



## Policy analysis

## Quantifying wildlife responses to conservation fencing in East Africa

Christine E. Wilkinson<sup>a,\*</sup>, Alex McInturff<sup>b</sup>, Maggi Kelly<sup>a</sup>, Justin S. Brashares<sup>a</sup><sup>a</sup> Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA, USA<sup>b</sup> Environmental Studies Program, University of California, Santa Barbara, CA, USA

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## ABSTRACT

The fencing of protected areas is increasing worldwide. However, the implementation of fences for conservation has outpaced scientific assessment of their effectiveness, non-target impacts, and long-term costs. We assessed landscape predictors of fence crossing sites and employed camera traps over a one-year period to investigate wildlife responses to a conservation fence around Lake Nakuru National Park, Kenya. Specifically, we measured the impact of the fence on wild mammal movement, and the temporal impacts of fence maintenance on wildlife crossings and behavior. Cameras captured more than 65,000 detections of animals approaching fences, with 3626 observed crossings over 2818 trap nights at 19 sites. Using these data, we developed a guide to classifying fence-specific mammal behaviors. Thirty-eight wild mammal species approached known weak points in the fence, and 27 species were recorded crossing the fence. No single environmental variable predicted detection or fence crossing points for all species, but seasonality, human activity, habitat visibility, and proximity to an adjacent protected area were each correlated with species-specific crossing locations. Additionally, breaches of repaired fence-crossing locations occurred within days of maintenance. We conclude that popular, 'one-size-fits-all', conservation fence designs may be ineffective and costly for restraining movement of many wildlife species. We recommend that those deploying conservation fences start with clearly articulated management goals, that fence maintenance be informed by taxa-specific tendencies to breach fences, and that managers consider the strategic creation of wildlife corridors, overpasses, or ungulate-proof fences to link fenced protected areas with surrounding habitat.

## 1. Introduction

Protected areas are a central component of conservation, and researchers, land managers, local communities, and politicians have advocated for the fencing of these areas to better safeguard their contents and to protect people living on their edges from conflict with wildlife (Hayward and Kerley, 2009; Packer et al., 2013). While fencing of protected areas, whether public or private, can be effective for reducing human-wildlife interactions and protecting animals and their habitats from unwanted incursions, these conservation fences come with significant economic and social costs (Ferguson and Hanks, 2012). Moreover, our understanding of the ecological consequences of fencing on wildlife communities is incomplete, with some species potentially benefiting over short or longer time scales (ecological 'winners'), while others may suffer (ecological 'losers'; Jakes et al., 2018; McInturff et al., 2020).

Conservation fences come in various forms but are typically composed of parallel lines of electrified wire that may be accompanied

by wire mesh. As reviewed elsewhere (McInturff et al., 2020), these structures will be beneficial to some species, detrimental to others, and easily ignored or breached by many. Ultimately, the effect of a fence on a species will be shaped by a combination of features of the fence and its surrounding environment (i.e., extrinsic factors) and physical and behavioral characteristics of the species in question (i.e., intrinsic factors).

Extrinsic factors affecting fence ecology include fence construction as well as patterns of fence maintenance, surrounding habitat and soil types, human disturbance, hydrology and season. The intrinsic factors that best predict species' response to fences are often as simple as mode of locomotion, body size, agility, strength and adaptations to dig or break through or under fences (Karhu and Anderson, 2006; Pirie et al., 2017). Capacity for problem-solving and searching can also be useful predictors. For example, in the case of species that seek and use fence openings created by other species (Stander, 1990; Kesch et al., 2014). The interplay of intrinsic and extrinsic drivers of fence interactions is evident, for example, among primate species that exhibit extreme

\* Corresponding author: 127 Mulford Hall, Berkeley, CA 94720, USA.

E-mail address: [christine.wilkinson@berkeley.edu](mailto:christine.wilkinson@berkeley.edu) (C.E. Wilkinson).

behavioral plasticity, physical dexterity, and a strong attraction to anthropogenic sources of foods that are often available in lands surrounding conservation areas (Fehlmann et al., 2017).

The taxa-specific permeability of fences directly and indirectly affects wildlife distributions and can ultimately lead to shifts in community structure and abundances both inside and outside of fenced areas (Cozzi et al., 2013; Massey et al., 2014). Specifically, by altering wildlife movement patterns at different spatial and temporal scales (Sawyer et al., 2020), fences can profoundly influence community composition and dynamics (Shamoon et al., 2018; Nickel et al., 2020). Fences can also affect population and community-level processes through direct mortality when wildlife become entangled in fences (Rey et al., 2012), or where predators use fences to corner or ambush prey (Dupuis-Desormeaux et al., 2016). Finally, fences may have less obvious impacts on wildlife by requiring energy expenditure to move around or through fenced areas (McInturff et al., 2020), or simply through the stress responses fences induce in wildlife as artificial, anthropogenic structures (Vanak et al., 2010). If wildlife show avoidance of fences similar to the avoidance observed in response to other anthropogenic structures and effects (Wang et al., 2017; Gaynor et al., 2018), the indirect impacts of fenced boundaries may be far reaching. In sum, the responses of wildlife to fences will be taxa-specific and even where fences may be effective in achieving conservation goals for targeted species, they may negatively impact the movement and survival of non-target species.

The fact that fences change in permeability over time as a function of maintenance investment adds yet another layer of complexity in predicting their longer-term effects on wildlife (Woodroffe et al., 2014; Massey et al., 2014). Fences are often exposed to harsh conditions and deteriorate quickly. In other cases, they may be actively sabotaged, broken down for snare wire, or simply not adequately and comprehensively maintained (Hoole and Berkes, 2010). Many terrestrial wildlife species patrol fence lines until they find a weakness (Cavalcanti et al., 2012), thus even small breaches may quickly result in major changes in fence permeability (Jori et al., 2011). Even where the structural integrity of fences is maintained, temporary disruptions in electrification can result in increased fence-crossing behavior from wildlife (McKillop and Sibly, 1988). In addition, many species exhibit high site fidelity to known fence crossing sites (Dupuis-Desormeaux et al., 2018), and may thus be likely to repeatedly return to dig through repaired holes. Thus, if maintenance budgets are low, as is typically the case for protected areas globally and notably in Africa (Pekor et al., 2019), fence permeability will steadily increase over time.

Assessing the long-term efficacy of conservation fences both for targeted ecological outcomes and economic sustainability is critical, yet, as outlined above, elusive (Hayward and Kerley, 2009). Much remains opaque regarding how and when wildlife cross fences, and how fence maintenance alters these behaviors through time. As the call for conservation fences and fenced protected areas increases globally, site-based, quantitative assessments of wildlife responses to fences must guide decisions on when and where it is effective to employ and maintain conservation fences. Here, we summarize our effort to quantify the responses of land mammals to conservation fencing in East Africa with the targeted goals of measuring animal behavior associated with fences broadly and the effects of fence maintenance on fence-crossing behavior. Specifically, we 1) tested for landscape-level predictors of wildlife fence crossing using documented crossing locations, and 2) employed camera traps along a conservation fence to address the following questions: a) How does fence-crossing behavior vary by taxa?, b) How do anthropogenic, ecological, and temporal factors influence fence crossing behavior?, and c) To what degree does fence maintenance alter fence-crossing behavior? Additionally, we provide a practical guide to classifying mammal behaviors around fences from camera trap images with the hope of fostering more uniformity among studies in fence ecology.

## 2. Methods

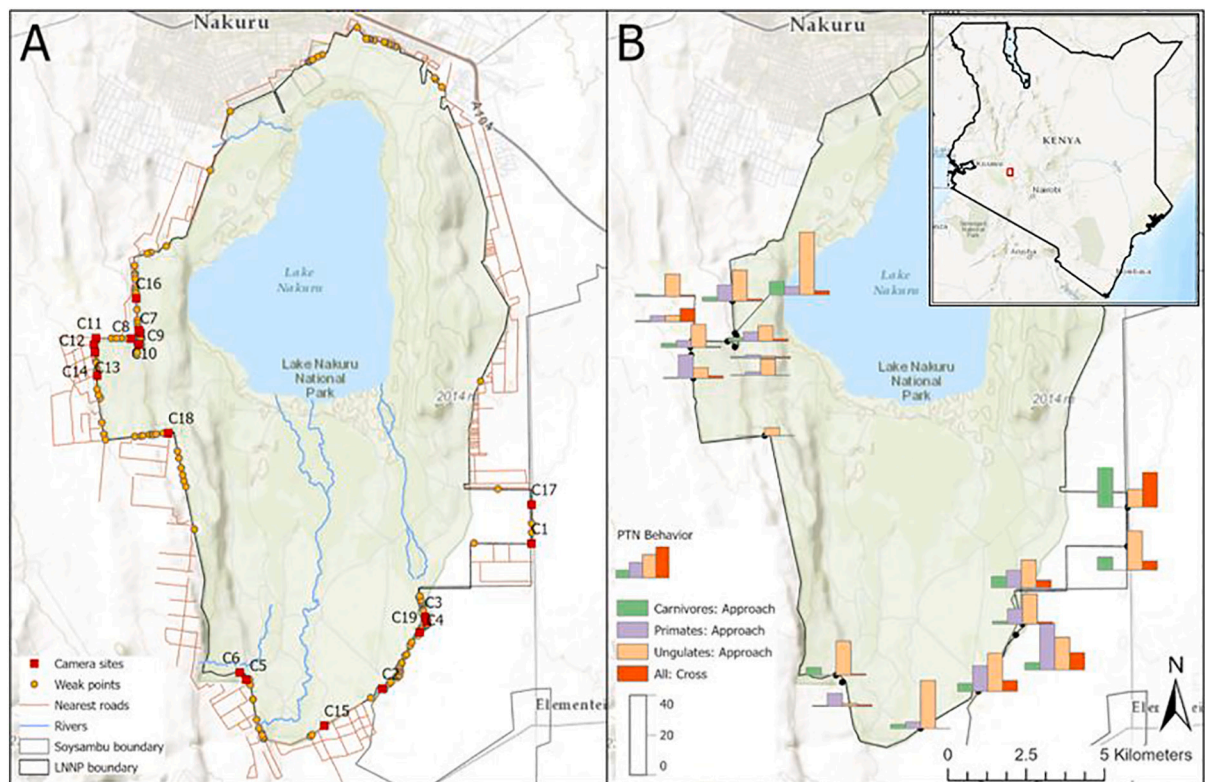
### 2.1. Study area

Our research was conducted at Lake Nakuru National Park (hereafter LNNP) in the Rift Valley of southwest Kenya (0.3562° S, 36.1002° E; inset Fig. 1). LNNP (188 km<sup>2</sup>) is one of only two fully fenced national parks in Kenya. Lake Nakuru encompasses nearly one third of the park (Elliot et al., 2020), leaving a land area of approximately 135 km<sup>2</sup>. The park lies directly adjacent to and west of the Soysambu Conservancy (190 km<sup>2</sup>), which is partially fenced and functions simultaneously as a private wildlife reserve and working ranch, housing 10,000 sheep, goats, and cattle. Dense agricultural settlements surround both LNNP and the adjacent conservancy, directly abutting their boundaries in many locations, and the nearby city of Nakuru, directly to the north of LNNP, is the fourth largest city in Kenya with a population of 570,000 in 2019. Lake Nakuru is classified as a UNESCO World Heritage and Ramsar site. This region supports multiple mammal species, including threatened and endangered species such as black rhinoceros (*Diceros bicornis*) and Rothschild's giraffe (*Giraffa c. camelopardalis*), as well as numerous carnivore species whose populations are stable or increasing despite heavy historical persecution (Ogutu et al., 2017). According to data on eight representative large mammal species, wildlife density inside of the national park is at least 20% higher than community lands outside (Ogutu et al., 2017), though Soysambu Conservancy maintains higher populations of most ungulates than LNNP (K. Combes, pers. comm., 5 July 2019). The region is characterized by a combination of savanna, woodland, and dense brush habitats, and experiences two major rainy seasons and two major dry seasons each year. Four rivers enter LNNP, three from the south and one from the northwest, and provide incomplete riparian corridors outside of the park.

The electrified LNNP perimeter fence was erected in 1986 to primarily “deter intruders and to keep rhinos within the sanctuary” (Lever, 1990), but it is also maintained to alleviate human-wildlife conflict and demarcate the park boundary (Kenya Wildlife Service, pers. comm.). The current fence, typical of conservation fences in sub-Saharan Africa, is 2.3 m tall and consists of 11 parallel electrified wires, with low tensile barbed wire below the bottom-most wire in select areas. Some portions of the fence, particularly those adjacent to Nakuru city, have a component of woven wire mesh that extends approximately 0.6 m above the ground and 1 m below ground to reduce wildlife crossing through digging. The perimeter is periodically walked and maintained by park employees. Maintenance includes cutting the grass directly beneath the fence wire, filling in holes with large stones, and replacing, adjusting, or tightening loose wire. The timing of maintenance events varies considerably across the year as a function of staff availability, budgets, and access to materials.

### 2.2. Camera trap placement and image classification

In June 2018, we used a handheld GPS to map the LNNP perimeter fence on foot and by vehicle. While mapping, we recorded signs of mammal crossings, including holes dug under the fence or signs of digging, hair in barbed wire, loose electric wire, tracks and paths crossing under the fence, signs of crop raiding from nearby farms (e.g., corn husks strewn in paths toward the park), and animals observed crossing the fence. We also relied on the expertise of Kenya Wildlife Service (KWS) rangers to find suspected weak points on the fence and assess whether mammals had recently crossed. We conducted this survey again in October 2018 and March 2019 to assess new weak points. Through these surveys, we identified 175 crossing points in the fence. Because carnivores were of special interest due to nearby human-carnivore conflict, camera traps were placed at 19 sites along the fence (Fig. 1a) that showed recent sign of carnivore crossings (scat, hair, tracks, and size of hole), but all 175 sites appeared similar in other characteristics, including signs of digging under the fence and game



**Fig. 1.** A map of Lake Nakuru National Park (188 km<sup>2</sup>) in western Kenya showing: A) sites of year-long camera trapping efforts and recorded weak points in the park's barrier fence, and B) per trap night detections and crossings of wild mammal taxa at camera sites over the study period.

trails extending in both directions into and out of the park. We deployed cameras (Bushnell TrophyCam E2, Bushnell, Overland Park, Kansas) at the 19 sites for varying periods from June 2018–June 2019, for a total of 2818 trap nights, after malfunctioning camera periods (where camera dates automatically reset and were incorrect) were excluded (paring the data from the total 3043 trap nights). Cameras were placed either directly on a pole of the perimeter fence or on a tree within the park facing the hypothesized crossing point. We configured the cameras for a two-exposure burst with a 15 s interval between bursts.

Photos were manually grouped by wildlife species as well as people, domestic animals, and detections of fence maintenance. Wildlife photos were placed into seven behavioral categories (Table 1): *Cross to LNNP* (2220 total images), *Cross from LNNP* (2073), *Straddle* (individuals from same group moving together on either side of the fence, 2733), *Implied cross* (observed closely approaching or trying to breach a fence opening or weak point- carnivores only, 5185), *Vigilant* (watchful directly across fence line for more than one photo burst, 1942), *Grazing/drinking* (grazing within 2 m of the fence, drinking from water gathered in a hole under the fence, 14,186), and *Undefined* (no indication of crossing and none of the above behaviors, 45,812). If at least one individual in a photo was crossing, the photo was classified as such. Because of limitations in camera sample size and photo capture settings, the 'straddle' behavior was recorded only for taxa such as primates, which crossed the fence frequently, quickly, and with ease. Though exhibited by multiple taxa, 'implied cross' was particularly important for carnivores, as they were most likely to exhibit fast, perpendicular movements through or under the fence which reduced the likelihood of photos capturing the exact moment of their crossing. *Implied cross* was assigned to images of carnivores that satisfied the following criteria: a) the animal was seen in a perpendicular orientation to the fence actively placing head near a gap, or pushing head through a gap, b) individuals of that species had been previously captured in an 'observed cross' at that gap, and c) there had been no fence maintenance since the species had been captured in



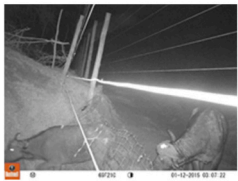




'observed cross' previously. Thus, recording *implied cross* addressed the limitations in camera settings that prevented detection of every crossing event. Nevertheless, to ensure transparency, we provide combined and separated analyses of confirmed ('observed cross') and hypothesized crossings ('implied cross').

### 2.3. Data analyses

#### 2.3.1. Landscape predictors of crossing points

To test for landscape predictors of wildlife crossing locations, we ran a logistic regression using the 175 observed fence crossing points and 700 randomly generated points along the fence line, assuming no additional crossing points were created after the 175 detected during the study period. We considered the following covariates: distance to Lake Nakuru, distance to rivers, road density, cost distance to Soysambu Conservancy boundary, human population density outside the park boundary, soil type, NDVI at the fence (e.g. for foraging or ambush- Dupuis-Desormeaux et al., 2016) the difference in NDVI inside and outside the fence, slope, and elevation (Suppl. Table 1). We scaled all continuous covariate values around zero using the *scale* function in the *base* package in R, and we used the *vif* function in the *car* package in R (R Core Team, 2018) to test for multicollinearity between variables. After eliminating any collinear variables, we used the *dredge* function in the *MuMIN* package in R to conduct model selection, retaining model variables within 2 delta AIC of the top model for model averaging (Burnham and Anderson, 2002). We tested the robustness of the top model by bootstrapping a calculation of the area under the receiver operating characteristics curve (AUC; Pearce and Ferrier, 2000). We randomly split the data into 80% training and 20% testing data, and calculated the AUC using the *performance* function in the *ROCR* package in R (R Core Team, 2018). We repeated this calculation 100 times, generating a range, a mean, and a standard deviation. Following Hosmer and Lemeshow (2000), we define AUC values below 0.7 as poor or

**Table 1**  
Classification of fence-specific mammal behaviors.

Behavior	Description	Applicable Taxa	Example
Undefined	Animal does not cross or exhibit any of the other classified behaviors	All taxa	
Cross into protected area	- Animal is seen on camera crossing into the national park  OR  - In 2-photo burst, animal is first outside of the park and then inside, with dust, etc. indicating motion through the fence	All taxa	
Cross out of protected area	- Animal is seen on camera crossing out of the national park  OR  - In 2-photo burst, animal is first inside of the park and then outside, with dust, etc. indicating motion through the fence	All taxa	
Straddle	- Animals of the same species are captured in one photo moving in parallel along opposite sides of the fence	All taxa, though more likely for social species	
Implied cross	- Animal actively tries to breach the weak point by sniffing, putting nose or other parts of body into gap  AND  - The same species was previously recorded crossing at this point and fence maintenance has not occurred	Carnivores	
Grazing/Drinking	- Animals graze within 2m of the fence  OR  - Animals drink from water pooled or flowing through the weak point hole	Grazing: Ungulates  Drinking: All taxa	
Vigilant	- Animal spends two or more consecutive 2-photo bursts standing and looking perpendicularly across the fence line with no other movement or behaviors	All taxa, though most visible and classifiable in species with medium to large body sizes.	

unacceptable, values between 0.7 and 0.8 as acceptable, and values greater than 0.8 as good or excellent.

### 2.3.2. Crossing behaviors

To test for predictors of animal crossing behaviors at the 19 camera sites, each site was classified according to the following categorical variables: human activity (high or low), adjacency to Soysambu Conservancy (adjacent or not adjacent), fence maintenance (maintained or not), and vegetation structure directly inside and outside of the crossing point (open grassland, mixed grassland, and dense shrub/forest). Human activity at each site was classified as a binary by quantifying per trap night detections of people and livestock (which were always accompanied by a herder); sites with per trap detections greater than or equal to 1 ( $n = 8$ ), indicating presence of an average of at least one person on camera per day, were classified as high human activity, and other sites ( $n = 11$ ) were classified as low human activity (Suppl. Fig. 1). Other independent variables considered were season (rainy or dry), time of day (night: 19:21–5:30, pre-dawn: 5:31–6:40, day: 6:41–18:19, twilight: 18:20–19:20), and body size (small:  $\leq 10$  kg, medium:  $>10$  kg and  $\leq 100$  kg, and large:  $>100$  kg). For the crossing response variable, behaviors were grouped as *No Cross*, which combined images scored as ‘vigilant’, ‘grazing/drinking’, and ‘undefined’; and *Cross*, which included images scored as ‘cross to LNNP’ and ‘cross from LNNP’. For carnivores, an additional analysis included images scored as ‘implied cross’ under the *Cross* designation. Because we were seeking to analyze behaviors, rather than individuals or populations, images were treated as independent regardless of timing; but if an animal’s confirmed or observed crossing occurred over two photos within the same burst, the two photos were only counted as a single crossing event. This allowed for a more accurate estimate of crossing behavior. For this behavioral analysis, we used the same methods outlined in Section 2.3.1 to test for multicollinearity, perform logistic regressions, determine best models (within 2 delta AIC), and retain variables for model averaging. We determined model strength by splitting data into 70% training and 30% testing data, and calculating AUC using the *predict* and *ROC* functions in the *pROC* package (R Core Team, 2018).

### 2.3.3. Temporal behavior

To determine influence of temporality on crossing behavior, we combined data from all camera sites and ran logistic regressions across pre-dawn, day, dusk, and night. Further, to determine temporal behavior and the temporal overlap coefficient (Dhat4 or Dhat1 depending on available behavior sample size for a particular species) for fence crossings by all species and by broad taxa across variables, we used the ‘overlap’ package in R (Meredith and Ridout, 2014). The effects of season, human activity, and adjacency on temporal fence approaches and crossings of carnivores, primates, and ungulates (Suppl. Table 3) were determined by comparing the smoothed bootstrapped mean overlap coefficient (10,000 resamples) and 95% confidence intervals between variables.

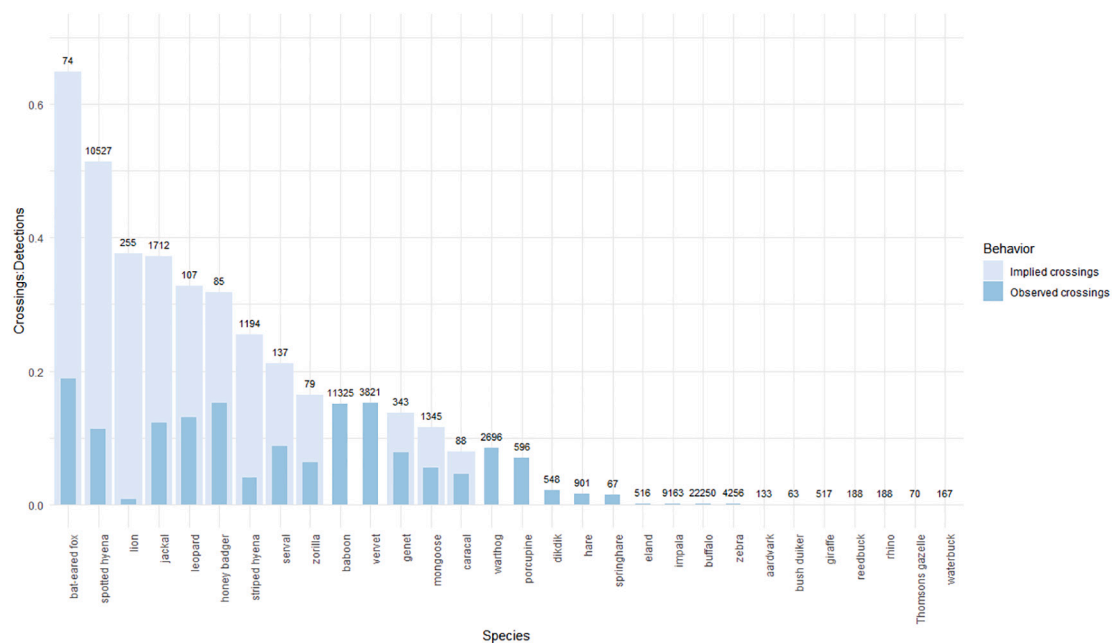
### 2.3.4. Fence maintenance and crossing behavior

The effects of fence maintenance were analyzed by subsetting the data from the 19 camera sites to equivalent periods before and after each maintenance event (these periods varied from 2 to 14 days before and after, dependent on camera and battery functionality), measuring daily confirmed and implied fence crossing behavior before and after maintenance, and conducting non-parametric  $\chi^2$  and Mann-Whitney *U* tests to determine differences in overall and site-level detections and crossings in the periods before and after maintenance.

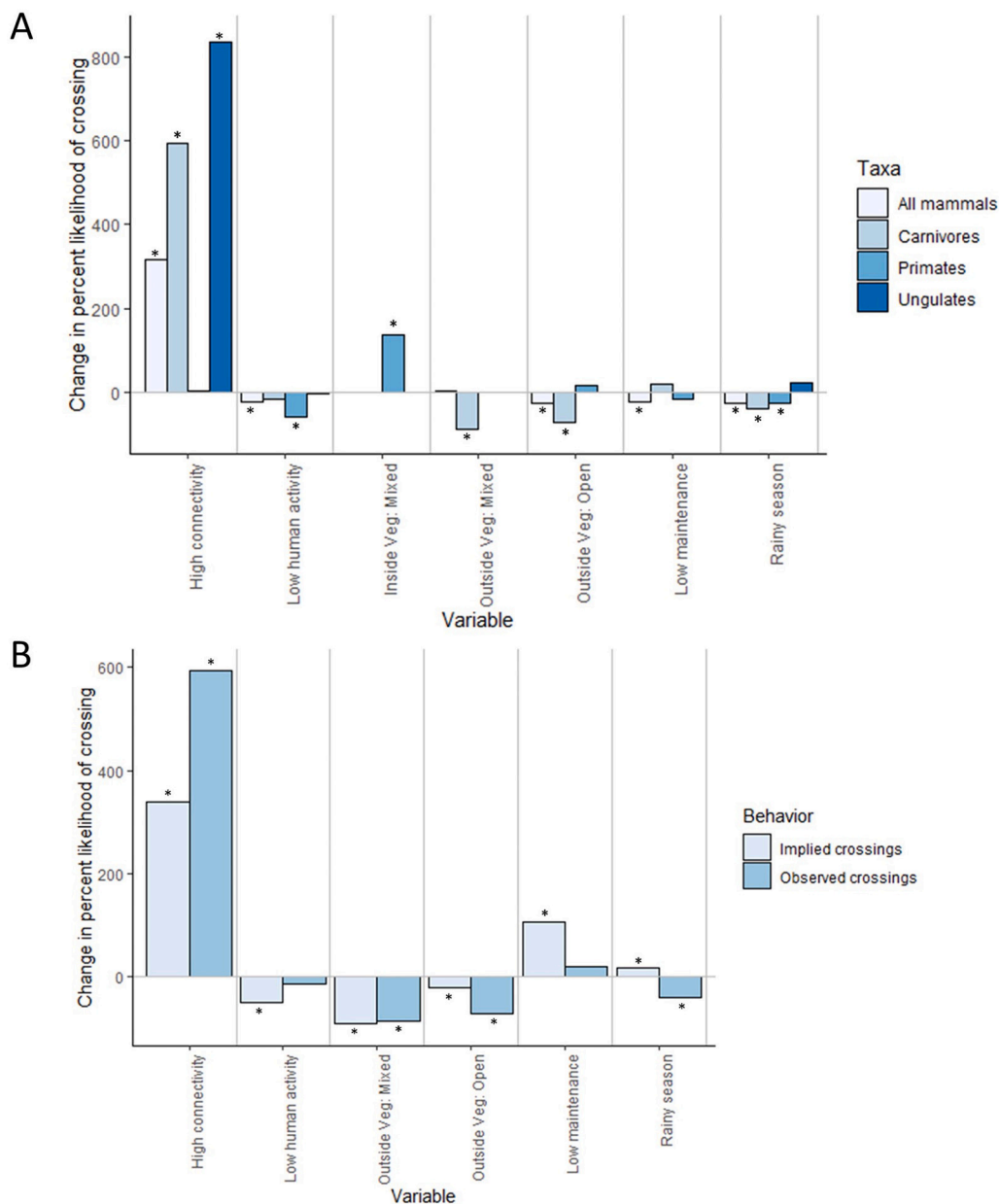
## 3. Results

### 3.1. Landscape predictors of fence-crossing

Following model selection, we identified three candidate models within 2 delta AIC of the top model, which included the following variables: NDVI at the fence, distance to rivers, distance to Lake Nakuru, slope, elevation, soil type, cost distance to the neighboring Soysambu Conservancy, and human population density (Suppl. Table 2). Soil type, NDVI, and distance to water were the strongest predictors. The weighted top model had a mean bootstrapped AUC of 0.73, indicating an acceptable, but not good or outstanding, diagnostic of the model.



**Fig. 2.** The ratio of observed and implied fence crossings to the total number of camera detections, in ranked order, labeled with total detections for each species. Light blue bars (shown for carnivores only) indicate cross:detection ratio where confirmed and implied cross behaviors have been combined, for carnivores only. Darker blue bars (shown for all species) indicate cross:detection ratio that includes only confirmed cross behaviors. Species with detection sample sizes lower than 60 have been excluded. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3.** (a) Percent likelihood ((odds ratio-1)\*100) of crossing after model averaging for each modeled group with binomial response variables *Cross Only* (“Cross to LNNP” and “Cross from LNNP” combined) and *No Cross* (“Vigilant”, “Grazing/Drinking”, and “Undefined”) and (b) percent likelihood of crossing for carnivores showing results where implied crossing behavior is also included in *Cross Only*. \* indicates variable significance ( $p < 0.001$ ). Inside and outside microhabitat vegetation both have a reference category of “dense”. Other reference categories, in order, are “high connectivity”, “high human activity”, “high maintenance”, “dry season”.

### 3.2. Assessment of crossing behavior

The 19 camera traps placed along the conservation fence recorded 65,560 photos of terrestrial mammals, with an average of 22.33 ( $\sigma = 12.8$ ) non-independent detections per trap night for all sites combined. Thirty-eight non-domestic mammal species (Suppl. Table 3) were detected (classified into ungulates: 12.9 detections/trap night on average; primates: 5.1 detections/trap night on average; carnivores: 5.2 detections/trap night on average; and aardvarks, hares, and rodents: 0.48 detections/trap night on average; Fig. 1b), and 27 of these species were recorded crossing the fence. Cameras at 17 of the 19 sites detected human-associated activity, such as people, fence maintenance, and livestock (1.5 detections per trap night on average) near the fence. Of the 11 species that did not cross the fence, most were ungulates (Suppl. Table 3). When including *implied cross*, the highest cross-to-detection ratio was seen in bat-eared fox (*Otocyon megalotis*) and spotted hyena, followed by all carnivore species except genet (*Genetta genetta*), mongoose (*Ichneumia albicauda* and *Herpestes ichneumon*), and caracal (*Caracal caracal*; Fig. 2). The average ratio of crossing to total detections

(Suppl. Table 4) across all species was 0.06 for confirmed crossings (*Cross*), and 0.14 when implied crossing behavior (*Implied cross*) was included for carnivores.

Models based on the camera data revealed that adjacency to the Soysambu Conservancy, body size, and vegetation inside the fence at the camera site were the strongest predictors of fence crossing in binomial logistic regressions (Fig. 3a, Suppl. Table 4). After testing for multicollinearity, the best model for all taxa combined (AUC = 0.834, *Cross*: *No Cross* = 3626:59365) retained all variables except fence maintenance. The strongest model for carnivores (AUC = 0.66, *Cross*:*No Cross* = 1232:13070) retained adjacency to Soysambu, body size, time of day, season, fence maintenance, and vegetation outside the fence at the camera site. The strongest carnivore model that included the *implied cross* detections retained human activity, body size, time of day, season, fence maintenance, and vegetation outside the fence at the camera site, and showed an improved model fit (AUC = 0.683, *Cross*:*No Cross* = 6130:8172). When including the *implied cross* behavior for carnivores, the effect of season flipped from negative to positive, the effects of maintenance increased, the effects of body size and vegetation outside

the fence crossing point were weaker, and the positive effect of adjacency nearly halved (Fig. 3b, Suppl. Table. 4). The strongest model for ungulates (AUC = 0.902, Cross:No Cross = 225:34850) retained body size, time of day, adjacency to Soysambu, and season. The strongest model for primates (AUC = 0.676, Cross:No Cross = 2112:9955) retained human activity, season, and vegetation inside and outside the fence at the crossing point. When combining all taxa, mammals were significantly less likely (OR = 0.749,  $p < 0.001$ ) to engage in crossing behavior at sites of low human activity than at sites of high human activity (Fig. 3, Suppl. Table 4).

### 3.3. Temporal behavior

From our logistic regression result, primates and ungulates were more likely to cross during the day, while carnivores were more likely to cross during the pre-dawn (Suppl. Table 4). Yet, at four sites that were directly adjacent to the conservancy with no road between the two protected areas (C2, C3, C4, C19), carnivores were less likely to cross at night (proportion of crossings = 0.6) than animals seen crossing at the adjacent sites (prop. of crossings at night = 0.87). Overlap analyses were pooled across the full study period after no seasonal differences in temporal behavior were found for any taxa. Overall, overlap analyses suggested that fence crossing behaviors coincided with other behaviors near fences for most species, yet there were notable exceptions for several species (Suppl. Fig. 2; Appendix S1). At sites of low human activity, carnivores showed more overall diurnal crossing behaviors than non-crossing behaviors (which were largely crepuscular and nocturnal); primates, meanwhile, exhibited marked noon-centered behaviors at sites of high human activity (Suppl. Fig. 3). Additionally, carnivores showed a trend of crossing out of LNNP in the evening, and crossing into LNNP in the morning (Suppl. Fig. 4).

### 3.4. Fence maintenance and crossing behavior

Camera data showed that 5 of the 19 sites experienced instances of fence maintenance (repair of wildlife crossing holes), for a total of 14 fence maintenance events. Fence maintenance events had no consistent impact on wildlife crossing ( $W = 115$ ,  $p = 0.43$ ) or overall detections ( $W = 102.5$ ,  $p = 0.84$ ) when combining all taxa. Both mammal detections and crossings increased in about half of post-maintenance events (Suppl. Fig. 5). Carnivores were the only group with a cumulative decrease in detections post-maintenance (before: 1162 detections, after: 614 detections), yet the decrease was not significant at the site level ( $W = 116$ ,  $p = 0.42$ ). Primates, rodents, and lagomorphs were cumulatively more likely to cross after fence maintenance events, while carnivores and ungulates were less likely to cross immediately post-maintenance (Pearson's  $\chi^2 = 26.67$ ,  $p < 0.001$ ).

## 4. Discussion

Our results revealed that the majority of mammal species detected by camera traps in Lake Nakuru National Park regularly crossed the park's boundary fence to and from the surrounding human-dominated landscapes. This suggests that many animals occurring within the park are subsidized by resources they acquire outside of its boundaries, or vice versa. Our methods offer a novel approach for quantifying wildlife responses to fencing, and our findings are consistent with surveys and frequent observations that report wildlife regularly passing in and out of the park (Kassilly et al., 2008, but see also Elliot et al., 2020). Our findings also echo indirect assessments that have shown fences are permeable to many wildlife species elsewhere in Africa (e.g., Pirie et al., 2017).

Of the 27 mammal species we recorded crossing the fence, carnivores and primates crossed most frequently, and crossing behaviors were strongly predicted by microhabitat at the crossing point, body size, and adjacency to the nearby Soysambu Conservancy. This result supports

other studies that have shown primates and carnivores frequently move over, under, and through fence lines (Pirie et al., 2017). Most ungulates, on the other hand, faced difficulties crossing. To our surprise, crossing frequency was unaffected by temporal patterns of fence maintenance. Below, we discuss the importance of these findings for animal behavior, conflict, connectivity, and conservation planning around fences.

### 4.1. Landscape predictors of fence crossing

In our landscape-scale study of predictors of fence-crossing locations, our analysis yielded only a moderately strong model, with soil type and water proximity among the strongest predictors. Having a model with only a moderately strong fit suggests that the factors affecting wildlife crossing sites varied sufficiently by species, space, and time to inhibit strong overarching predictions. Nevertheless, we conclude from this model that fences placed in soil types that are amenable to digging will require constant investment in maintenance (Kesch et al., 2014). Even if managers install and bury mesh or other specialized material to inhibit digging, maintenance will still be required (Hoare, 1992; Gusset et al., 2008). Finally, due to their topography, rivers and smaller waterways provide easy crossing points under fences for animals, even for very large-bodied species such as Cape buffalo (*Syncerus caffer*). In our study area, as for many others (e.g., Jori et al., 2011), fences placed along or crossing waterways were prone to degradation due to the physical disturbance and erosion caused by running water in the rainy season, which gave way in the dry season to sunken riverbeds or small rivulet-caused dips that served as wildlife highways beneath fences. Soil type was our variable most associated with erosion-potential, and was one of the strongest predictors of fence gaps in our model. NDVI, meanwhile, may have factored strongly in our model due to certain species using the fence for foraging or ambush (Dupuis-Desormeaux et al., 2016). Future studies may have more success in identifying landscape correlates of crossing points by focusing on crossings observed in a single season or by a targeted subset of species rather than combining all points that showed evidence of crossing by any species.

The vegetative cover at crossing point factored strongly in the best models for primates, carnivores, and all taxa combined, indicating that microhabitat was an important component of whether and where an animal chose to cross the fence. Carnivores and all taxa combined preferred crossing points with dense vegetation outside of the park (as opposed to open or mixed), and primates preferred crossing points with mixed vegetation inside of the park (as opposed to open or dense). This could be because wildlife prefer predictable cover when crossing out of the park into a risky landscape, while they may prefer not to cross into dense cover within the park where there is more risk of ambush by wild predators (see Boinski et al., 2003; Stears and Shrader, 2015). The act of crossing underneath the fence wire inherently requires at a minimum a brief moment of vulnerability, including the hazard of being stuck in the wire, and wildlife may be choosing microhabitat to mediate their risks during the crossing moment. Due to the likely importance of immediate cover, managers seeking to maximize connectivity by opening up portions of the fence may consider locating several small but safe microhabitat crossings rather than focusing money and effort on a few longer stretches of fence that aim toward broader landscape variables.

### 4.2. Wildlife crossing by taxa

Detections from our 19 camera traps revealed that nearly all of the larger (i.e.,  $> 1$  kg) mammal species known to occur in the national park were seen at the fence line, and most of the species that approached the fence also crossed. Species that did not cross the fence nonetheless exhibited marked interest in gaps and holes (i.e., were recorded pointedly approaching gaps), but apparently could not easily pass through them. This hypothesis is supported by other studies that have shown wildlife may spend considerable time seeking to breach fences (Connolly et al., 2009) even if they are likely to be unsuccessful due to body size

and lack of agility (Mbaiwa and Mbaiwa, 2006).

Our use of cameras and a precise classification scheme for fence-specific behaviors allowed us to build an understanding of detailed movements and behavioral patterns of select species around the fence line. For example, many carnivores recorded in our study appeared to exit the park during the evening and returned in the morning. The change in model results when including *implied cross* for carnivores also suggests that fine-scale timing of fence crossings (i.e. hesitancy) may be influenced by ecological and anthropogenic variables. Though carnivores may be able to adapt to and even thrive in human-dominated areas (Chapron et al., 2014), they may need nearby protected areas to serve as a population source (Lamb et al., 2020) or as a temporal refuge from human influences and persecution (Gaynor et al., 2018). The fact that carnivores appear to regularly utilize areas shared by local human communities emphasizes the necessity of community engagement, education, and interventions aside from fences to ensure their persistence, as has also been noted in areas surrounding unfenced protected areas (Dickman et al., 2014; van Eeden et al., 2018). Finally, the ease with which primates crossed the electrified fence, particularly baboons (*Papio anubis*) and vervet monkeys (*Chlorocebus pygerythrus*), both by digging underneath and climbing over and through, raises the question of whether restricting their movements is ever a realistic goal of conservation fencing. Our study is far from alone in reporting such a result; in fact, in their survey of the relevant literature, Junker et al. (2019), could find no evidence of fences containing baboons (*Papio* sp.) or other cercopithecine monkeys.

#### 4.3. Anthropogenic and ecological factors influencing crossing behavior

Within the 19 camera trap sites, mammals showed more likelihood of exhibiting crossing behavior at sites that were adjacent to Soysambu Conservancy, but also preferred to cross (rather than exhibiting other behaviors) at sites with high human activity. Adjacency to Soysambu appeared to be one of the strongest drivers of crossing behavior within the 19 sites, yet the pattern of crossing preference at sites of high human activity held true even for camera trap sites that were not adjacent to the conservancy. Analysis of the camera data revealed no strong overall predictors of crossing behavior at specific sites for all primates or all carnivores. Ungulates, however, showed a strong relative increase in crossing behavior at camera trap sites adjacent to the neighboring Soysambu Conservancy, and this appeared to drive the all-taxa model. This pattern matches our prediction because the conservancy is a large tract of protected habitat that might also serve as a corridor to other protected lands to the southeast. Furthermore, while most carnivores and primates in LNNP are capable of tolerating and utilizing adjacent human-dominated areas (Fehlmann et al., 2017; Pirie et al., 2017), attractive surrounding habitat for ungulate species may be limited to the conservancy. Future studies in this region and elsewhere should further assess ecological and anthropogenic drivers of fence crossing through deployment of additional cameras for a longer study period.

#### 4.4. Temporality of wildlife crossing

Our results showed contrasting temporal trends in fence crossing behavior. At a seasonal scale, primates and carnivores were less likely to cross in and out of the park in the rainy season than in the dry season, contrary to what we expected given that animals in arid landscapes tend to move farther in the rainy season when they are less restricted by access to water (Kesch et al., 2014; Koziarski et al., 2016). It is possible that better foraging opportunities in the park during the rainy season make staying in the park a more attractive option at this time, but additional research is required to test this idea.

Surprisingly, primates and ungulates appeared to be most active in the middle of the day at sites with high human activity, for crossing and other behavior. This is in contrast to carnivores in this study, as well as other studies that have found human activity pushes wildlife to be more

nocturnal (Gaynor et al., 2018). It is likely that human activity, which was highest in the early morning and early evening at these camera sites, was pushing primate and ungulate activity into the heat of the day. This might have negative consequences for energetics of the affected species, since crossing a fence is inherently risky, but crossing at noon on the equator is likely much more energetically costly than doing so at other times of the day (see McFarland et al., 2019). Additionally, many primate and ungulate species appeared to rely on a thin line of habitat along the inner boundary of the park for grazing and other needs, and human activity outside of the fence impacted the temporality of their non-crossing behaviors even within the park. Human activity thus seemed to attract crossings spatially but altered crossings and other behaviors temporally. Designated buffer zones of wildlife habitat and vegetation around fenced protected areas, rather than allowing human development to directly abut the fence, may allow wildlife to maintain their normal temporal activity without being impacted or influenced by people.

#### 4.5. Fence maintenance

We found little evidence for the effectiveness of fence maintenance in stopping or even slowing wildlife crossings. After maintenance occurred, wildlife tended to resume crossing at the same site within 24 h, and in some places, crossings increased in the period following maintenance. The small number of maintenance events and maintained sites in our study likely contributed to the absence of clear patterns in our results. Maintenance events were intermittent and without predictability, and there were relatively few maintenance events (14) over the course of the study, leading to a limited dataset from which to draw conclusions about maintenance effects. However, it is clear from our camera detections that wildlife exhibited strong fidelity for crossing points, as shown at another site in Kenya (Dupuis-Desormeaux et al., 2018). In our study, digging species, such as spotted hyena, were commonly seen undoing maintenance efforts (typically by moving stones placed in fence gaps) within hours of their execution. This suggests that at least some species would rather exert energy breaking through or digging in a well-used crossing site than creating a new hole elsewhere, a concern that has been raised in the past (Hoare, 1992) but not quantified until now. The tenacity of wildlife seeking to cross a given fence segment, the well-noted challenges of supporting regular fence maintenance efforts (Pekor et al., 2019), and the lack of a clear effect of maintenance in reducing wildlife crossing suggest protected area managers should carefully consider the opportunity costs of erecting new fences (Durant et al., 2015). As has been argued elsewhere (e.g., Creel et al., 2013), conservation funding targeted for fencing may have greater positive impact when applied instead to manage buffer areas and engage local communities to foster human-wildlife coexistence (Dickman et al., 2014).

#### 4.6. Measuring the effectiveness of conservation fencing

Any rigorous study of conservation fencing will likely show a mix of successes (e.g., containment of focal species, reduction of human activity) and failures (e.g., unabated crop raiding, negative impacts on non-focal species); thus, perhaps the fairest assessment of a fence's efficacy is a comparison of outcomes in relation to the stated goals of fence construction (McInturff et al., 2020). However, identifying the exact goals of fencing is often difficult, particularly when fences have been in place for decades. Several justifications have been put forth for the construction and maintenance of the perimeter fence at LNNP. One original goal of the fence was to prevent rhinoceros and Cape buffalo from entering community lands, which it appears to have largely achieved, with the exception of one consistent buffalo crossing point. Our findings suggest other large ungulates, such as eland (*Taurotragus oryx*) and zebra, are also mostly contained within the park's fence, though they too were recorded crossing on several occasions. A second stated



purpose of the fence was to prevent carnivore-livestock and primate-crop interactions (Kassily et al., 2008). Our results suggest the fence is not effectively performing this function. Baboons and vervet monkeys cross the fence each day and baboons were regularly reported crop-raiding in nearby farms (Kenya Wildlife Service, pers. comm.). Furthermore, we documented that every large carnivore species in LNNP crossed the perimeter fence. Regardless of the biological realities, nearby human communities perceive the fence as being effective at containing wildlife (C. Wilkinson, unpub. data), and perceptions can be a key component to alleviating human-wildlife conflict (Dickman et al., 2014; Ohrens et al., 2019). The efficacy of the fence in achieving the goal that most directly inspired its original creation at LNNP, to prevent poaching of rhinoceros (Lever, 1990), was not analyzed in this study and would be difficult to decouple from the effects of other anti-poaching activities of the Kenya Wildlife Service.

## 5. Conclusions

Contrary to previous assertions (Kassily et al., 2008; Elliot et al., 2020), we found that a diverse array of wildlife readily found their way in and out of Lake Nakuru National Park. Some may interpret this finding as suggesting fences have fewer ecological impacts than is often claimed, however, it may also undermine justifications for investment in fences in the first place. Ultimately, measures of success and failure with regard to conservation fencing will be context-dependent and only relevant where the intended goals of fencing are clearly articulated (e.g., written into management plans) and regularly revisited over time. The outlined goals for a particular conservation fence should identify and differentiate between species and processes within an ecosystem the fence is intended to contain from those for which ongoing permeability or connectivity is desired. Such forward-thinking and inclusive planning will require a detailed understanding of the responses of a diversity of species to different types of conservation fences over space and time. Ideally, an integration of ecological and economic costs and benefits of conservation fences, as well as analyses of potential alternatives to fences such as community outreach or the creation of buffer areas, will prevent short-sighted, short-lived, and ineffective fencing efforts.

## CRedit authorship contribution statement

**Christine E. Wilkinson:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Funding acquisition, Project administration. **Alex McInturff:** Methodology, Formal analysis, Writing – review & editing, Visualization. **Maggi Kelly:** Conceptualization, Writing – review & editing, Visualization. **Justin S. Brashares:** Conceptualization, Methodology, Validation, Writing – review & editing.

## Declaration of competing interest

The authors have no conflict of interests to declare.

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## Appendix A. Supplementary data

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## References

- Boinski, S., Kauffman, L., Westoll, A., Stickler, C.M., Cropp, S., Ehmke, E., 2003. Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*). *Behaviour*, 140, 1421–1467.
- Burnham, K.P., Anderson, D.R., 2002. *Model selection and inference: A practical information-theoretic approach*, 2<sup>nd</sup> Ed. Springer.
- Cavalcanti, S.M.C., Crawshaw, P.G., Tortato, F.R., 2012. Use of electric fencing and associated measures as deterrents to jaguar predation on cattle in the Pantanal of Brazil. In: Somers, M.J., Hayward, M.W. (Eds.), *Fencing for Conservation: Restriction of Evolutionary Potential or a Riposte to Threatening Processes?* Springer Science + Business Media, Berlin, Germany, pp. 295–310.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andren, H., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346, 1517–1519.
- Connolly, T.A., Day, T.D., King, C.M., 2009. Estimating the potential for reinvasion by mammalian pests through pest-exclusion fencing. *Wildl. Res.* 36, 410–421.
- Core Team, R., 2018. R: A language and environment for statistical computing. In: R Foundation for Statistical Computing. Austria. URL, Vienna. <https://www.R-project.org/>.
- Cozzi, G., Broekhuis, F., McNutt, J.M., Schmid, B., 2013. Comparison of the effects of artificial and natural barriers on large African carnivores: implications for interspecific relationships and connectivity. *J. Anim. Ecol.* 82, 707–715.
- Creel, S., Becker, M.S., Durant, S.M., M'Soka, J., Matandiko, W., Dickman, A.J., Zimmermann, A., 2013. Conserving large populations of lions - the argument for fences has holes. *Ecol. Lett.* 16, 1413–e3.
- Dickman, A., Hazzah, L., Carbone, C., Durant, S.M., 2014. Carnivores, culture and 'contagious conflict': multiple factors influence perceived problems with carnivores in Tanzania's Ruaha landscape. *Biol. Conserv.* 178, 19–27.
- Dupuis-Desormeaux, M., Davidson, Z., Pratt, L., Mwololo, MacDonald S.E., 2016. Testing the effects of perimeter fencing and elephant enclosures on lion predation patterns in a Kenyan wildlife conservancy. *PeerJ* 4, e1681.
- Dupuis-Desormeaux, M., Kaaria, T.M., Mwololo, M., Davidson, Z., MacDonald, S.E., 2018. A ghost fence-gap: surprising wildlife usage of an obsolete fence crossing. *PeerJ* 6, e5950.
- Durant, S.M., Becker, M.S., Creel, S., Bashir, S., Dickman, A.J., Beudels-Jamar, R.C., Pettorelli, N., 2015. Developing fencing policies for dryland ecosystems. *J. Appl. Ecol.* 52, 544–551.
- van Eeden, L.M., Crowther, M.S., Dickman, C.R., Macdonald, D.W., Ripple, W.J., Ritchie, E.G., Newsome, T.M., 2018. Managing conflict between large carnivores and livestock. *Conserv. Biol.* 32, 26–34.
- Elliot, N.B., Bett, A., Chege, M., Sankan, K., de Souza, N., Kariuki, L., Gopalaswamy, A. M., 2020. The importance of reliable monitoring methods for the management of small, isolated populations. *Conservation Science and Practice* 2, e217.
- Fehlmann, G., O'Riain, J., Kerr-Smith, C., Hailes, S., Luckman, A., Shepard, E.L.C., King, A.J., 2017. Extreme behavioural shifts by baboons exploiting risky, resource-rich, human-modified environments. *Nat. Sci. Rep.* 7, 15057.
- Ferguson, K., Hanks, J., 2012. The effects of protected area and veterinary fencing on wildlife conservation in South Africa. *Parks* 18, 49–58.
- Gaynor, K.M., Hohnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360, 1232–1235.
- Gusset, M., Ryan, S.J., Hofmeyr, M., van Dyk, G., Davies-Mostert, H.T., Graf, J.A., Somers, M.J., 2008. Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa. *J. Appl. Ecol.* 45, 100–108.
- Hayward, M.W., Kerley, G.I.H., 2009. Fencing for conservation: restriction of evolutionary potential or a riposte to threatening process? *Biol. Conserv.* 142, 1–13.
- Hoare, R.E., 1992. Present and future use of fencing in the management of larger African mammals. *Environ. Conserv.* 19, 160–164.
- Hoole, A., Berkes, F., 2010. Breaking down fences: recoupling social-ecological systems for biodiversity conservation in Namibia. *Geoforum* 41, 304–317.
- Hosmer, D.W., Lemeshow, S. (Eds.), 2000. *Applied Logistic Regression*. John Wiley and Sons, New York, New York, USA.
- Jakes, A.F., Jones, P.F., Paige, L.C., Seidler, R.G., Huijser, M.P., 2018. A fence runs through it: a call for greater attention to the influence of fences on wildlife and ecosystems. *Biol. Conserv.* 227, 310–318.
- Jori, F., Brahmabhatt, D., Fosgate, G.T., Thompson, P.N., Budke, C., Ward, M.P., Ferguson, K., Gummow, B., 2011. A questionnaire-based evaluation of the veterinary cordon fence separating wildlife and livestock along the boundary or the Kruger National Park, South Africa. *Preventive Veterinary Medicine* 100, 210–220.
- Junker, J., Kuhl, H.S., Orth, L., Smith, R.K., Petrovan, S.O., Sutherland, W.J., 2019. Primate conservation. In: Sutherland, W.J., Dicks, L.V., Ockendon, N., Petrovan, S. O., Smith, R.K. (Eds.), *What Works in Conservation 2019*. Open Book Publishers, Cambridge, UK, pp. 439–491.
- Karhu, R.R., Anderson, S.H., 2006. The effect of high-tensile electric fence designs on big-game and livestock movements. *Wildl. Soc. Bull.* 34, 293–299.
- Kassily, F., Tsingalia, H.M., Gossow, H., 2008. Mitigating human-wildlife conflicts through wildlife fencing: a Kenyan case study. *Wildl. Biol. Pract.* 4, 30–38.

- Kesch, K., Bauer, D.T., Loveridge, A.J., 2014. Undermining game fences: who is digging holes in Kalahari sands? *Afr. J. Ecol.* 52, 144–150.
- Koziarski, A., Kissui, B., Kiffner, C., 2016. Patterns and correlates of perceived conflict between humans and large carnivores in Northern Tanzania. *Biol. Conserv.* 199, 41–50.
- Lamb, C.T., Ford, A.T., McLellan, B.N., Proctor, M.F., Mowat, G., Ciarniello, L., Boutin, S., 2020. The ecology of human-carnivore coexistence. *PNAS* 117, 17876–17883.
- Lever, C., 1990. Lake Nakuru black rhinoceros sanctuary. *Oryx* 24, 90–94.
- Massey, A.L., King, A.A., Foufopoulos, F., 2014. Fencing protected areas: a long term assessment of the effects of reserve establishment and fencing on African mammalian diversity. *Biol. Conserv.* 176, 162–171.
- Mbaiwa, J.E., Mbaiwa, O.I., 2006. The effects of veterinary fences on wildlife populations in Okavango Delta, Botswana. *International Journal of Wilderness* 12, 17–41.
- McFarland, R., Barrett, L., Costello, M., Fuller, A., Hetem, R.S., Maloney, S.K., Henzi, P. S., 2019. Keeping cool in the heat: behavioral thermoregulation and body temperature patterns in wild vervet monkeys. *Am. J. Phys. Anthropol.* 171, 407–418.
- McInturff, A., Xu, W., Wilkinson, C.E., Dejid, N., Brashares, J.S., 2020. Fence ecology: frameworks for understanding the ecological effects of fences. *BioScience* 70, 971–985.
- McKillop, I.G., Sibly, R.M., 1988. Animal behavior at electric fences and the implications for management. *Mammal Rev.* 18, 91–103.
- Meredith, M., Ridout, M., 2014. **overlap: Estimates of coefficient of overlapping for animal activity patterns. R package version 0.2.3.**
- Nickel, B.A., Suraci, J.P., Allen, M.L., Wilmers, C.C., 2020. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biol. Conserv.* 241, 108383.
- Ogutu, J.O., Kuloba, B., Piepho, H., Kanga, E., 2017. Wildlife population dynamics in human-dominated landscapes under community-based conservation: the example of Nakuru Wildlife Conservancy, Kenya. *PLoS One* 12, e0169730.
- Ohrens, O., Santiago-Ávila, F.J., Treves, A., 2019. The twin challenges of preventing real and perceived threats to human interests. *Human–Wildlife Interactions: Turning Conflict into Coexistence* 23, 242.
- Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M., Polasky, S., 2013. Conserving large carnivores: dollars and fence. *Ecol. Lett.* 16, 635–641.
- Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* 133, 225–245.
- Pekor, A., Miller, J.R.B., Flyman, M.V., Kasiki, S., Kesch, M.K., Miller, S.M., Lindsey, P.A., 2019. Fencing Africa's protected areas: costs, benefits, and management issues. *Biol. Conserv.* 229, 67–75.
- Pirie, T.J., Thomas, R.L., Fellowes, M.D.E., 2017. Game fence presence and permeability influences the local movement and distribution of South African mammals. *Afr. Zool.* 52, 212–227.
- Rey, A., Novaro, A., Guichon, M.L., 2012. Guanaco (*Lama guanicoe*) mortality by entanglement in wire fences. *J. Nat. Conserv.* 20, 280–283.
- Sawyer, H., Lambert, M.S., Merkle, J.A., 2020. Migratory disturbance thresholds with mule deer and energy development. *J. Wildl. Manag.* 84, 930–937.
- Shamoon, H., Maor, R., Saltz, D., Dayan, T., 2018. Increased mammal nocturnality in agricultural landscapes results in fragmentation due to cascading effects. *Biol. Conserv.* 226, 32–41.
- Stander, P.E., 1990. A suggested management strategy or stock-raiding lions in Namibia. *S. Afr. J. Wildl. Res.* 20, 37–43.
- Stears, K., Shrader, A.M., 2015. Increases in food availability can tempt oribi antelope into taking greater risks at both large and small spatial scales. *Anim. Behav.* 108, 155–164.
- Vanak, A.T., Thaker, M., Slotow, R., 2010. Do fences create edge effects on the movement patterns of highly mobile mega-herbivore? *Biol. Conserv.* 143, 2631–2637.
- Wang, Y., Smith, J.A., Wilmers, C.C., 2017. Residential development alters behavior, movement, and energetics in an apex predator, the puma. *PLoS One* 12, e0184687.
- Woodroffe, R., Hedges, S., Durant, S.M., 2014. To fence or not to fence. *Science* 344, 46–48.