bhola et al., 2012).

A particular threat of changing surface water and animal aggregations on wildlife and livestock health is disease transmission. Aggregations around water, especially during dry periods and in arid areas (Hayward & Hayward, 2012; Valeix et al., 2007), may

increase indirect pathogen transmission via contaminated water and forage (Titcomb, Mantas, et al., 2021; Zvidzai et al., 2013). While prior studies have quantified the potential for elevated indirect parasite transmission at water sources (e.g. Ndlovu et al., 2018; Titcomb, Mantas, et al., 2021), more data are needed on the risks of direct interspecific contacts at water, especially for wildlife-livestock interactions. This is especially important given that directly transmitted parasites may pose a greater extinction risk to wild mammals than other transmission routes (Pedersen et al., 2007). Climate change has direct impacts on pathogens, particularly vector-borne and environmentally transmitted pathogens whose survival may be limited by hot temperatures. However, for directly transmitted pathogens, climatic effects on host movement patterns may be especially important. Increasing temperatures may drive more frequent water use by many different animals, especially highly water dependent species (Valeix, 2011); however, the extent of increasing interspecific contacts is unknown. Given some evidence that wildlife and cattle can temporally partition water use (Ayeni, 1975; Valls-Fox et al., 2018), it is plausible that intensifying water use may be decoupled from contact rates such that interspecific direct contacts remain constant. However, we lack data enabling us to predict the degree to which temperature and rainfall affect interspecific contact rates.

The effects of changing temperatures and water dynamics on large herbivore movements have implications for wildlife and livestock health and human-wildlife conflict. Large wild and domestic herbivores must balance food and water needs while competing with other species (Odadi et al., 2007, 2009). For example, highly water dependent animals, such as elephants, may displace other species at water sources (Valeix et al., 2007), potentially creating distinct temporal water foraging niches across taxa. Likewise, cattle and other livestock frequently overlap with and are replacing wildlife in many savanna systems (Hempson et al., 2017; Ogotu et al., 2016), and they may displace or compete with wildlife for water during dry, hot periods. Indeed, cattle have been shown to displace wildlife around water sources (De Leeuw et al., 2001), although contact may be minimised by temporal niche partitioning (Valls-Fox et al., 2018). This competition can have serious implications for human-wildlife conflict; for example, in a large survey conducted in Tsavo, Kenya, respondents reported that wildlife water foraging was a major source of damage to farms and livestock (Makindi et al., 2014). Wildlife-livestock competition may be particularly relevant in ecosystems where artificial water sources support high cattle abundance and provide new water foraging

opportunities for wildlife. A better understanding of these interactions and conflicts could help develop management strategies that balance both livestock and wildlife needs in changing climates.

In this study, we used a two-year water manipulation experiment at a mixed cattle ranch and wildlife conservancy to examine how water influences animal aggregation and contact rates. We used camera traps positioned around five groups of filled water sources, experimentally drained water sources, and matrix (non-water) sites to quantify the extent to which water sources increased interspecific contacts. We then examined how daily temperature and monthly rainfall modified hourly probability of total and species-specific contact. We expected interspecific contacts to be elevated around filled water sources relative to drained water sources and matrix sites, and that hot and dry conditions would increase this effect. We also expected the most water dependent animals to show the strongest aggregation and contact patterns in response to increased temperature and decreased rainfall.

2 | MATERIALS AND METHODS

2.1 | Study system

Fieldwork was conducted at Ol Pejeta Conservancy (0.0043°S, 36.9637°E), a 360 km² mixed wildlife conservation area and cattle ranching property. Ol Pejeta is a fenced conservancy with wildlife corridors along its northern border, and it is also an actively-managed ranch featuring approximately 7000 Boran cattle that graze across the property and are herded to bomas overnight. Ol Pejeta is a semi-arid savanna home to at least 24 large herbivore species, including plains zebra (*Equus quagga*), impala (*Aepyceros melampus*), Cape buffalo (*Syncerus caffer*), reticulated giraffe (*Giraffa camelopardalis*), African elephant (*Loxodonta africana*) and common warthog (*Phacochoerus africanus*). Large predators, including lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), spotted and striped hyenas (*Crocuta crocuta* and *Hyaena hyaena*), and leopards (*Panthera pardus*) are also present. Camera trapping was conducted alongside a two-year water manipulation study in the western half of the property, where an array of artificial water pans are maintained for livestock and wildlife use, described by (Titcomb, Mantas, et al., 2021). In brief, five pairs of water pans (10 pans total) were selected from the array: in each pair, one pan was randomly designated as a permanently-filled control water pan, and the other pan was experimentally drained. Each water pan in a pair was located within 2 km of the other pan, and the pair was grouped with a 'matrix' site randomly located 1 km from the filled control pan and at least 1 km from any water source. The distance between pairs ranged from 3 to 16 km. Experimentally manipulated pans were drained from October 2016 to January 2018.

Fieldwork was conducted with the necessary permissions granted by the Kenyan National Commission for Science, Technology, and Innovation (NACOSTI/P/16/0782/10585) and the Kenya Wildlife

Service (KWS/BRM/5001). Animals were passively sampled using unbaited camera traps; thus, this study did not require ethical approval from an animal ethics committee.

2.2 | Camera trapping methods

One camera trap (Moultrie A-30 and Moultrie M-880) was set and checked monthly at each water pan and matrix site for the 2-year duration of the study (August 2016–September 2018). Camera trapping included approximately 3 months of data before water was drained, 16 months of data when water was removed, and 9 months of data after refilling. Cameras were set at knee height to take three images when they sensed heat or movement, with a minimal delay (1–5 s) between bursts. To ensure consistency in camera detections, walk tests were used to position cameras to have 12–15 m detection distances across sites. Cameras were aimed to completely capture the water pan and remained in a fixed position during the study. In total, the dataset included 5631 days of data (hereafter, 'trap days') after filtering deployments that had been shifted or displaced.

2.3 | Image processing

We adapted methods described by (Titcomb, Mantas, et al., 2021), in which members of the public counted animals that were present in each image burst using the online UK/USA-based Zooniverse citizen science platform. Each burst received at least five public classifications. Because a small number of misidentifications could inflate contact estimates, we applied additional stringent rules to determine consensus identifications for this study. First, we considered an animal present if ≥80% of public classifications said so. For other images we used the identification assigned by any of the top five users for the project (each >5000 identifications). We assigned IDs to remaining non-consensus images (11%) using information from photographs that were taken immediately before or after the non-consensus image. Most non-consensus images involved an animal standing very close to the camera, so we grouped each camera's image bursts into 5-min trigger sets and assigned the most common high-confidence identification within that trigger set to any non-consensus image.

The burst nature of camera trapping makes it difficult to assess physical contact between individuals. Moreover, many directly transmitted pathogens do not require physical contact but close spatial proximity. Therefore, we defined an interspecific contact as more than one species occurring within the same trigger set. We defined a trigger set as a sequence of images in a burst that occurred within 5 min of each other in a single location. Thus, if any images in a burst contained another species, we assumed that entire burst to contain interspecific contact between all species observed in any of those burst images. When successive bursts led to >1 h of continuous activity (<0.04% of all triggers), we created separate triggers for each hour.

2.4 | Temperature measurements

Many camera trap models record ambient temperature; however, these data are frequently discarded due to concerns over temperature accuracy compared to dedicated weather monitoring tools (Meek et al., 2014). Recent remote sensing studies have shown that when averaged across cameras, daily temperatures can have higher baseline temperature values but very high correlations with nearby weather station readings, providing high potential for tracking wildlife and climate simultaneously (e.g. Hofmeester et al., 2020). Given the focus of our study on relative temperature changes within days and over the course of a year, we extracted all temperatures recorded by camera traps and averaged them across cameras per hour of the study period. Specifically, we calculated mean hourly temperature across the five study locations ($n=15$ cameras). For each hour that cameras were active but no animal initiated a trigger sequence (and thus recorded a temperature), we added rows denoting zero activity for each species and location. We imputed temperatures for hours with no temperature data (6% of the dataset) using a linear model containing categorical predictors for month, hour and year (model $R^2=0.94$). To account for confounding effects of temperature and light on animal aggregation patterns, as well as estimation issues due to sparse contact data at matrix sites at night, we filtered the dataset to daylight hours (7:00am–6:00pm) but we present night-time results for species with sufficient data in Tables S2–S6. To validate temperature data, we compared mean hourly camera trap temperature readings to average temperatures collected concurrently for 2 weeks from small, remote HOBO(c) loggers (Onset, MA), with one hung from a tree at each of the five locations. Data were highly correlated (Pearson's $r=0.97$, $p<0.001$), but camera traps overestimated temperatures by 0.39°C on average and by 1.66°C during the daytime, potentially because HOBOS were typically in shaded areas, while camera traps were more exposed to sunlight. Therefore, we calculated bias-adjusted temperatures using a linear model containing average HOBO data as the response and the interaction between hour (coded as a factor) and average camera temperature as predictors.

To further explore temperature patterns in the context of projected climate changes, we calculated the mean temperature for each day of the study and classified the top 25% as 'hot days' versus the remaining 75% 'other days' (threshold = 23.48°C). Averaged across daylight hours, hot days were 0.75°C (1.53°C for raw data) warmer than other days and 0.5°C (1.01°C for raw data) warmer across all hours of the day, corresponding to projected mean monthly temperature increases of 0.54 – 0.74°C by 2021–2039 in this region under IPCC climate model SSP2-4.5 (a 'middle road' scenario) (World Bank Group, 2024). No hot days were observed in August. The highest proportion of hot days occurred during October and the long dry season (January–March) (Figure 1).

Monthly rainfall totals were provided by the OI Pejeta Ecological Monitoring Unit. We found that the proportion of hot days per month was inversely correlated with monthly rainfall totals (Spearman's $\rho=-0.45$, $p=0.02$) (Figure 1).

2.5 | Statistical methods

2.5.1 | Effect of water on total interspecific contacts

We fit three models to parse apart drivers of total contact rates in relation to water manipulation: (1) a linear model using mean daily total triggers as a response, (2) a generalised linear mixed model (GLMM) with a binomial error structure using interspecific triggers as 'successes' and single-species triggers as 'failures' using *glmmTMB* (Brooks et al., 2017), and (3) a linear model using mean daily interspecific triggers. We included treatment (filled, drained or matrix), status (pre, during or post) and their interaction as fixed effects and month and location as random effects. We conducted hypothesis tests within experimental phases and with a Tukey adjustment for multiple comparisons using *emmeans* (Lenth, 2020).

To test whether the composition of interspecific contacts changed significantly due to water draining (as opposed to consistent

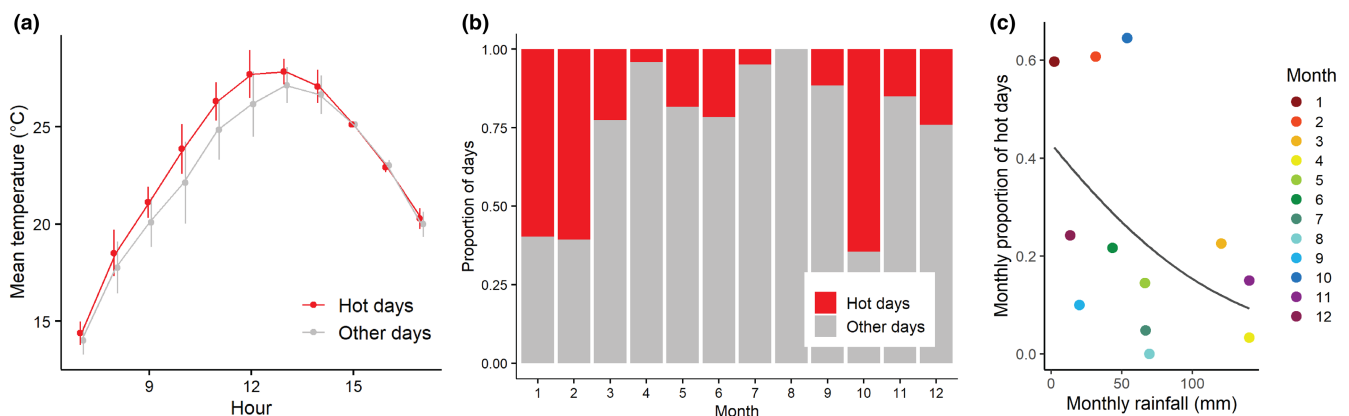


FIGURE 1 (a) Temperature during daylight hours (means \pm SD) for the hottest 25% of days ('hot days') in red and other days in grey. (b) The proportion of days per month that were classified as hot, with the highest proportions occurring during the hot dry season (January–March). (c) Monthly proportion of hot days correlated with monthly rainfall.

reductions across all species), we built one undirected unipartite network for all interactions at filled water sources, and one undirected unipartite network for all interactions at drained water sources using *igraph* (Csardi & Nepusz, 2006). We then performed a Chi-square test of proportions using the weighted edgelist of the two graphs to test whether contact composition shifted independently of the number of contacts.

2.5.2 | Effect of temperature and rainfall on hourly contact probability

We tested the effects of temperature and rainfall on hourly interspecific contact probability at filled and drained water pans using both continuous hourly temperature and monthly rainfall data and binary hot/other day and wet/dry month designations to improve interpretability. To compare across well-represented species across treatments and temperatures, we focused on seven common species (cattle, elephants, buffalo, plains zebra, giraffe, warthog, and impala) that accounted for 85% of triggers. Given that 'pre' and 'post' periods had significantly fewer trap days and covered different seasons, we restricted analyses to cameras running during the 15-month 'during' period.

Total interspecific contact probability

To test whether average hourly temperature, monthly rainfall and water status corresponded to hourly interspecific contact probability across all herbivores, we used a binomial GLMM with a binary response designating whether or not an interspecific contact occurred for each hour that a camera trap was running. Fixed effects included temperature, treatment, and their interaction, as well as rainfall, treatment and their interaction. We compared models using logarithmic and polynomial temperature terms, but found an unmodified temperature coefficient was most parsimonious using AICc. We included random effects of hour, month and location. We repeated this analysis of contact probabilities using binary hot/other day and wet/dry month variables and their interaction with treatment, using hour, month and location as random effects. We also ran both sets of models using night-time data.

Species-specific inter- and intraspecific contact probability

To test whether hourly intra- and interspecific trigger probabilities at water pans corresponded to temperature and rainfall, we used hot/other day and wet/dry month classifications as covariates. For each focal species, we aggregated data by calculating the number of hours with ≥ 1 interspecific contact and the total hours that a camera was deployed for each hour of the day, hot/other day, wet/dry month, treatment and location. We fit a binomial GLMM with hourly interspecific contact as the response and hot/other day, water status (drained, filled or matrix site) and their interaction as fixed effects, as well as the wet/dry period covariate and its interaction with water status. Location and hour were random effects. We tested residuals using the DHARMA package (Hartig, 2020) and found that including

an intercept-only zero-inflation term improved model fits across species. We repeated analyses with night-time data.

3 | RESULTS

Our dataset included 24,196 triggers of 15 mammalian herbivore and 3 mammalian omnivore (warthogs, baboons and humans) species and 3137 interspecific contacts. Mammal communities differed across treatments: filled and drained water sources had 1.5 times the mean species richness per deployment compared to matrix sites (mean \pm SE for filled water pans, drained pans and matrix sites = 10.6 ± 1.6 , 10.1 ± 1.43 , and 7.6 ± 1.6 , respectively). Because human-cattle contacts were closely linked due to herding practices, we excluded humans from contact analyses.

3.1 | Effect of water on total interspecific contacts

We found that total triggers per trap day, proportion of interspecific triggers and total interspecific triggers per trap day were higher at water sources relative to matrix sites prior to experimental water draining (Table S1). After experimental pans were drained, total triggers decreased and interspecific trigger probability was halved relative to filled pans (OR = 0.48, $p < 0.001$; Figure 2a; Table S1), such that the resulting number of daily interspecific contacts at drained water was lower than at filled water (0.52 ± 0.21 vs. 1.45 ± 0.19). However, refilling water in drained pans did not restore interspecific contacts to pre-experiment levels within the study timeframe (Figure 2a; Table S1). We saw a non-significant increase (~40%, $p = 0.24$) in total interspecific triggers at filled water sources after paired water sources were drained, likely due to water availability at other nearby pans.

The composition of contacts differed between filled and drained pans during the experimental phase of the study ($\chi^2 = 1606.1$, $p < 0.001$). Interactions involving cattle or elephants accounted for a larger proportion of total contacts at filled water pans relative to drained water pans (Figure 2b,c).

3.2 | Effect of temperature and rainfall on hourly contact probabilities

3.2.1 | Total interspecific contact probability

At filled pans during the day, hourly probability of any interspecific contact significantly increased from 2.9% at 15°C to 13.6% at 30°C (Table S2). This trend was not significant at night-time. With decreasing rainfall, hourly interspecific contact probability increased at filled pans during day and at drained pans at night. These trends were not significant for matrix sites (Table S2). Our model using binarised hot versus other days and wet versus dry periods supported these findings, and showed that during hot,

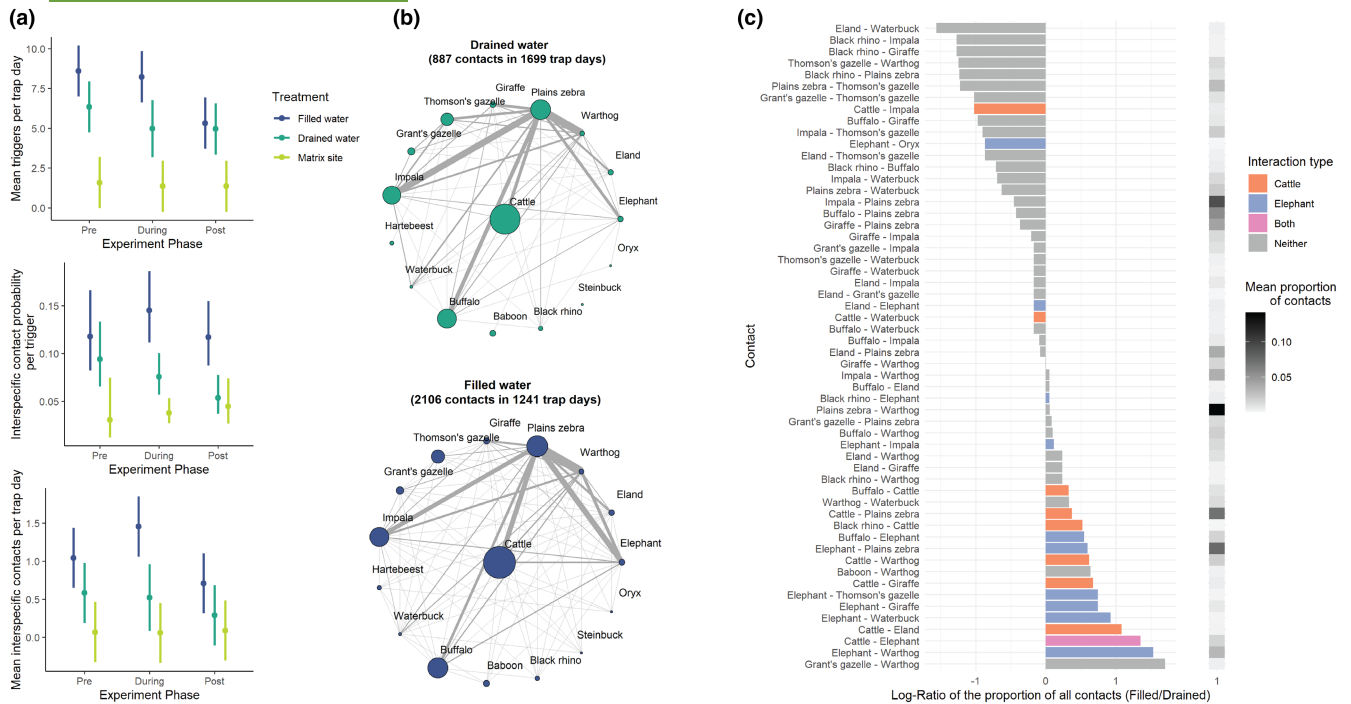


FIGURE 2 (a) Total triggers per trap day, interspecific contact probability per trigger and total interspecific contacts per trap day for treatments and experimental phases. Drained and filled water pan measurements were comparable before draining and were higher than matrix sites. Draining reduced total triggers per trap day, contact probability per trigger and total contacts per trap day. However, refilling water did not immediately increase contacts. See [Table S1](#) for post-hoc comparison details. Approximate per-capita triggers per trap day are provided in [Figure S1](#). (b) Interspecific contact networks at drained and filled water pans during the experiment. Edges are weighted by the proportion of contacts and nodes are scaled by square-root of abundance. There were more (~2.4x) total contacts at permanent water sources. (c) Network edges for filled versus drained pans, with any interaction involving cattle or elephants shown in orange or purple, respectively. Positive values indicate an increased proportion of total contacts comprised by a given interaction.

dry periods, hourly interspecific contact probability at filled water pans was >50 times that at matrix sites, and nearly five times that at drained pans ([Table S3](#)). During wetter and cooler periods, hourly interspecific contact probability at filled water pans was still higher than at matrix sites and drained pans, but to a lesser extent (OR=13.3, OR=3.1; [Figure 3](#); [Table S3](#)).

3.2.2 | Species-specific contacts

Species-specific investigations of water use yielded further insights into interspecific contacts ([Figures 4](#) and [5](#); [Tables S4–S6](#)). We found that both water dependent and water independent species showed increased hourly interspecific contact probability at water on hot and dry days. Specifically, we found that giraffes had more interspecific contacts at filled water pans on hot days versus other days (OR=3.66, $p < 0.001$), but to a lesser extent during dry versus wetter months (OR=1.60, $p = 0.03$). Impala were also more likely to come into contact with other species at filled water sources on hot days versus other days (OR=2.59, $p < 0.001$), but not during dry versus wet months (OR=1.29, $p = 0.11$). Interestingly, impala also visited drained water pans at higher rates on hot days and dry periods (OR=2.06 hot vs. other, $p < 0.001$; 2.58 dry vs. wet, $p < 0.001$). Cattle, which are frequently herded to water by

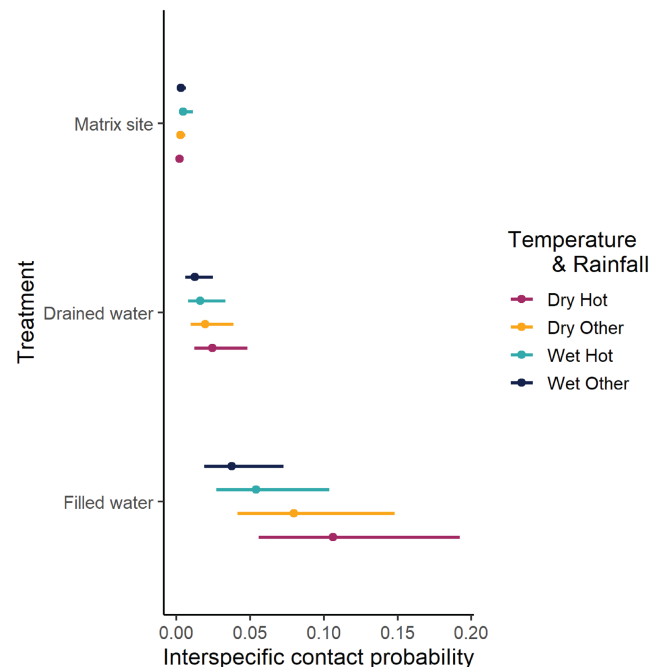


FIGURE 3 Probability of any interspecific contact per hour, across water treatments, temperature, and rainfall conditions. Filled water pans in dry and hot conditions had the highest interspecific contact probability. Bars show $\pm 95\%$ confidence levels.

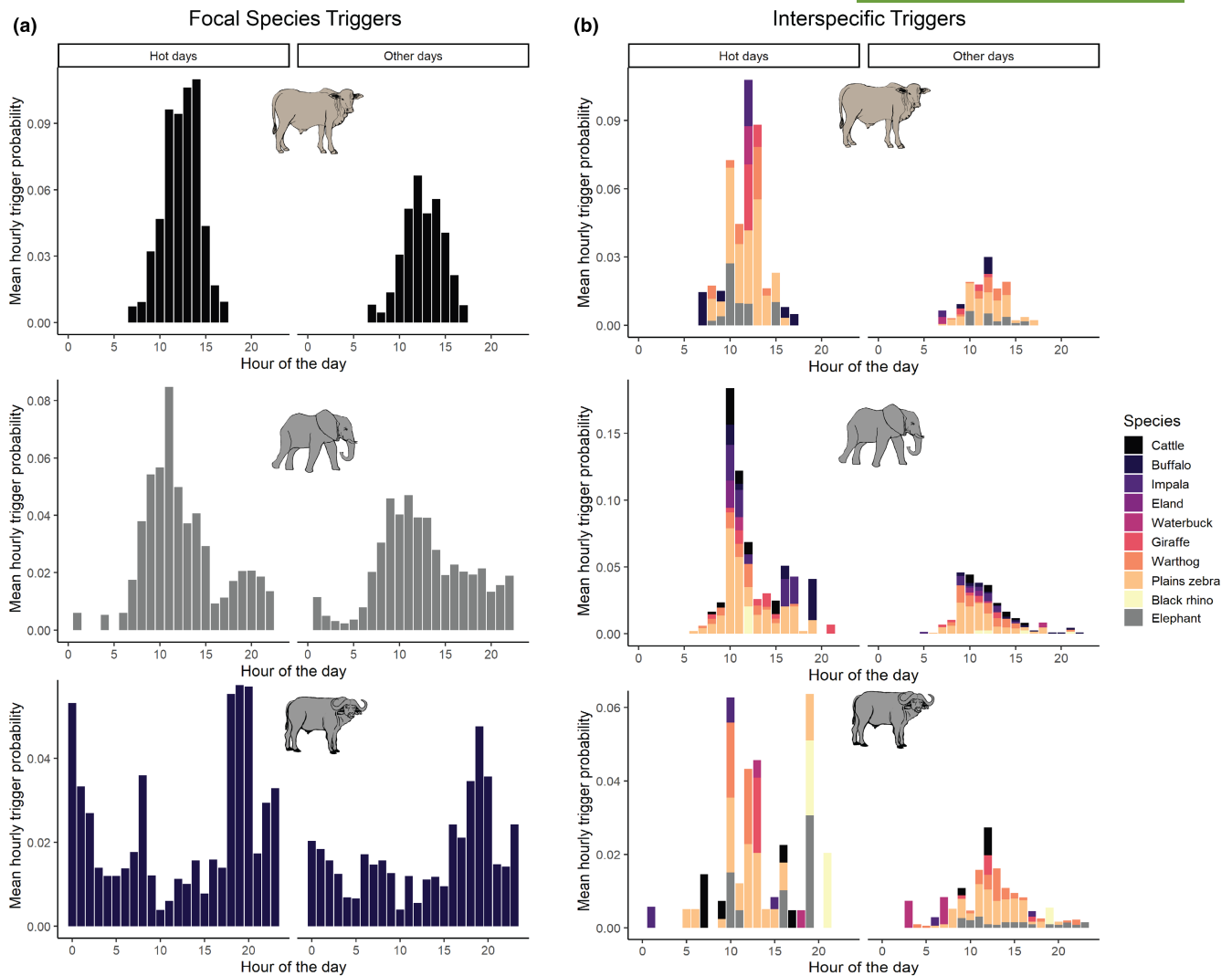


FIGURE 4 (a) Hourly mean trigger probability for cattle (top row), elephants (middle row) and buffalo (bottom row) for hot days (left-hand plots within panels) versus other days (right-hand plots within panels) at filled pans during the experiment. (b) Hourly mean trigger probability for contacts between cattle, elephants, and buffalo and other species (colours in bars) for hot days versus other days at filled pans during the experiment. Interactions with >1 additional species are split to individual interactions, resulting in larger stacked interspecific contact probabilities during high-activity hours. Across all species except buffalo, interspecific contacts peaked around midday and were highest on hot days at filled water pans. Plots showing side-by-side contacts for all focal species are provided in [Figure S2](#).

humans, had more than twice the hourly interspecific contact probability at filled pans on hot days versus other days ($OR = 2.03$, $p < 0.001$), and had similar increases for dry versus wet months ($OR = 1.81$, $p < 0.001$). Elephants were also more likely to encounter other species at filled water pans under hot conditions ($OR_{hot vs. other days} = 1.61$, $p < 0.001$), but their contact patterns were not predicted by monthly rainfall. Interestingly, buffalo were the only species without increased hourly interspecific contact probability at water sources under increased temperatures during the day. However, this pattern was apparent at night ($OR_{hot vs. other days} = 2.25$, $p = 0.04$). Night-time trends were similar to daytime trends for other species, although far fewer interspecific contacts reduced their significance ([Table S4](#)).

4 | DISCUSSION

Our results demonstrate that interspecific contact rates are elevated at water sources relative to matrix sites and drained water and that this effect is amplified at higher temperatures (hottest 25% of days across the year) and during drier months. Specifically, all focal species except buffalo increased activity around filled water sources on the hottest 25% of days and during dry months, resulting in higher hourly interspecific contact probability (approximately 2–3-fold). Additionally, our findings show complex and nuanced responses displayed by a diverse community of mammals in response to changing water supply and temperatures.

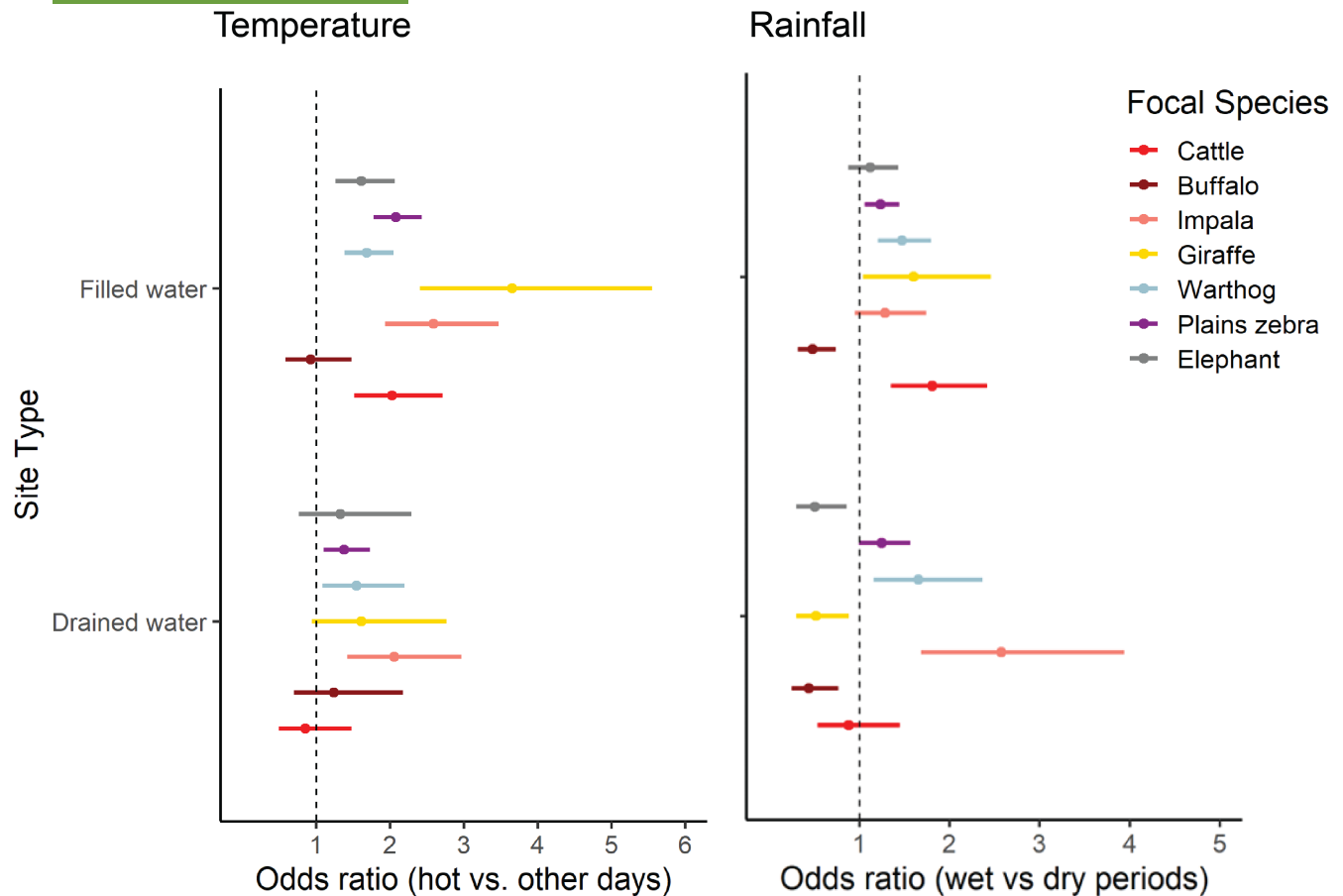


FIGURE 5 Odds ratios and 95% confidence intervals for mixed species contact for dry periods versus wet periods and hot versus other days from binomial models fit to data in Figure 4 and Figure S2. Points and intervals to the right of the vertical grey line indicate higher odds of a camera trap trigger at a given location during a dry versus wet month (for rainfall) or for hot days versus other days (for temperature).

4.1 | Effect of water on total interspecific contacts

Our finding that total camera triggers were elevated at water sources relative to matrix sites aligns with previous observational work documenting high animal activity rates around water, but extends this work by showing an elevated proportion of triggers with interspecific contacts around water. This indicates that temporal niche partitioning does not reduce total contact rates despite shifts in species-specific interactions. However, we found some evidence that temporal partitioning may occur at new or newly re-established water sources, as interspecific contacts did not increase within 6 months of water re-instatement in our experiment. One explanation is that species most likely to be captured in a single-species trigger (i.e. cattle and elephants) heavily aggregated around newly-refilled water sources, potentially excluding other species. Previous studies have indicated that elephants may exclude other animals around water in some contexts (Valeix et al., 2007), and that wildlife and cattle temporally partition water (Sitters et al., 2009). Alternatively, less water-dependent species may take longer to shift foraging behaviours to additional water sources: an important consideration for managers seeking to reduce aggregations by establishing new water points.

We found that the composition of interspecies contacts changed when water was removed, and this effect was driven by changes in elephant and cattle movements. Interestingly, several herbivore species still overlapped at drained water pans, potentially because drained pans may provide food resources in the form of grazing lawns in certain contexts (Titcomb, Amooni, et al., 2021), or because they were slower to adapt to water changes than human-herded cattle or elephants that rapidly adjust movements in response to water availability (Chamaillé-Jammes et al., 2013).

4.2 | Effect of temperature and rainfall on hourly contact probabilities

As expected, interspecific contact probability around water increased with temperature and during dry months, but, contrary to our hypothesis, the magnitude of this change did not follow species-specific expectations based on water dependency. These findings suggest that increased temperatures and aridity that are likely under future climate change scenarios are also important for dry-adapted species. These results contrast with a study in Hwange National Park, in which highly water-dependent grazers used water sources

more intensely than browsers during a dry year than a wet year (Valeix, 2011). One explanation for this is that animals may have moved to other areas over a longer period, while our results show temperature and rainfall responses on a granular time scale in which baseline animal activity remained relatively consistent, as shown by matrix site results (Table S4). Conservancy fencing also likely limited animal emigrations, resulting in more frequent water access at other water sources.

While we observed increased hourly interspecific contact probability at water sources on hot days for cattle, cattle had consistently high levels of aggregation near water, potentially due to routine grazing and water visitation patterns via human management. Elephants, a species of concern for wildlife conflicts, were also more likely to come into contact with another species at filled water pans on hot versus other days. By examining the hourly distribution of water visitation times, we noted that elephants tended to visit water earlier than cattle, suggesting that elephants may have adapted to routine cattle behaviour (Figure 4). By contrast, other studies have found that in the absence of cattle, elephants tend to access water during peak afternoon when temperatures are warmest (Hayward & Hayward, 2012; Valeix et al., 2007).

We also found intriguing behavioural patterns among other species, particularly buffalo. Buffalo-cattle interactions are important because they share diseases such as bovine tuberculosis, foot and mouth disease, and malignant catarrhal fever (Kock et al., 2014). However, our results showed that buffalo rarely foraged for water during the middle of the day and that they maximised activity during early morning or evening. Notably, 35% of buffalo activity at filled water pans occurred between 6 pm and 7 am. This behaviour decreases competition for water and reduces direct contacts that may lead to disease transmission. However, we note that buffalo and cattle still regularly visited the same water sources and thus have considerable risks of environmentally transmitted and vector-borne pathogens (Amulyoto, 2020; Titcomb et al., 2023).

In this study, we explored the relationship between temperature and rainfall and water-foraging patterns, although hot days typically fell during the long dry season when rainfall was also scarce. Our results show that both temperature and rainfall are related to water foraging, but we note that rainfall analyses are conducted on a monthly scale, and thus may miss intramonth nuances in water availability. In the context of likely climate changes, rainfall predictions are highly uncertain, with conflicting projections (Funk et al., 2008; IPCC, 2014), but dry and wet periods are likely to become more extreme (Funk et al., 2008), potentially driving higher contact rates than predicted here during hot days in the dry season (Caravaggi et al., 2020). In this study, we investigated two dimensions of climate (temperature and monthly rainfall), but note that future work is needed to connect additional complexities of climate change, like extreme weather events and variability to animal movements and contact rates.

There are several limitations of this study to consider. First, we found that temperature data can be aggregated and averaged

across multiple camera traps as coarse, long-term data, but they must be bias-corrected using ground-truthed data, as suggested by Hofmeester et al. (2020). Second, we categorised 'hot days' using temperatures across the year since mean monthly temperatures varied by 2–3°C; however, stratifying 'hot days' within season may also be important in temperate climates. Third, camera detection rates can vary with temperature such that detections decrease when background temperatures are similar to animal body temperatures (McIntyre et al., 2020). This may mean that we underestimated relative abundance and interspecific contacts during the hottest periods, causing hot/dry day results to be conservative and that true aggregating effects may be higher.

4.3 | Conclusions and management implications

Our analyses show that in temperatures aligning with a likely future warming scenario (0.54–0.74°C by 2021–2039), interspecific contact rates at water increase for most species (by approximately two- to threefold), with dry periods exacerbating this aggregation. These findings have important implications for resource partitioning, mitigating wildlife conflict, and managing disease transmission under climate change. In the context of the recent 30×30 global initiative—a worldwide effort to conserve at least 30% of land and sea by 2030—it is more important than ever to identify and mitigate wildlife conflict in ways that also support human livelihoods in biodiverse systems such as East African savannas. Promoting sustainable wildlife-cattle systems in this region will help to achieve this goal, but risk of direct and indirect disease transmission is a major obstacle. Given that water sources present an acute transmission hotspot in a small space, transmission risks may be mitigated by flexible water access management, rather than complete separation of wildlife and livestock. We suggest that managers consider that during hot and dry periods, wildlife-cattle interactions increase substantially, and that maintaining wildlife-only water sources within a shared landscape may provide an opportunity to reduce competition and disease sharing opportunities at the livestock-wildlife interface.

AUTHOR CONTRIBUTIONS

Viviana Martinez and Georgia Titcomb conceived the analytical ideas and designed methodology. Georgia Titcomb and Hillary Young conceived and designed fieldwork components, with logistical support and guidance from Benard Gituku. John Naisikie Mantas, Jenna Hulke, Nickson Ndiema and Georgia Titcomb collected the data. Viviana Martinez, Georgia Titcomb, Malik Elkouby, Joelle CantoAdams, Serena Yeh, Adam VanLeeuwen and Asher Thompson analysed the data. Viviana Martinez and Georgia Titcomb led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data and code to replicate analyses are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.02v6wwqc5> (Titcomb et al., 2024).

STATEMENT OF INCLUSION

Our study brings together authors from a wide variety of career stages from both the United States of America and Kenya, where the field research was carried out. Fieldwork was conducted by both Kenyan and US researchers and involved guidance and input from stakeholders at OI Pejeta Conservancy. All co-authors from all backgrounds participated in manuscript preparation. Where relevant, literature published by scientists from the East African region was cited.

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SUPPORTING INFORMATION

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

Table S1: Effects of water manipulation on interspecific contact rates.

Table S2: Effect of temperature and rainfall on interspecific contact rates using continuous predictors.

Table S3: Effect of temperature and rainfall on interspecific contact rates using binary predictors.

Table S4: Effect of temperature on species-specific contact rates at water sources and matrix sites.

Table S5: Treatment effects on species-specific contact rates in different temperatures.

Table S6: Effect of rainfall on species-specific contact rates at water sources and matrix sites.

Figure S1: Per capita triggers per trap day by treatment.

Figure S2: Intra- and interspecific hourly activity at water sources and matrix sites for focal species.

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