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Human-wildlife conflict in Rwanda: Linking ecoregion, changing conservation status and the local communities' perception

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ABSTRACT

For densely populated and low-income countries, human-wildlife competition (better known as human wildlife conflict; HWC) is an increasing challenge to both biodiversity conservation and local communities' wellbeing. This study examines HWC (crop raiding and livestock depredation) in Rwanda — one of the most densely populated countries in the world. Specifically, two socio-ecological contexts were compared: i) two agriculturist communities dwelling around the isolated forest fragments of Gishwati and Mukura Forest, i.e., protected, afro-montane rain forest patches in the west of Rwanda, and ii) a savannah dwelling pastoralist community in the Eastern savannah, a semi-arid rangeland in the east. We related results from camera trapping to those obtained from semi-structured interview surveys of local communities to assess wildlife abundance and the reliability of wildlife damage compensation claims. We investigate the predominant nuisance species at each study site, the type and amount of crop/livestock damage caused, the communities' tolerance towards such damage, and the different levels of response to the impairment. In the Eastern savannah and around Mukura Forest, relative species abundance obtained from interview surveys corresponded to that found using camera traps, but strongly deviated near Gishwati Forest, where farmers reported significantly higher crop losses than near Mukura Forest or in the Eastern savannah. Main nuisance species around Gishwati and Mukura Forest were primates, mainly targeting maize, while in the Eastern savannah rodents and primates caused most damage, mainly on beans. Livestock (chicken) losses in the Eastern savannah region were caused by mongooses, around Gishwati and Mukura Forest by genets. Communities near Gishwati were significantly less tolerant towards wildlife damage than near Mukura Forest or in the Eastern savannah, suggesting that ecoregion or a changing conservation status had no effect on HWC. Accordingly, people around Gishwati used stronger retaliative responses to repel wildlife than near Mukura or in the Eastern savannah.

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1. Introduction

An ever-increasing encroachment of human activities into previously undisturbed areas and a growing competition for limited natural resources (space, food, and livelihood) lead to increasing human–wildlife competition and an aggravated human-wildlife coexistence (hereafter referred to as human wildlife conflict, HWC; Madden, 2004; Peterson et al., 2010; Frank and Glikman, 2019) in many regions of the world. HWC appears in the context of a dynamic, socio-ecological system in which humans and nature act as opposing poles (Mosimane et al., 2014). HWC refers hereby to negative interactions between humans and wild animals, with undesirable consequences for both, people and their resources on the one hand, and wildlife and its habitats on the other (Treves et al., 2006). If not mitigated, HWC can lead to retaliations and a generally negative attitude towards nature, making it a major obstacle for wildlife conservation; Woodroffe et al., (2005); Frank et al., (2019)). HWC commonly manifests as crop raiding (S. K. Mc Guinness, 2016) or livestock depredation (Michalski et al., 2006; Kuiper et al., 2022), human casualties (Acharya et al., 2016; Gulati et al., 2021), competition between wild herbivores and domestic livestock (Mekonen, 2020; Marino and Rodríguez, 2022) or the transmission of zoonotic diseases (Standley et al., 2012), all of which can cause substantial damage and induce significant economic—and

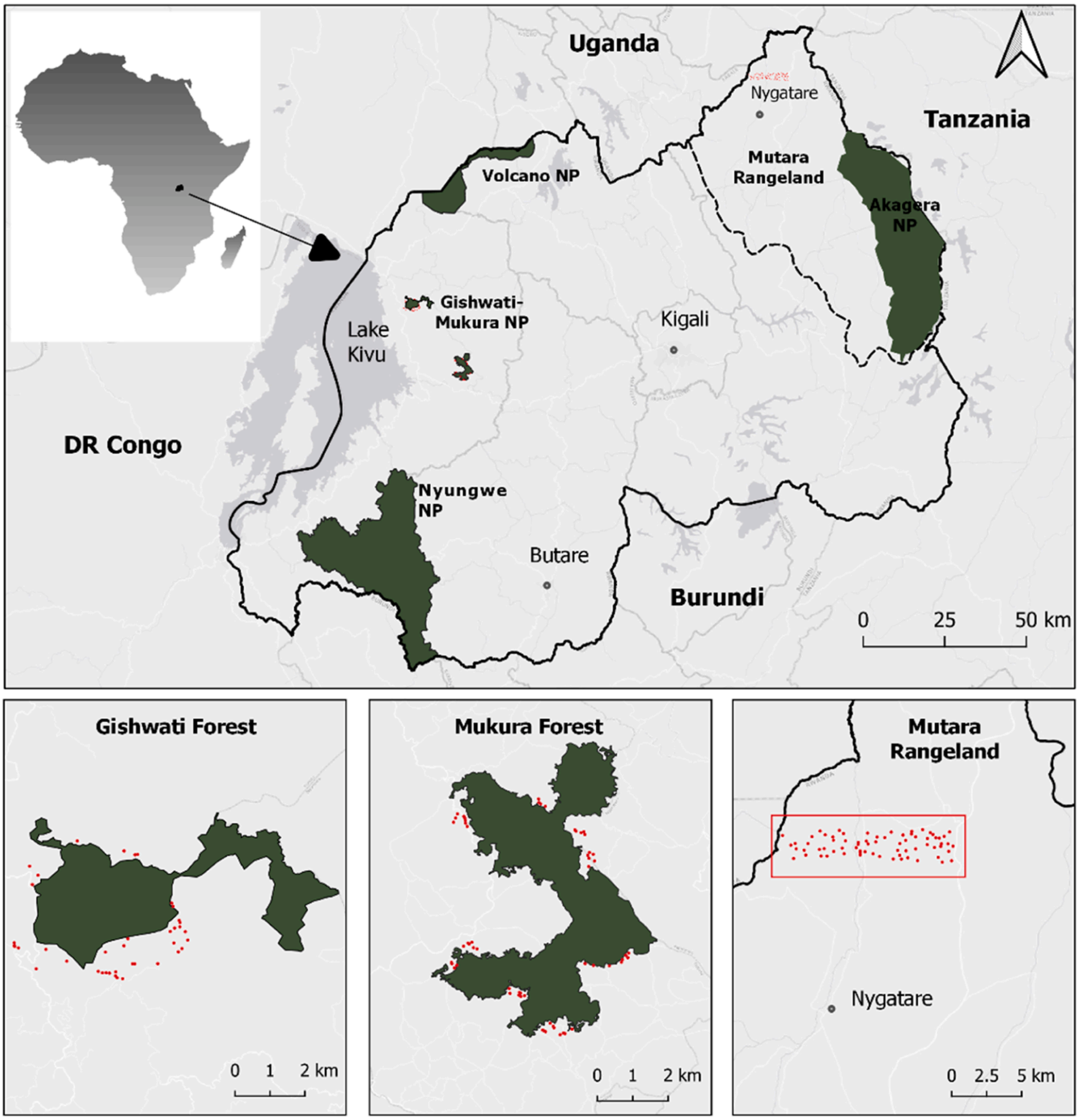

Fig. 1. The location of Rwanda in Africa (inlet) and the expansion of national parks in Rwanda (green). Bottom row shows study areas, i.e., Gishwati Forest (left), Mukura Forest (centre) and the Eastern savannah (right). Interview locations are depicted by red dots. Camera trapping locations were located inside Gishwati and Mukura Forest (see Sun et al., 2022) and within the interview area of the Eastern savannah (red rectangle).

personal—losses to local communities (Lamarque, 2009; Nyhus, 2016; Benjamin-Fink, 2019; Dunnink et al., 2020).

HWC is particularly evident in rural Africa where wildlife habitat often intermingles with human settlements, pasture for livestock, or agriculture (Lamarque, 2009; Benjamin-Fink, 2019), and where human activities frequently reach well beyond the borders of protected areas, making HWC inevitable (Mosimane et al., 2014; Stoldt et al., 2020). Rwanda is a small land-locked African country that has seen a doubling of its human population size in the past three decades, reaching an average density of 503 inhabitants/km^2 in 2022 (NISR, 2023a, 2023b). Currently, about 70 % of Rwandans work in the agricultural sector, which contributes to one third of the country's gross domestic product (FAO, Food and Agriculture Organization of the United Nations, 2023). Tea and coffee are the main cash crops for export, while plantains, ground nuts, Irish and sweet potatoes, maize, and beans are common subsistence crops (FAO, Food and Agriculture Organization of the United Nations, 2023). Against this background, HWC is a widespread challenge in Rwanda (Kanyamibwa, 2013).

Compared to neighbouring countries such as Tanzania, Uganda or Kenya, studies on HWC in Rwanda are scarce (Mnzava and Sirima, 2022). In Rwanda, HWC occurs mainly in the mountainous forest regions of the west (i.e., Volcanoes National Park [NP]: Plumptre, (2002); Kalpers et al., (2010); Mc Guinness, (2014); Cyubahiro et al., 2015; Bikorimana and Mupenzi, (2023); Ndayishimiye et al., 2023 and Gishwati-Mukura NP: (S. Mc Guinness and Taylor, 2014; Tuyisingize et al., 2022), but also in the Eastern savannah region (REMA, Rwanda Environment Management Authority, 2015), i.e., the degazetted parts of Mutara Game Reserve and Akagera NP, today administratively merged as Gatsibo and Nyagatare District. In the past, crop raiding around Volcanoes NP was largely accredited to African buffalo (*Synceros caffer,* Cyubahiro et al., 2015) and the endangered golden monkey (*Cercopithecus mitis kandti;* Ndayishimiye et al., 2023), while HWC in the Eastern savannah was attributed to competition between wild herbivores and domestic livestock (Bariyanga et al., 2016; Banamwana et al., 2021). In the forest biome, HWC was mainly perceived to influence food security, whereas concerns among pastoralists revolved primarily around human health (Udahemuka et al., 2022; Sabuhoro et al., 2023).

In this study, we attempted to link ecoregion, changing conservation status and the local communities' perception to better understand HWC (i.e., crop raiding and livestock depredation) in Rwanda. Specifically, we selected two socio-ecological contexts, i.e., the local pastoralist community inhabiting the Eastern savannah, a semi-arid rangeland where the conservation status negatively changed from national park (game reserve) to pastoral rangeland (Kanyamibwa, 1998), and two local forest communities living adjacent to Gishwati and Mukura Forest where the conservation status positively changed from forest reserve to national park and UNESCO biosphere reserve (Kisioh, 2015; Ordway, 2015; RDB, 2020).

Numerous studies have focused on the comparison of two methods to establish relative species abundance rates whereby one was the use of local ecological knowledge (Anadón et al., 2009; Pérez-Peña et al., 2012; Camino et al., 2020; Madsen et al., 2020; Braga-Pereira et al., 2022). In a first step, we therefore compared ecological data on wildlife obtained from camera trapping with the observations of the respective community. Local communities have accumulated a long-standing, intimate ecological knowledge of their environment (local ecological knowledge *sensu* Joa et al., 2018), and their expertise is increasingly applied in conservation and ecosystem management (Berkes et al., 2000; Gilchrist et al., 2005; Brook and McLachlan, 2008; Davis and Ruddle, 2010). On the one hand, the community's ecological knowledge could be used by the Rwanda Development Board (RDB) and other institutions in charge of wildlife management, namely national park or local authorities (Republic of Rwanda, 2011; Ministry of Trade and Industry, 2013) to estimate the status of wildlife in, and—more importantly—outside protected areas. On the other hand, these governmental institutions could use our approach to at least broadly gauge the reliability of community claims for wildlife damage compensation (Ogra and Badola, 2008; Songhurst, 2017). Secondly, we described and quantified the damage of mammalian wildlife on crops and livestock. Here we compared damage occurrence and the severity of HWC between savannah and forest biome and between areas of changed conservation status. Finally, we asked whether the local community's tolerance (or intolerance) towards wildlife damage—and the

Table 1
Main nuisance species and the damage they caused (percentage crop or livestock losses) in the Eastern savannah and near Gishwati and Mukura Forrest.

Study site		Beans	Maize	Sweet potatoes	Ground nuts	Sorghum	Cassava	Irish potatoes	Peas	Chicken	Honey
Eastern savannah	Incidence rate (%)	50.0 %	27.5 %	6.9 %	20.6 %	2.9 %	5.9 %	-	-	36.3 %	-
	Main nuisance species	small mongooses and impala	vervet monkey, hare, baboon	-	rodents, small mongooses	-	-	-	-	large mongooses	-
Gishwati Forest	Incidence rate (%)	50.0 %	98.3 %	28.3 %	-	-	-	16.7 %	13.3 %	23.3 %	6.7 %
	Main nuisance species	chimpanzee, L'hoest & golden monkey, tree squirrels	chimpanzee, L'hoest & golden monkey, jackal	chimpanzee, L'hoest & golden monkey	-	-	-	chimpanzee, L'hoest & golden monkey	chimpanzee, L'hoest & golden monkey, tree squirrel	genet	chimpanzee
Mukura Forest	Incidence rate (%)	20.7 %	96.6 %	-	-	-	-	3.5 %	-	31.0 %	-
	Main nuisance species	L'hoest monkey, giant-poached rat	L'hoest monkey, jackal	-	-	-	-	L'hoest monkey	-	genet	-

respective responses—differed between socio-ecological contexts.

2. Materials & methods

2.1. Study area

Our study area comprised three study sites situated within two socio-ecological contexts (see above). One study site was located in the northern part of the Eastern savannah (1°10'S, 30°20'E, 1400 m asl; Fig. 1), i.e. the part of the rangeland that was proclaimed as the Mutara Game Reserve in 1935, but opened for livestock grazing in 1971 and finally degazetted in 1997 (Vande weghe, 1990). The Eastern savannah is part of the Akagera ecosystem, a savannah roughly extending between the western shores of Lake Victoria and the forests of the Congo-Nile divide (Kindt et al., 2014). The eastern savannah is mainly inhabited by pastoralist communities, with an average population density of 373 inhabitants/km^2, substantially lower than the national average (NISR, 2023a, 2023b). The natural vegetation is heavily degraded (Wronski et al., 2017), but still comprises the indigenous plant community of the Akagera ecosystem (native grass species with *Acacia* trees and thicket clumps; Vande weghe, 1990; Kindt et al., 2014). Land use in the Eastern savannah was dominated by traditional pastoralism (mainly Ankole cattle), but gradually gives way to intensification by means of confined grazing (zero-grazing, cut-and-carry), silvopastoral land and subsistence agriculture (MINAGRI, 2018). About 50 large mammal species were historically reported from the Eastern savannah, including several antelopes, plains zebra (*Equus quagga*), black rhino (*Diceros bicornis*), as well as their predators. Only the smaller species (e.g., small antelopes, genets, mongooses, jackals and baboons) have persisted until today (Apio et al., 2015; Sun et al., 2018; this study).

The other two study sites were located around Gishwati Forest (1°49 S, 29°22 E) and Mukura Forest (1°59 S, 29°31 E (since 2015 merged as the Gishwati-Mukura NP and integrated into the UNESCO Gishwati-Mukura biosphere reserve) at an altitude of 2300–2700 m in Rutsiro District of western Rwanda (Fig. 1). The region has an average population density of 565 inhabitants/km^2, i.e., slightly higher than the Rwandan average (NISR, 2023a, 2023b) and is predominantly inhabited by agricultural communities. The two forest fragments (Gishwati and Mukura Forest) comprise afro-montane rainforest of various levels of intactness, while the National Park as a whole also includes tea plantations, cattle pasture (silvopastoralism) and small patches of secondary forest or woodlot plantations (REMA, Rwanda Environment Management Authority, 2015). Both forest patches have a history of deforestation extending over the past 70 years, during which 98 % of the original forest was cleared (Arakwiye et al., 2021). Today, the National Park has a core area of 34.3 km^2 (Gishwati: 14.4 km^2, Mukura: 19.9 km^2) surrounded by a buffer zone of 9.9 km^2 (REMA, Rwanda Environment Management Authority, 2015; UNEP-WCMC, United Nations Environment Program-World Conservation and Monitoring Centre, 2020). Primarily, the park was set up to protect remaining populations of endangered Eastern chimpanzee (*Pan troglodytes schweinfurthii*) and golden monkey (*Cercopithecus mitis kandti*; Plumptre et al., 2007). While the camera trapping study was conducted within the native forest core areas of Gishwati and Mukura Forest, the interview survey was carried out in the communities directly adjacent to each forest fragment (Fig. 1).

2.2. Camera trapping

In the rural parts of the Eastern savannah (Fig. 1), six camera trapping grids with 16 locations at an interval of 300 m were established in the interview area (see below), to obtain information on the relative abundance of ground-dwelling, mammalian nuisance species. The study period extended from November 2017 to May 2018, ranging from one to three months per study plot. The camera trapping effort was 136 days revealing a total of 113 independent photographic events of 9 medium- to large-sized, ground-dwelling mammals. The vegetation in each camera trapping grid comprised mainly of natural, but degraded (overgrazed), savannah vegetation typical for the Akagera ecosystem (see above) and was representative for most parts of the Eastern savannah region. Captured ground-dwelling mammals were identified to species level using Dorst and Dandelot (1970), Halthenorth and Diller (1977) and Kingdon et al. (2013), and subsequently grouped into independent photographic events. An 'event' was determined as a sequence of images occurring after an interval of at least one hour from the previous image of a certain species (Tobler et al., 2008). Species accumulation curves (based on a species-by-sampling-unit incidence matrix) were constructed using the 'specaccum' function in the 'vegan' package in R (Development Core Team 2023, (Oksanen et al., 2001), to identify whether the camera trapping effort was sufficient to confidently assign site-specific non-appearance of each mammal species detected in the study area. Subsequent analysis followed those described in Sun et al. (2022).

To capture the ground dwelling mammal fauna representative for Gishwati and Mukura Forest—and thus for the nuisance species causing HWC around the two forest patches—two camera trapping grids with 16 locations at an interval of 300 m were established in the two core areas of natural, pristine Afromontane rain forest habitat (Gishwati: 10 May to 17 November 2017, Mukura: 4 December 2017 to 11 May 2018; Sun et al., 2022). Thus, in all cases each camera grids covered an area of 1.2 km × 1.2 km, corresponding to a density of one camera per 0.05 km^2. The camera trapping effort (2704 days for Gishwati Forest and 2050 days for Mukura) yielded a total of 254 independent photographic events of eight medium- to large-sized, ground-dwelling mammals, while that of Mukura Forest yielded a total of 93 independent photographic events of six species. This information was provided in in Sun et al. (2022).

2.3. Questionnaire-based interviews

Parallel to the camera trapping study, we conducted a semi-structured questionnaire-based interview survey at each study location. This approach ensured that standard questions were asked during each interview, enabling direct comparisons and maintaining data

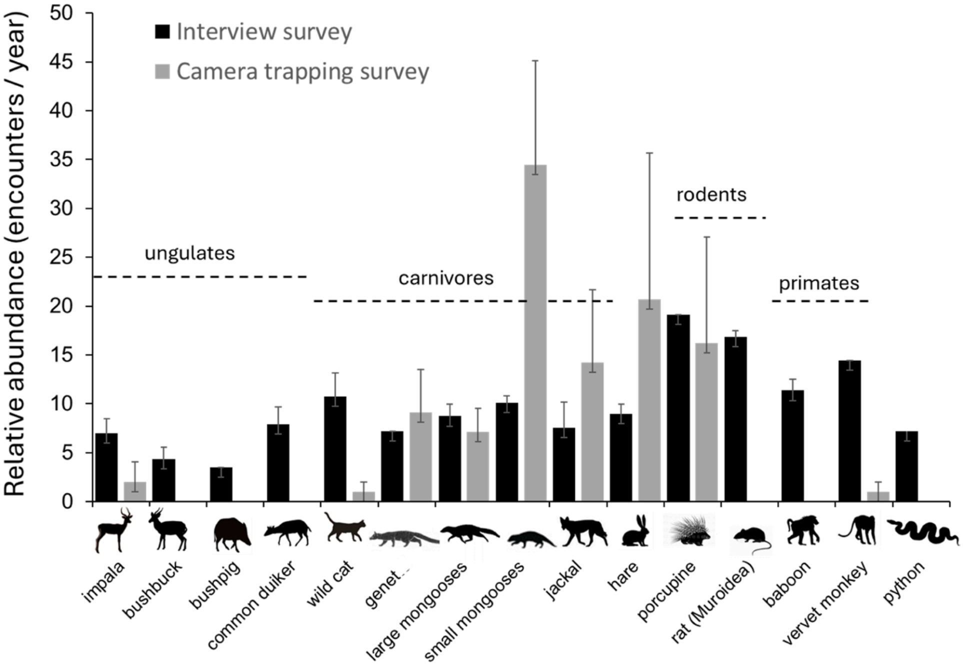

Fig. 2. Relative abundance indices of wildlife species obtained from interview (black) and camera trapping surveys (shaded) in the Eastern savannah.

quality. At the same time, it allowed the interviewer to ask additional questions if a new or interesting line of topics arose, a flexibility which is essential for exploring the interface between conservation science and policy (Young et al., 2014, 2018). The method was successfully piloted and applied during a previous study in the Eastern savannah (Apio et al., 2015).

Interviewees were arbitrarily approached in the field, including mainly two predefined target groups known to spend extended periods on their farm or pasture and thus being the most likely to report on wildlife encounters (key informant sampling *sensu* Newing, 2010), i.e., subsistence farmers and cattle owner (or their herdsmen). In the Mutara rangeland, 94 participants agreed to be interviewed, including 53 male and 41 female respondents. Adjacent to Gishwati and Mukura Forest, 120 participants were interviewed, including 58 male and 2 female respondents in Gishwati, and 55 male and 5 female respondents in Mukura. Only adult respondents aged 25–40 years were interviewed.

Prior to conducting interviews, participants were asked to confirm their informative consent (*sensu* Silvermann, 2013) after being informed about the purpose of the study and their anonymity. Interviews were carried out by one interviewer conversant with the local language (Kinyarwanda). Each interview started with the identification of the interviewee (gender, age and occupation, but not the identity), some 'icebreaker' questions, and lasted for approximately 20 minutes (Bryman, 2004). Questions were designed in a manner to not lead or bias the respondent to answer in favour of the researcher (Bryman, 2004). Photographs of mammalian nuisance species potentially occurring at each study site were presented, to ask which species were regularly encountered on the respondent's land. Respondents who did not know any species were not interviewed. Subsequently, closed-format questions (Gomm, 2008) were asked to obtain information on the abundance of each nuisance species, i.e., the time since the respective species was last encountered and the frequency of encounters during the last 12 months. It was further inquired whether the identified nuisance species caused any damage (no damage *versus* damage), and if yes, what kind of damage. Next, we asked how interviewees responded to wildlife damage encounters (intolerant *versus* tolerant), and how they reacted to prevent wildlife damage including five response levels (see below).

2.4. Statistical analysis

In a first step, we related abundance data generated from camera trapping to those obtained from interview surveys to check for possible inconsistencies. A relative abundance index was calculated as the square root-transformed number of annual encounters obtained from interview surveys. The corresponding index of relative abundance obtained from camera trapping was calculated as the number of independent photographic events divided by the number of active camera trapping days and multiplied by 365, i.e., the number of camera trapping events per 365 days. A Wilcoxon-Mann-Whitney test was applied to test for differences between the two relative abundance indices (interview survey *versus* camera trapping study) at each study site.

The analysis of HWC was solely based on interview data obtained at each study site. A descriptive analysis was carried out to identify the predominant nuisance species and the main type of damage caused. Nuisance species were defined as wild mammals that either raided one or several types of crops or that killed livestock or poultry. Wildlife damage incidence rates were calculated as the percentage of interviewees who encountered any damage (Table 1). For further analysis, nuisance species were grouped into four

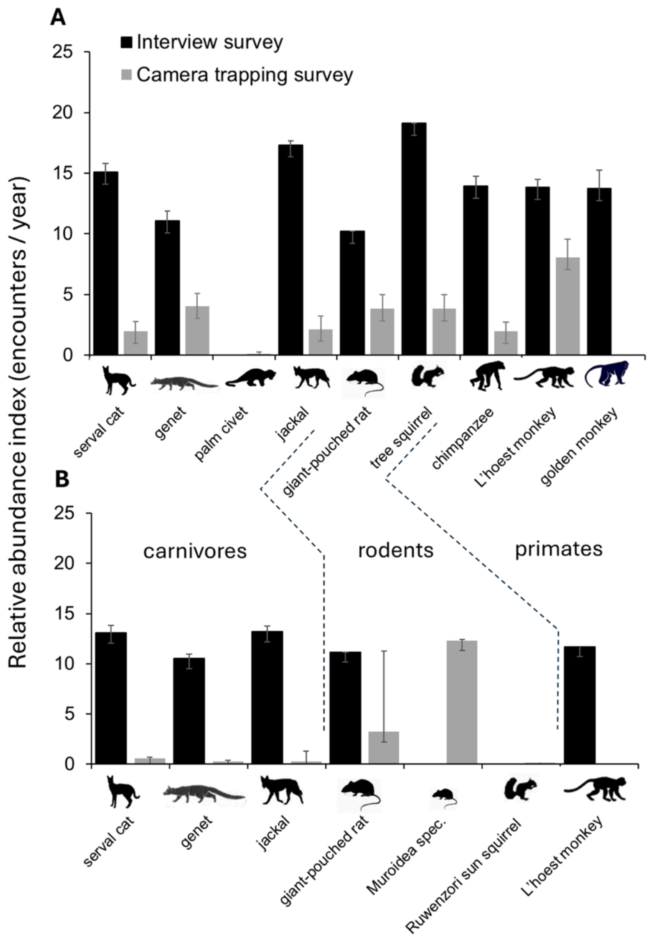

Fig. 3. Relative abundance indices of wildlife species obtained from interview (black) and camera trapping surveys (shaded) in Gishwati (A) and Mukura Forest (B).

groups, namely carnivores, primates (including chimpanzees), ungulates, and rodents. To test what factors affected the occurrence of damage, we applied a binomial generalized linear mixed model (GLMM), including the 'occurrence of damage' (damage [1] *versus* no damage [0]) as the dependent variable, 'study site' and 'wildlife group' as fixed factors, the 'species relative abundance' as a covariate, and the 'interviewee ID' as a random factor. Furthermore, we included all two-way interaction terms between fixed factors and the covariate. Subsequently, we ran a second binomial GLMM to examine the tolerance of local communities towards the damage caused by nuisance species, including 'intolerance' (tolerant [0] *versus* intolerant [1]) as the dependent variable, 'study site' and 'wildlife group' as fixed factors, the 'species relative abundance' as a covariate, and the 'interviewee ID' as a random factor. We again included all two-way interaction terms between fixed factors and the covariate. Both binomial GLMMs were fitted using the R library package 'lme4' (Bates et al., 2014). Finally, an Ordinal Logistic Regression Model (Ordered logit) was computed to analyse how local communities responded to repeated wildlife damage using an ordinal response level as the dependent variable. The hierarchy was based on human effort (time expenditure), i.e., no reaction [0], using dogs to guard crops or livestock [1], using noise to repel wildlife [2], chase wildlife using stones and sticks [3], and retaliation through capture or dispatch [4], whereby each category was assumed to be mutually exclusive and that crop/livestock-related responses fit into only one category. 'Study site' and 'wildlife group' were included as fixed factors, 'species relative abundance' as a covariate, and 'interviewee ID' as a random factor. This model was fitted using the R library package 'Ordinal' (Christensen, 2023). For all three models described above, we followed a model construction process that initially built a series of models including all possible combinations of fixed factors, covariate, interaction terms, and the random factor. Model selection was carried out using the R library package 'MuMIn' (Barton and Barton, 2015) which is based on the Akaike Information Criterion values corrected for small sample size (AICc) and the value of the model weight. The most parsimonious model was identified by having the lowest AICc (yet highest model weight), and a ΔAICc > 2.0 compared to the second-best fitting model. If multiple top-ranked models exhibited significant similarities (ΔAICc ≤ 2.0), a model averaging procedure was implemented.

Finally, we used the Pearson's Chi-squared test (as a post-hoc test) to examine whether the altered conservation status had an impact on the damage occurrence caused by nuisance species, and the local community's tolerance (or intolerance) towards nuisance species. All data analyses were carried out using R (version 4.3.2).

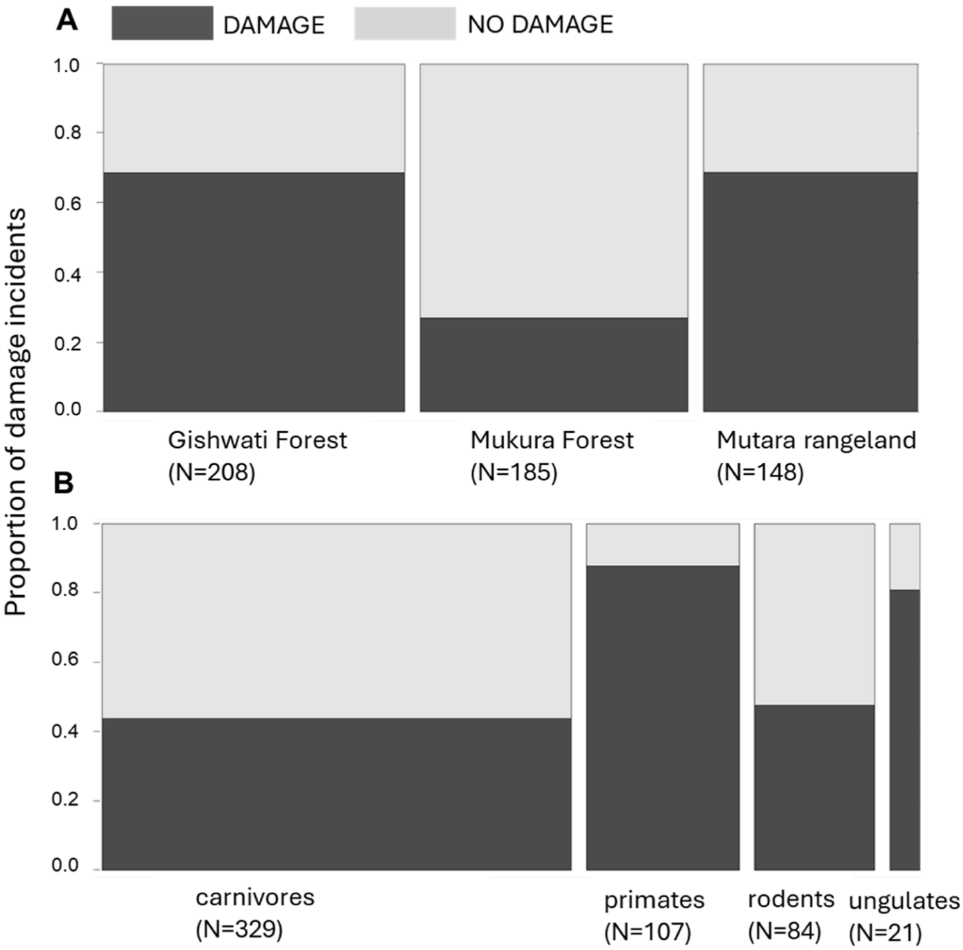

Fig. 4. Proportion of damage (no damage) incidents experienced by local communities around Gishwati and Mukura Forests, and in the Eastern savannah. The width of stacked bars reflects the number (N) of human-wildlife encounters at each study site. B) Proportion of damage incidents caused by four taxonomic units. The width of stacked bars reflects the number (N) of human-wildlife encounters per each taxonomic group.

Table 2
Averaged model results from the two best performing binomial GLMMs (Supplementary material: Table A1) fit by maximum likelihood (Laplace Approximation): (1) Damage (yes [1] *versus* no [0]) ~ Study sites + Wildlife group + Relative abundance + Study sites × Wildlife group + Relative abundance × Wildlife group + Study sites × Relative abundance + Interviewee ID; (2) Damage (yes [1] *versus* no [0]) ~ Study sites + Wildlife group + Relative abundance + Study sites × Wildlife group + Relative abundance × Wildlife group + Interviewee ID.

Binomial dependent variable	Independent variables	Estimate	SE	Z-value	*P*
Damage	Intercept	−0.37	0.24	1.57	0.117
[yes: 1 *vs* no: 0]	Study site: Mukura Forest	−0.72	0.31	2.32	**0.020**
	Study site: Eastern savannah	1.30	0.39	3.32	**0.001**
	Wildlife group: primates	20.73	1785	0.01	0.991
	Wildlife group: rodents	−1.10	0.95	1.15	0.252
	Wildlife group: ungulates	−0.17	0.99	0.18	0.861
	Relative abundance	0.68	0.26	2.65	**0.01**
	Mukura Forest × Primates	−19.54	1785	0.01	0.991
	Eastern savannah × Primates	−20.56	1785	0.01	0.991
	Mukura Forest × Rodents	0.44	1.19	0.37	0.712
	Eastern savannah × Rodents	0.54	1.14	0.48	0.633
	Primates × Relative abundance	−0.03	0.74	0.05	0.963
	Rodents × Relative abundance	1.08	0.42	2.53	**0.011**
	Ungulates × Relative abundance	−0.76	0.72	1.05	0.293
	Mukura Forest × Relative abundance	−0.20	0.31	0.66	0.509
	Eastern savannah × Relative abundance	−0.48	0.45	1.07	0.286

Table 3
The top fitted binomial GLMM with the lowest AICc value (Supplementary material: Table A2): Intolerance (yes [1] *versus* no [0]) ~ Study sites + Wildlife group + Relative abundance + Study sites × Wildlife group + Interviewee ID.

Binomial dependent variable	Independent variables	Estimate	SE	Z-value	*P*
Intolerance [yes: 1 *vs* no: 0]	Intercept	−0.216	0.193	−1.117	0.264
	Study site: Mukura Forest	−0.776	0.273	−2.847	**0.004**
	Study site: Eastern savannah	0.324	0.328	0.987	0.324
	Wildlife group: Primates	3.424	0.622	5.507	**< 0.001**
	Wildlife group: Rodents	0.106	0.704	0.150	0.881
	Wildlife group: Ungulates	0.120	0.513	0.234	0.815
	Relative abundance	0.378	0.112	3.368	**0.001**
	Mukura Forest × Primates	−2.343	0.768	−3.051	**0.002**
	Eastern savannah × Primates	−2.431	1.340	−1.814	0.070
	Mukura Forest × Rodents	−0.994	0.959	−1.037	0.300
	Eastern savannah × Rodents	−0.830	0.803	−1.034	0.301

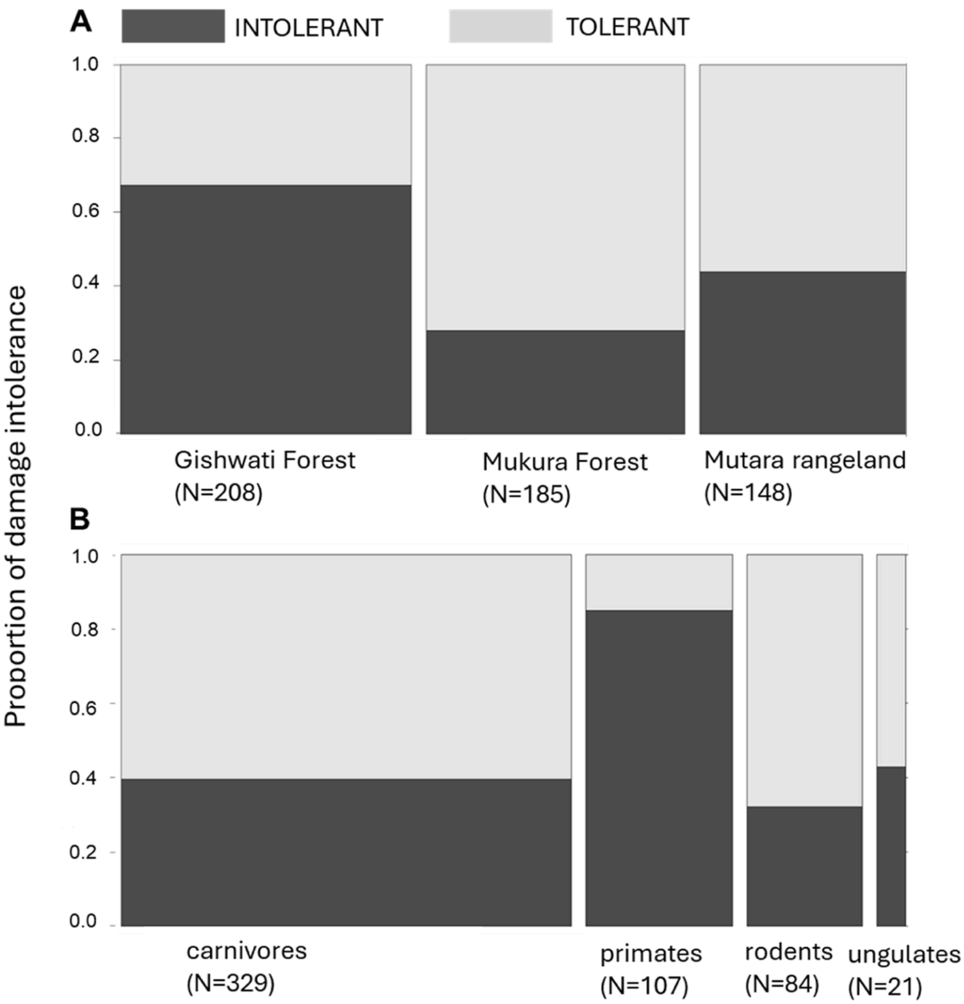

Fig. 5. Proportion of tolerance (*vs* intolerance) to wildlife damage experienced by local communities around Gishwati and Mukura Forests, and in the Eastern savannah. The width of stacked bars reflects the number (N) of human-wildlife encounters at each study site. B) Proportion of tolerance (*vs* intolerance) to wildlife damage caused by four taxonomic units. The width of stacked bars reflects the number (N) of human-wildlife encounters per each taxonomic group.

Table 4
Averaged model results from the two best performing Ordinal Logistic Regression Models (Supplementary material: Table A3): (1) Response (no reaction [0], using dogs to displace wildlife [1], using noise to repel wildlife [2], chase wildlife using stones and sticks [3], and retaliation through capture or dispatch [4]) ~ Study sites + Wildlife group + Relative abundance + Study sites × Wildlife group + Relative abundance × Wildlife group + Study sites × Relative abundance + interviewee ID, (2) Response (as above) ~ Study sites + Wildlife group + Relative abundance + Study sites × Wildlife group + Study sites × Relative abundance + Interviewee ID. The random effect of interviewee ID had a variance of < 0.001 and was therefore omitted.

	Variables	Estimate	SE	Z-value	*P*
Response to damage	0 | 1	0.35	0.22	1.61	0.11
	1 | 2	0.75	0.22	3.43	**< 0.001**
	2 | 3	2.69	0.27	10.05	**< 0.001**
	3 | 4	4.97	0.39	12.86	**< 0.001**
Independent variables	Study site: Mukura Forest	−1.04	0.30	3.44	**< 0.001**
	Study site: Eastern savannah	0.13	0.31	0.44	0.66
	Wildlife group: Primates	2.82	0.33	8.48	**< 0.001**
	Wildlife group: Rodents	0.19	0.80	0.24	0.81
	Wildlife group: Ungulates	0.76	0.88	0.67	0.39
	Relative abundance	0.67	0.23	2.95	**0.003**
	Mukura Forest × Primates	−2.05	0.58	3.51	**< 0.001**
	Eastern savannah × Primates	−2.50	0.89	2.82	**0.005**
	Mukura Forest × Rodents	−1.00	1.12	0.89	0.37
	Eastern savannah × Rodents	−0.53	0.92	0.58	0.56
	Mukura Forest × Relative abundance	−0.04	0.32	0.13	0.89
	Eastern savannah × Relative abundance	−0.63	0.43	1.47	0.14
	Primates × Relative abundance	−0.39	0.39	1.00	0.32
	Rodents × Relative abundance	0.34	0.34	1.00	0.32
	Ungulates × Relative abundance	0.72	0.72	1.00	0.32

3. Results

3.1. Interview vs camera trapping data

Questionnaire-based interviews of the local pastoralist community in the Eastern savannah (94 interviewees) revealed 148 human-wildlife encounters (on average one interviewee encountered one to three wildlife taxa), comprising 16 ground-dwelling mammals, namely impala (*Aepyceros melampus*), bushpig (*Potamochoerus larvatus*), bushbuck (*Tragelaphus scriptus*), common duiker (*Sylvicapra grimmia*), baboon (*Papio anubis*), vervet monkey (*Chlorocebus pygerythrus*), large mongooses (banded mongoose, *Mungos mungo* and white tailed mongoose, *Ichneumia albicauda*), small mongooses (slender mongoose, *Herpestes sanguineus* and dwarf mongoose, *Helogale parvula*), wildcat (*Felis lybica*), blotched genet (*Genetta maculata*), side-stripped jackal (*Lupulella adusta*), porcupine (*Hystrix cristata*), cape hare (*Lepus capensis*) and rats (Muroidea spp.). Nine of these taxa were also captured by the camera traps, including impala, vervet monkey, wildcat, small mongooses, large mongooses, genet, side-stripped jackal, porcupine, and cape hare. A Wilcoxon-Mann-Whitney test revealed a substantial, but insignificant difference in relative species abundance between interview survey and camera trapping ($W = 158$, $p = 0.06$; Fig. 2).

Around Gishwati Forest, the interview survey (60 interviewees) revealed 208 human-wildlife encounters. Encountered wildlife species comprised eight mammal species, i.e., chimpanzee, golden monkey, L'hoest monkey (*Allochrocebus l'hoesti*), serval cat (*Leptailurus serval*), servaline genet (*Genetta servalina*), side-stripped jackal, tree squirrel (*Funisciurus* cf *carruthersi*) and giant pouched rat (*Cricetomys* cf *kivuensis*). Apart from golden monkey, all above species were detected by camera traps. Near Mukura Forest, the interview survey (60 interviewees) revealed 158 human-wildlife encounters. Encountered wildlife species comprised five mammal species, namely L'hoest monkey, serval cat, servaline genet, side-stripped jackal, and giant pouched rat. Besides these, camera traps inside the forest also detected the tree squirrel. For Gishwati Forest, the Wilcoxon-Mann-Whitney test revealed a statistically significant deviation in relative species abundance between interview survey and camera trapping ($W = 72.5$, $p < 0.01$; Fig. 3a) but a non-significant difference for Mukura Forest ($W = 32$, $p = 0.37$; Fig. 3b).

3.2. Human-wildlife conflict: damage

In the Eastern savannah, 94 respondents were interviewed, of which 89 (i.e., 94.7 %) claimed to have experienced crop damage or livestock loss. Among 148 human-wildlife encounters, 102 crop raiding incidents were observed (68.9 %; Fig. 4a). Beans had the highest incidence rate of 50 %, followed by maize and ground nuts with an incidence rate of 27.5 % and 20.6 %, respectively (Table 1). Rats (Muroidea spp.) were the main nuisance taxa, responsible for 37.3 % of beans and 50 % of maize losses. The only targeted livestock species, i.e., chicken, had a damage incidence rate of 36.3 %, where larger mongooses accounted for 81 % of all incidents (Table 1). Around Gishwati Forest, all 60 interviewees claimed to have experienced crop damage or livestock loss by one or more nuisance species. Among 208 human-wildlife encounters, 145 HWC incidents were recorded (69.7 %, Fig. 4a). In Mukura Forest, only 29 people (out of 60; 48 %) complained about wildlife damage, and from 158 human-wildlife encounters, 42 HWC incidents were reported (26.6 %; Fig. 4a). Chimpanzee, golden monkey and L'hoest monkey were the main crop raiders around Gishwati Forest, whereas around Mukura Forest, only L'hoest monkey was flagged as a nuisance species (Table 1). Maize was the most frequently damaged crop around both forests, with an incidence rate of 98.3 % and 96.6 %, respectively (Table 1). The incidence rate for chicken losses near Gishwati Forest was 23.3 %, while that around Mukura Forest was 31 %. All chicken damage reported near Gishwati or Mukura Forest was attributed to servaline genets (Table 1).

The two best performing, binomial GLMMs demonstrated a good fit (Supplementary material: Table A1), prompting a model averaging procedure. The averaged GLMM revealed communities living in the Eastern savannah experienced more damage incidents than those around Gishwati or Mukura Forest (Table 2), where damage incidents were significantly more likely close to Gishwati Forest than near Mukura Forest (Table 2). Moreover, animals with a high relative abundance caused significantly more damage than those with low abundance. This pattern was particularly pronounced in rodents, where the damage incidence rate significantly corresponded to a relatively high abundance (Table 2, Fig. 4b). 'Interviewee ID' showed a variance smaller than 4 %, suggesting this random effect could be ignored when interpreting our data.

Damage incidence rates were significantly different between changing conservation status and thus between savannah and forest biome (Pearson's Chi-squared test: $\chi^2 = 16.23$, $df = 1$, $P < 0.001$). The post-hoc test, corrected by the Bonferroni method, showed communities living in the Eastern savannah—where the conservation status had diminished—experienced higher damage than communities in the forest biome. In the forest biome—where the conservation status had improved—communities experienced significantly lower damage than expected ($\varepsilon = 4.12$, $P < 0.001$).

3.3. Human-wildlife conflict: intolerance

Around Gishwati Forest, 141 of 145 reported damage incidents (i.e., 97.2 %) were not tolerated by the interviewees. A similar rate was found around Mukura Forest (40 of 42 damage incidences were not tolerated, i.e. 95.2 %. Tolerance towards wildlife damage in the Eastern savannah was considerably higher (59 of 101 damage cases were not tolerated, i.e., 58.4 %). However, a Pearson's Chi-squared test revealed no significant differences in the community's tolerance between forest and savannah communities or between changing conservation states (Pearson's Chi-squared test: $\chi^2 = 0.86$, $df = 1$, $P = 0.35$).

The best fitted binominal GLMM (Supplementary material: Table A2) revealed that communities living near Mukura Forest were significantly more tolerant towards wildlife damage than those near Gishwati Forest (Table 3, Fig. 5a). Interviewees stated that they were less tolerant towards damage caused by primates (including chimpanzees) than to that caused by rodents, carnivores, or ungulates (Table 3, Fig. 5b). The interviewee ID had a variance less than 0.01 %, suggesting this random effect could be ignored when interpreting our data. Moreover, communities were generally less tolerant towards species with high relative abundance (e.g., murids), than to species with a low relative abundance, such as ungulates (Table 3, Fig. 5b).

3.4. Human-wildlife conflict: response

A model averaging procedure applied to the two best-performing Ordinal Logistic Regression Models (Supplementary material: Table A3), revealed the local community around Mukura Forest reported significantly less repelling or retaliative responses than the other two study sites. A higher relative abundance of nuisance species, particularly the presence of primates increased the odds of local communities towards more aggressive responses (Table 4). Specifically, the communities living around Gishwati Forest reported significantly more antagonistic responses towards primates than those in the Eastern savannah or around Mukura Forest (Table 4). Interviewee ID had a variance of less than 0.01 %, suggesting that this random effect could be omitted from our analysis.

4. Discussion

In this study, we set out to assess wildlife abundance and the reliability of wildlife damage compensation claims and to explore HWC in two social-ecological contexts, linking ecoregion, changing conservation status and the local communities' perceptions. Although we could not directly assess actual compensations claims of communities—HWC data are not recorded on a regular basis—our findings showed that the mammalian wildlife species abundance recorded through interview surveys was consistent with data obtained from camera traps in the Eastern savannah and around Mukura Forest, while near Gishwati a statistically significant deviation was observed. Our analyses further showed that local communities showed different tolerance and response to the HWCs. Communities near Gishwati Forest reported significantly higher instances of crop loss, displayed a considerably lower tolerance towards wildlife-induced damage, and employed more aggressive retaliatory measures against wildlife compared to those near Mukura Forest or in the Eastern savannah. We discuss these findings in the context of (1) comparing data from interview and camera trapping surveys, (2) type and amount of damage, (3) local communities' tolerance towards damage, and (4) the communities' response to damage.

4.1. Interview vs camera trapping data

Evaluating the accuracy of wildlife damage claims could enhance public confidence in compensation programs (López-Bao et al., 2017). The primary purpose of verification is to establish trust among the public regarding the fairness of decisions and compensation schemes (Young et al., 2016; Riley et al., 2018; Anthony, 2021), preventing fraud and ensuring that compensation reaches the appropriate individuals genuinely affected by wildlife damage. Social trust, i.e., the readiness to depend on managing authorities, policymakers, and implementers of interventions, is essential for the effective management of HWC (Cvetkovich and Winter, 2003;

Stern, 2008). Vice versa, for managing authorities it is important to control and verify the claims of local communities (P. Nyhus et al., 2003; Karanth et al., 2018; Anthony, 2021). Contrasting relative wildlife abundance obtained from camera trapping to that reported by local communities could hereby act as a proxy to verify the odds of crop damage and to increase social trust (Nyhus et al., 2005; Nyhus, 2016; Van Vliet et al., 2023).

Our results indicate that most wildlife taxa encountered by the local pastoralist community of the Eastern savannah indeed occur in the area and may cause the proclaimed damage (Fig. 2). By contrast, the relative species abundance reported around Gishwati Forest was significantly higher than that recorded by camera traps inside the forest (Fig. 3a). Surprisingly, such deviation was not established for Mukura Forest (Fig. 3b), suggesting that the ecological knowledge of adjacent communities—at least around Gishwati Forest—seems to be a rather unreliable source to indirectly assess species abundance, and that putative claims for government compensation might be exaggerated. The discrepancy between the two forests may be attributed to a noticeably higher wildlife abundance in Gishwati Forest (Sun et al., 2022; this study), causing more complains and thus intensified HWC. The deviation between forest and savannah biome is puzzling since the abundance and diversity of wildlife and the proportion of wildlife damage incidences in the Eastern savannah was as high as that near Gishwati (Fig. 4a). This might indicate reports from communities living around Gishwati are less precise, or the camera trapping method is less suitable in (former) forest habitats. The latter is unlikely since the relative abundance obtained from interviews near Mukura Forest well matched the relative abundance obtained from camera trapping. Our results show that even at a small spatial scale, the effectiveness of using local ecological knowledge to estimate forest mammal abundances can vary considerably, an observation also reported by Parry and Peres (2015) who monitor tropical-forest wildlife over large spatial scales in Brazil.

The effectiveness of cameras at capturing crop-raiding events was acknowledged as an efficient and low-cost alternative to direct observation (or interview surveys) and was recommended as a long-term, large-scale monitoring method to assess crop damage by primates in South Africa (Walton et al., 2022). By contrast, a comparative study in the Amazon rain forest showed that local ecological knowledge was effective in estimating vertebrate abundance across a wide range of taxa and forest environments. Local ecological knowledge was compared to line-transect surveys, highlighting that it can help to calibrate abundance estimates and capture species that are infrequently seen during foot surveys but are commonly observed by local people during their daily activities (Braga-Pereira et al., 2022). Other studies compared the use of camera traps and farmer reports to study the crop raiding in Indonesia or the Democratic Republic of Congo, stressing that the comparison of camera trap data and farmer reports provides valuable information to mitigate HWC (Zak and Riley, 2017; Van Vliet et al., 2023). However, a word of caution should be raised here: Humans are like a walking camera trap, therefore increasing the likelihood of encounters which may have biased our results (Van Vliet et al., 2023). On the other hand, camera traps work throughout the day, while humans spend about half their time resting, unlikely to encounter wildlife (Van Vliet et al., 2023). Given the above, we propose that both, community reports and stratified camera trapping, are decent methods to study HWC, specifically to verify and assess crop (and/or livestock) damage and should be viewed as complimentary approaches (Zak and Riley, 2017; Camino et al., 2020; Lamelas-López and Marco, 2021; Walton et al., 2022).

4.2. Human-wildlife conflict: damage

Like in many other African countries (Hill and Wallace, 2012; Benjamin-Fink, 2019; Long et al., 2020; Tamrat et al., 2020; Raphela and Pillay, 2021), crop raiding on maize, beans as well as livestock depredation on chicken were the most prevalent causes for HWC in our study areas (Table 1). However, the proportion of reported wildlife damage incidents differed between study areas.

Rwanda set forest landscape restoration as a national priority (Cohen-Shacham et al., 2016), making Gishwati and Mukura Forest receive high conservation attention and an improved conservation status as national park and UNESCO biosphere reserve (Kisioh, 2015; Ordway, 2015; RDB, 2020). By contrast, in large parts of the Eastern savannah, the conservation status aggravated from national park (or game reserve) to a degraded rangeland with pasture for grazing cattle and subsistence agriculture (Kanyamibwa, 1998). Damage incidence rates—as reported in this study—were significantly different between changing conservation states and thus between savannah and forest biome, i.e., rangeland communities experienced a significantly higher damage than forest residents (Table 2). HWC in African savannah biomes usually involves crop damage by large herbivores resource competition between herbivores and domestic livestock (Butt and Turner, 2012; Fynn et al., 2016; Pozo et al., 2021; Barroso and Gortázar, 2024) or livestock depredation and threats to human safety caused by large predators (Lamarque, 2009; Muir, 2010; Dickman, 2013; LeFlore et al., 2019; Kuiper et al., 2022). Given that larger herbivores and their predators were eliminated from the Eastern savannah soon after the protected areas were degazetted (Kanyamibwa, 1998), the community feedback unrevealed in our study was unexpected. Parts of the former savannah were transformed to cattle ranches, allowing the remaining wildlife species (i.e., smaller ungulates, primates, rodents and meso-predators; Apio et al., 2015; Wronski et al., 2015; Bariyanga et al., 2016; this study) to persist and raid on subsistence crops or prey on poultry. This finding implies that the elimination of larger nuisance species and the downgrading of conservation states does not necessarily reduce HWC (Suratissa, 2021). In forest habitats, by contrast, HWC is due to habitat loss and human encroachment, resulting in crop damage mostly caused by primates (Dickman, 2013; Dore et al., 2017; Hill, 2017; Siljander et al., 2020; Kolinski and Milich, 2021).

Resource competition between wildlife and livestock, or attacks on livestock and humans play a minor role (Naughton-Treves, 1998). Given that damage incidence rates near the forest were lower than in the Eastern savannah does not necessarily imply that the improved conservation status (national park and biosphere reserve) could be held accountable. The comparatively low damage incidence rates reported from near Mukura Forest, instead indicate wildlife populations to be depleted (Sun et al., 2022; this study) and that a higher wildlife abundance around Gishwati Forest consequently leads to more crop damage.

Primates were the most damaging nuisance species at all study sites, which was not unexpected since HWC between primates and

Fig. 6. A servaline genet (*Genetta servalina*), allegedly killed as a retaliative response to poultry depredation near Gishwati Forest in Rwanda. © Laura Kmoch.

subsistence farmers—not only in Africa but across the world—is well documented (e.g., Strum, 1994; Hill and Wallace, 2012; Hill, 2017). Particularly the forests of the Albertine Rift region are known for their primate diversity, but also for an increasing human primate conflict (Plumptre et al., 2007; Webber et al., 2007; Lamarque, 2009). In Rwanda, a recent study carried out by Ndayishimiye et al. (2023) found 95 % of the local farmers interviewed nearby Volcanoes NP to have faced crop damage caused by the golden monkeys, while 36 % admitted repelling monkeys by throwing stones and making noise. Near Gishwati Forest, Tuyisingize et al. (2022) reported 72 % of farmers to have faced crop losses by primates, namely chimpanzees, golden and L'hoest monkeys. Moreover, a recent study by Rundus et al. (2022) reported on chimpanzees to ever more leaving Gishwati Forest and to forage in maize fields close to the forest edge. These studies are in line with our results, whereby it should be noted that a relatively large number of interviewees reported on a moderate damage caused by small carnivores, while a relatively small number of respondents experienced primate incursions causing serious damage (Fig. 4b).

4.3. Human-wildlife conflict: tolerance

Regarding the communities' tolerance towards wildlife damage (Serenari, 2024), our analysis neither revealed a significant difference between forest and savannah biome nor between changing conservation states. Though, communities living near Mukura Forest were significantly more tolerant towards wildlife damage than those near Gishwati Forest (Table 3, Fig. 5a). Interviewees asserted to be less tolerant towards crop damaging primates than to damage caused by rodents, carnivores, or ungulates (Table 3, Fig. 5b). This finding can be accredited to the fact that local communities around Mukura Forest—with a relatively low primate abundance—were significantly more tolerant towards primate damage than communities adjacent to Gishwati Forest which had a relatively high primate abundance.

The attitude of communities living near protected areas is an important but often overlooked peril for effective conservation strategies (Conover and Conover, 2001; Thirgood et al., 2005; Kansky et al., 2016; Mogomotsi et al., 2020). HWC threatens human welfare, health and safety, and can have severe economic and social costs that undermine conservation efforts (Newmark et al., 1993; Distefano, 2005). Indeed, our findings suggest that HWC around Gishwati (and Mukura) Forest may hamper conservation efforts and poses a great challenge to the persistence and survival of wildlife in the newly established National Park. Frequent negative human wildlife interactions made local communities resent the park, mainly due to crop raiding primates, adding to food insecurity, and making the patience of local farmers vanish (Mc Guinnes & Taylor 2014; Serenari, 2024). Such objections are in line with reports from other protected forest areas in Rwanda, namely Nyungwe and Volcanoes NP, where a negative community attitude towards chimpanzee and golden monkey poses a conservation threat owing to retaliative actions such as illegal hunting or deliberate habitat deprivation (Hasabwamariya, 2018; Haggblade et al., 2019; Ndayishimiye et al., 2023). In the Eastern savannah, the electro-fencing of the modern Akagera NP significantly decreased HWC with larger herbivores (Bariyanga et al., 2016; Banamwana et al., 2021). Although nuisance encounters with small animals persist, our study showed that the communities' attitude towards wildlife in the Eastern savannah was moderately positive. Whether a community tolerates crop damage (or livestock depredation), or whether it resists conservation efforts does not solely depend on monetary benefits but might be related to nonmonetary paybacks creating positive emotions (e.g., living with wildlife, cultural values, meaning, learning, or spiritual values; Muguchu, 2013; Kansky et al., 2021). Despite the considerable damage encountered by rangeland communities (Fig. 2, Tables 1, 2), the moderate tolerance towards wildlife might be best explained by this 'crowding-in' effect. This was not unexpected since it could be argued that such nonmonetary values rank higher in pastoralist communities, where the nomadic lifestyle and the wellbeing of livestock resulted into a higher socio-cultural value and thus the willingness to tolerate a co-existence with wildlife (Hill and Webber, 2010; Laverty et al., 2019).

4.4. Human-wildlife conflict: response

HWC poses a major challenge to conservation and can trigger preventive or retaliatory responses (Treves et al., 2006; Dickman, 2010). Such responses include using dogs, noise or stones to repel wildlife, or the application of traditional measures such as burning wild animal dung, putting scarecrows, or spreading concoction around fields (Mwamidi et al., 2013). Other methods to repel nuisance species involve digging wildlife trenches or constructing electric fences—such as that built around Akagera NP—to deter large herbivores and their predators. Smaller species however, such as mongooses, genets, primates or rodents cannot be controlled using such methods (MacKenzie, 2012; Mwamidi et al., 2013; Rusoke and Rwetsiba, 2019). Lethal control measures involving snaring, retaliatory shooting, poisoning or capture, have been widely used throughout history to mitigate HWC and to eliminate sources of damage (Conover and Conover, 2001; Thirgood et al., 2005; Woodroffe et al., 2005; Nyhus, 2016; Fig. 6). Such human-induced mortality affects not only the population viability of some of the most endangered species but also has broader environmental impacts on ecosystem equilibrium and biodiversity (Treves et al., 2006).

Our study attempted to quantify and analyse communities' responses to HWC in Rwanda for the first time. Local communities near Mukura Forest reported significantly less repelling or retaliative responses than those living around Gishwati Forest or in the Eastern savannah (Table 4). Across all three study sites, an increase in relative wildlife abundance, particularly the presence of primates, strongly corresponded to an increasing severity of peoples' response towards the damaging species. This finding indicates that threatened species, such as chimpanzees and L'hoest monkey, attract most negative community responses, confirming an acknowledged conservation dilemma, i.e., species most exposed to conflict are also most prone to extinction (Thirgood et al., 2005; Woodroffe et al., 2005; Nyhus, 2016). However, lethal control measures were not reported by any respondent, which may be owed to the fact that primates receive a considerable conservation attention by Rwandan authorities and the international conservation community, and that consuming primate meat is a taboo in the local communities' culture (O'Brien et al., 2014).

Legal and ethical approval

All procedures were performed in compliance with relevant laws and institutional guidelines of Republic of Rwanda and have been approved by the appropriate institutional committee(s).

Ethics

If this manuscript involves research on animals or humans, it is imperative to disclose all approval details

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Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03550.

Data availability

The authors do not have permission to share data.

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