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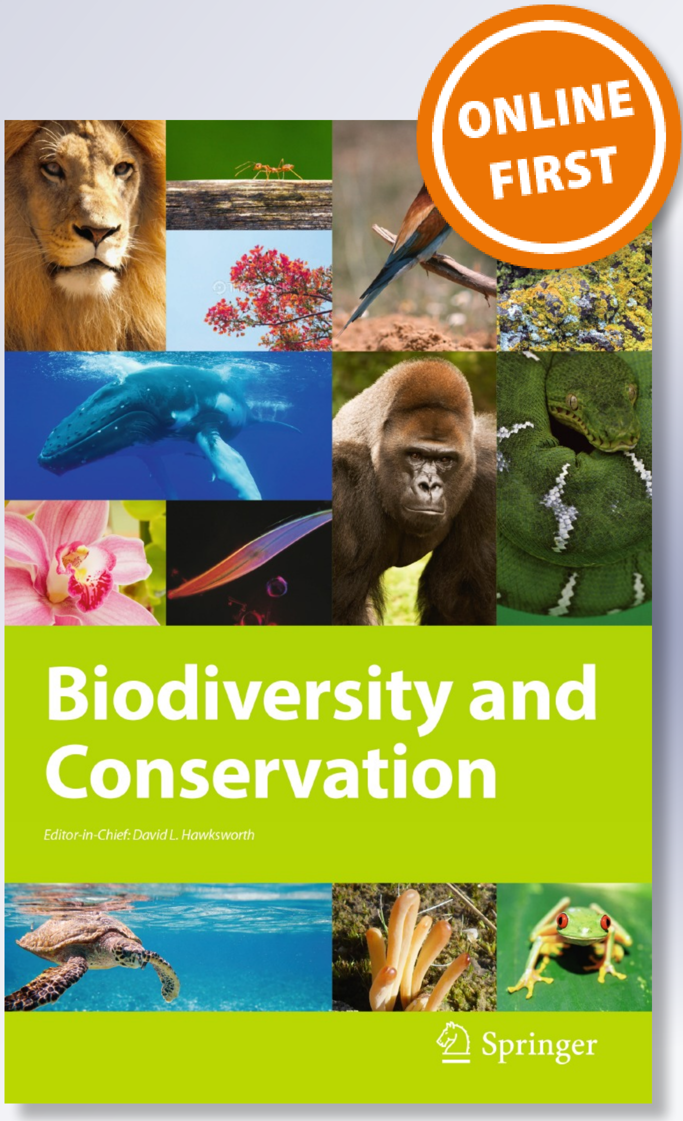

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ORIGINAL PAPER

Seasonality, crop type and crop phenology influence crop damage by wildlife herbivores in Africa and Asia

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Abstract Wildlife species damaging crops can cause substantial losses to farmers and at the same time create negative attitudes against wildlife and conservation efforts that may result in negative interactions against wildlife and lead to human-wildlife conflicts (HWCs). For the analysis of negative interactions between humans and terrestrial wildlife species, a globally applicable scheme for monitoring was developed and applied over 6 years in study areas of two Asian (Nepal and India) and two African (Zambia and Tanzania) countries. Factors influencing crop consumption by eight different groups of herbivores were monitored and analyzed using generalized linear models. Seasonality, crop availability, type and the phenological stage of the crop seem to play an important role in the crop damaging behavior of herbivores. Crop consumers such as elephants (*Loxodonta africana* and *Elephas maximus*), zebra (*Equus quagga* spp.) and boars/hogs (*Sus scrofa, Potamocherus larvatus* and *Phacochoerus africanus*) show preferences for harvested and/

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or maturing crops. Rhinos (*Rhinoceros unicornis*) and antelopes/deer (*Taurotragus oryx, Aepyceros melampus, Boselaphus tragocamelus* and *Axis axis*) damage the highest numbers of fields with crops at an intermediate growth stage. The findings of this study can inform management of HWCs in areas where people and wildlife coexist. Furthermore, this study demonstrates the benefits of standardized HWC assessments in order to compare data from different continents and between different species to be able to draw generalized conclusions for the management of HWC.

Keywords Crop raiding · Crop preferences · Human-wildlife conflict management · Human-wildlife conflict database · Land-use planning · Conflict mitigation

Introduction

With rising awareness about the importance of the interaction between wildlife and people, more and more conservation organizations are focusing on this topic (Hoare 2012; Madden 2004; Osborn and Parker 2003; Peterson et al. 2010). Human-wildlife conflict (HWC) generally refers to situations where "wildlife impacts humans negatively (physically, economically, or psychologically), and where humans likewise negatively impact wildlife" (Draheim et al. 2015). This definition includes the fact that interactions between wildlife and people can cause damage and costs to both sides and can even result in disagreements between different groups of people (human–human conflicts) (Madden 2004; Marshall et al. 2007).

When wildlife damage crops, human properties, or lives, this can negatively influence the attitude towards wildlife and conservation issues (Kansky and Knight 2014; Sukumar 1991). This is especially the case in rural landscapes close to wilderness and conservation areas, where people and wildlife compete for the same natural resources such as water, grazing land and space for cultivation, and losses to wildlife can be substantial. For people who depend on natural resources and are without economic alternatives, such damage can have catastrophic dimensions (Thirgood et al. 2005). Increasingly, organizations are working towards reducing negative wildlife impacts on humans, and simultaneously to create higher acceptance and reduce animosities towards conservation efforts (Hoare 2012; King et al. 2011; Lichtenfeld et al. 2014; Ogra and Badola 2008). The development of effective strategies to reduce crop damage by wildlife species needs to be based on detailed and systematic research, taking into consideration ecological and social factors. The French based organization Awely developed a standardized system to assess and analyze damage by wildlife (crop damage, property damage, livestock predation and accidents with humans), as well as the socio-economic setting in which they appear, for any species in any terrestrial ecosystem (Gross and Fulconis 2009). This system has been tested in two African and two Asian countries (Zambia and Tanzania, and India and Nepal, respectively). The main purpose of this HWC assessment scheme is to facilitate the analysis of wildlife damage based on standardized monitoring to understand which factors are related to wildlife damage so that their occurrence becomes more predictable in time and space (Hoare 1999; Karanth et al. 2012). Understanding the factors influencing crop consumption by herbivores is an important step in designing effective crop protection methods and has relevance for the management of HWCs in the vicinity of national parks or other areas where people and wildlife coexist.

Here, we analyze crop damage data (pre-harvest) collected over 6 years in two Asian and two African regions to identify factors that influence the frequency and severity of crop damage by wild herbivores. To structure the analysis, four questions were defined: (1) Which wildlife species are the most frequent crop raiders? (2) Does the frequency of crop consumption change throughout the seasons? (3) Does the phenology of crops influence the frequency of crop consumption by wildlife species? (4) Which crop types are damaged through consumption, and which through trampling?

Materials and methods

Study sites

This study was carried out in four different regions adjacent to national parks in two African and two Asian countries. Data were collected continuously throughout the years from January 2009 to December 2014 in three defined study areas (Zambia, Nepal and India) and from January 2010 to December 2011 in Tanzania. The shorter study period in Tanzania occurred due to an unforeseen lack of funding. All farms suffering from crop damage were included in the study.

South Luangwa/Zambia (SL): South Luangwa National Park (9050 km^2) is located in the Luangwa valley in the Eastern Province of Zambia. To its east, the Luangwa River forms the natural boarder to the adjacent Lupande Game Management Area (4840 km^2), which is subdivided into six chiefdoms (Nshimbi and Vinya 2014). The study area (2800 km^2) encompasses five chiefdoms (Kakumbi, Malama, Mnkanya, Msoro and Nsefu) located at 13°05′S to 13°32′S and 31°33′E to 31°57′E (Fig. 1a), in the Lupande Game Management Area. The area holds a large elephant (*Loxodonta africana*) population as well as large populations of other herbivores such as African buffalo (*Syncerus caffer*), puku (*Kobus vardonii*), Crawshay's zebra (*Equus quagga crawshayi*), impala (*Aepyceros melampus*) and common hippo (*Hippopotamus amphibius*) (Frederick 2009). The rainy season (RS) occurs from December to April, with annual rainfall of < 830 mm, followed by a cooler, green and dry intermediate season (IS) from May to July and a very hot dry season (DS) from August to November (Astle et al. 1969). Small-scale subsistence farming areas with rain fed fields are interspersed with natural habitat. About 45.4% of the Game Management Area is utilized for living, agriculture and infrastructure (Watson et al. 2014). The overall population density is 11.6 people/km^2 (CSO 2012). Maize (*Zea mays*), sorghum (*Sorghum bicolor*), finger-millet (*Eleusine coracana*), pumpkin (*Cucurbita* spp.), groundnut (*Arachis hypogea*), and cotton (*Gossypium herbaceum*) are cultivated on rain fed fields (Nyirenda et al. 2011).

Tarangire/Tanzania (TA)

The Tarangire National Park of Tanzania (2800 km^2) is located in northern Tanzania and is part of the Tarangire-Manyara Ecosystem encompassing 35,000 km^2 (Prins 1987). The data collection in TA was conducted east of Tarangire National Park, in the community of Loibor Siret in Simanjiro District, with a total land holding of 550 km^2 (Lichtenfeld et al. 2014), located at 04°08′S to 04°64′S and 36°18′E to 36°43′E (Fig. 1b). The area belongs to one of East Africa's most important wildlife habitats with large numbers of migratory ungulates (Kissui 2008; Prins 1987) such as the eastern white-bearded wildebeest

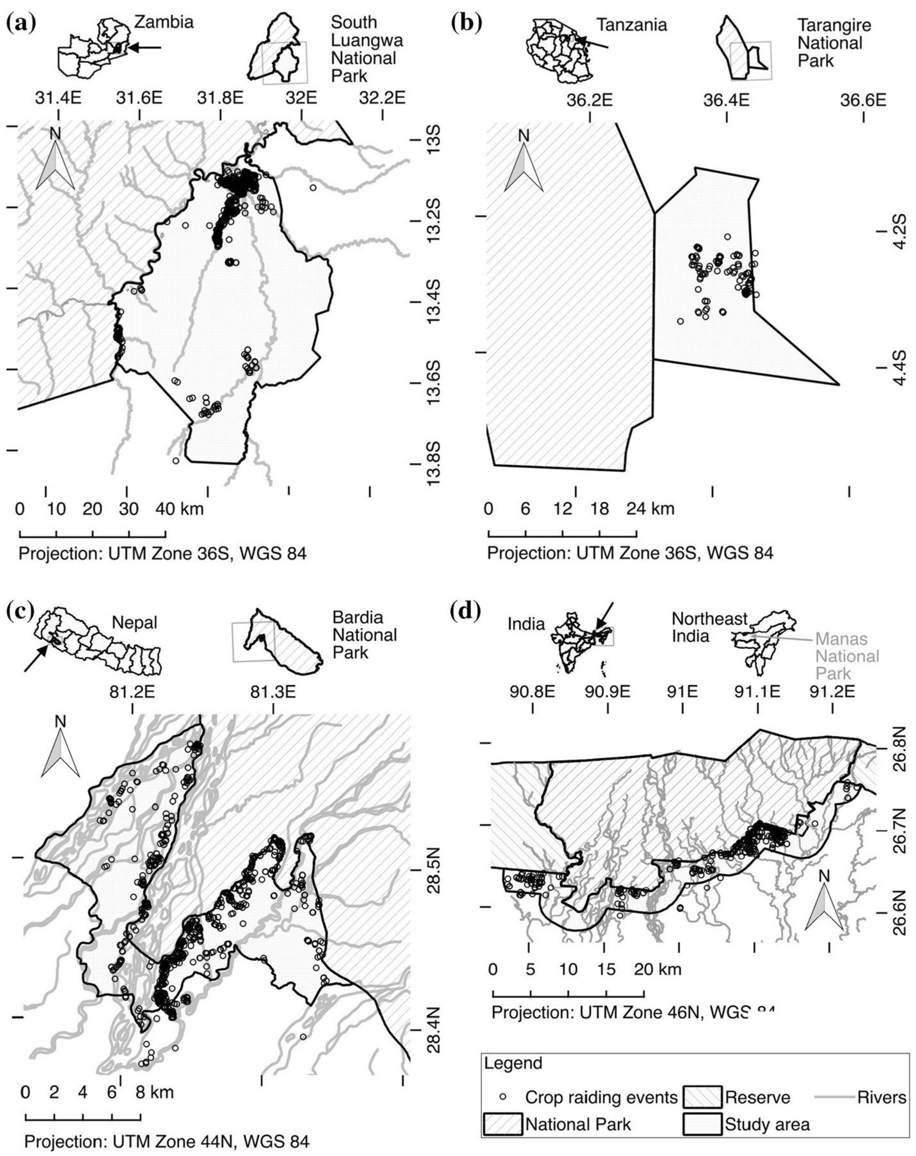

Fig. 1 Distribution of crop raiding events in the study areas **a** SL (South Luangwa/Zambia), **b** TA (Tarangire/Tanzania), **c** BA (Bardia/Nepal), **d** MA (Manas/India). Permanent water bodies (rivers) are indicated as grey lines. Few crop raiding events located outside of the study area were included in the study

(*Connochaetes taurinus albojubotus*), Burchell's zebra (*E. quagga burchellii*), Thomson's gazelle (*Eudorcas thomsonii*), Grant's gazelle (*Nanger granti*) and impala (Prins 1987). Abundant large herbivores in this area include African elephants, African buffalo and common eland (*Taurotragus oryx*) (Kissui 2008). With an annual rainfall between 450 and 600 mm the study area lies in the semi-arid ecological zone (Lichtenfeld 2005; Pratt et al. 1966). The long RS from March to June is followed by a long DS from July to October.

Short rains can occur in the months from November to February (IS), but not reliably (Kissui 2008; Lichtenfeld 2005). With seven people per km^2, the Simanjiro District is one of the least populated districts of Tanzania (Davis 2011). The most dominant ethnic group is the Kisongo Maasai (Cooke 2007), who traditionally performed transhumant pastoralism (Baird and Leslie 2013), but today agricultural activities have increased, especially the farming of maize, groundnuts and beans (*Phaseolus vulgaris*) (Cooke 2007).

Bardia/Nepal (BA)

The Bardia National Park (968 km^2) is located in the lowlands of Nepal. South of the national park a buffer zone was created in 1997, encompassing 17 Village Development Committees, the smallest political unit in rural Nepal (Thapa 2010). The study area BA (170 km^2) is located in the Western part of the buffer zone, comprising four Village Development Committees (Manau, Pashupatinagar, Gola and Pathabhar) on the Western bank of the Geruwa River and four (Suryapatuwa, Thakurdwara, Shivapur and Neulapur) on the Eastern side, located at 28°35′N to 28°22′N and 81°06 E to 81°19′E (Fig. 1c). The national park holds a high density of wildlife and the most abundant ungulate is the spotted deer (*Axis axis*), followed by the hog deer (*A. porcinus*) and barking deer (*Muntiacus muntjak*). A small population of blue bull or nilgai (*Boselaphus tragocamelus*), the largest Asian antelope, is also found here. With 20–30 individuals, this area holds the largest number of resident elephants (*Elephas maximus*) in Nepal, as well as a small population of reintroduced greater one-horned rhinoceros (*Rhinoceros unicornis*) (Flagstad et al. 2012; Wegge et al. 2009). The climate is influenced by the monsoon with rainfalls between July and October (RS) with around 1500 mm annually (Dinerstein 1979). The cool, mostly dry, green season from November to February (IS) is followed by the hot DS from March to June, during which severe water deficiency can occur (Flagstad et al. 2012; Jackson et al. 1994). With about 306 people/km^2 (Thapa and Chapman 2010), the southern buffer zone of Bardia National Park is densely populated. Subsistence farming of paddy (*Oryza sativa*), wheat (*Triticum aestivum*), maize, lentils (*Lens culinaris*) and mustard (*Brassica campestris*) are the main agricultural activities (Studsrod and Wegge 1995; Thapa Karki 2013). In the eastern part of the study area fields and farms are located directly at the forest border and, on the western part, the river forms the natural boundary to agricultural land.

Manas/India (MA)

Manas National Park (500 km^2) is located in the state of Assam, India. In the north it shares a border with the transboundary Royal Manas National Park (1057 km^2) of Bhutan and to the west and east it is framed by forests of the Manas Tiger Reserve (2840 km^2) (Goswami and Ganesh 2014). Towards the south private agricultural and community lands and villages directly border Manas National Park. As no buffer zone or other protection category exists in the vicinity of Manas National Park, the study area MA was defined as a 3 km wide belt (180 km^2) comprising the first line of villages and their farmlands directly bordering the national park and a small part of the Tiger Reserve further west. This belt includes a total of 156 villages (Sarma et al. 2015), located at 26°48′N to 26°36′N and 90°46′E to 91°16′E (Fig. 1d). Due to its various habitats Manas National Park is home to a wide diversity of fauna, including pygmy hog (*Porcula salvania*), hispid hare (*Caprolagus hispidus*) and Asian elephant. Ungulates, such as wild water buffalo (*Bubalus arnee*), gaur (*Bos gaurus*), hog deer and wild boar (*Sus scrofa*) are abundant (Goswami and Ganesh 2014). A small population of greater one-horned rhino has been reintroduced within the past decade. Assam is influenced by the southwest monsoon with heavy rains from June to September (RS) with annual rainfalls of 3000–4000 mm (Dikshit and Dikshit 2014) followed by a cool dry green season (October/November IS_1). The winter season from December to February (DS) has the driest months of the year, whilst from March to May pre-monsoon rains occur (IS_2) (Jhajharia et al. 2012). With approximately 1280 people/km^2 the study area is heavily populated. Paddy cultivation and farming of black gram (*Vigna mungo*), mustard seeds and jute (*Corchorus* spp.) are the main agricultural activities. Betel nut (*Areca catechu*), banana (*Musa* spp.), and vegetables are cultivated in homestead gardens (Sarma et al. 2015).

Collection of data on HWCs

The HWC assessment was carried out through observations of the crop damage by local trained independent enumerators (HWC officers) as well as structured interviews with victims. For each study area, 2 (TA) to 8 (SL) HWC officers were trained by the corresponding author during a week's course on interviewing standards, measuring of damage, identification of wildlife tracks and estimation of costs of damage (Fulconis and Gross 2011). The number of HWC officers varied per size and accessibility of the study area, so that every HWC officer was able to cover all villages/farming blocks at least twice a month. A local HWC coordinator supervised and monitored the HWC officers throughout the year. Follow-up training was conducted annually by the corresponding author and data reliability was verified on site. Each HWC officer was equipped with a set of HWC Assessment Forms (Appendix A in Supplementary material), a GPS handheld (Garmin 60), a digital camera (Fuji Finepix XP50), a mobile phone and a bicycle or motor bike. As proactive reporting by victims was not reliable (Howe et al. 2010), voluntary HWC informants were identified in each village or cluster of the study area to inform the trained HWC officers about the occurrence of damage. After the HWC officers were informed about a wildlife damage, assessment was carried out within 24 h. Further, regular site visits (at least twice a month), including to remote areas, were conducted by HWC officers. Information on HWCs was recorded on forms (see Appendix A in Supplementary material) and entered into the Awely HWC database based on Windows Access 2007 by the HWC coordinators.

The assessment scheme developed by Awely incorporates the IUCN data collection protocol for Human Elephant Conflict Situations in Africa (Hoare 1998), but was further developed to encompass any terrestrial wildlife species causing damage. The scheme includes crop damage (crops on farmland damaged by herbivores), property damage (houses, food storages, livestock shelters, fences or vehicles damaged mostly by large herbivores), livestock predation (livestock injured, killed and/or displaced by predators) and/or accidents leading to human injuries or death. Data were collected with a set of five different forms with open and close-ended questions (Appendix A in Supplementary material). For this particular study, data from only three forms (General Conflict Information, Crop Raiding and Brief Conflict Assessment) were used. For each damage event, one assessment was carried out. Similarly, as proposed by Naughton-Treves (1998), we defined a crop damage event as damage by an individual or group of one wildlife species during one time period (e.g., one night) in a defined area. For example, elephants damaging the fields of four different farmers in one night were recorded as one damage event with four occurrences of crop damage. In this way, spatial autocorrelation is reduced, which could result from clustered damage events by one species individual or group (Songhurst and Coulson 2014).

The movement of an individual or group of wildlife species was determined by reading the tracks. In cases when it was unknown, whether the same individual/group had caused the damage, multiple damage events were considered. The first form (*General Conflict Information*) took into consideration the ecological and geographical components of the conflict (location, time, species, number of individuals etc.) and was filled once for each damage event. The damage then was assessed further, focusing on the damage per victim. For damage to fields, whether the wildlife had fed on the crops or had just walked through them, the *Crop Raiding Form* was used. Data and GPS location as well as crop type and its stage of growth was recorded. A special focus was laid on the identification of the destruction type. Damaged crops that showed any bite mark of herbivores (twigs, stems, leaves, fruits, cobs or roots) was defined as "crops eaten", damaged crops that showed no bite marks at all, but were damaged by being pushed over and stepped upon, without feeding, were defined as "trampled". Crops that were both trampled and fed upon were regarded as eaten. In cases where the crops were already harvested and deposited on the field, this form was also applied. Where crops had been stored in granaries or other kinds of building, the *Property Damage Form* was used. However, these data were not included into this pre-harvest study. In case conflicts could not be visited by the HWC officer in due time, the information was recorded in the *Brief Conflict Assessment Form.* This form only captures a condensed version of the damage, and was also used in cases where victims were not willing to give detailed information. Capturing these conflicts despite the lack of detailed information was important to obtain a maximum coverage of conflicts in one area.

Mapping of crop damage

For each conflict event we recorded the location at its center with a global positioning system unit (Garmin GPS 60) with an accuracy of 15 m. We mapped crop damage events for each of the four study areas, using the Quantum GIS Geographic Information System, Version 2.14.3 Essen (QGIS Development Team 2016).

Analysis of crop damage data

We formed eight species categories, to compare crop damage frequencies per season, stage of growth during consumption and kind of damage per crop type by wildlife species throughout different study areas (Table 1). All analyses were calculated with R version 3.2.5 (R Core Team 2016) using Generalized Linear Models (GLM). To identify the seasons with the highest and lowest frequencies of crop damage, we used data on crop damage events per study area, species category and season, which were included as factors into the model. The influence of the season on crop damage frequency was analyzed in general over all study areas and years. For this analysis we used a quasipoisson distribution (with a log-link function), accounting for overdispersion in the data. Varying lengths per season in the respective study areas were taken into account (Appendix B Table 1 in Supplementary material), by including the length of each season per study area (in months) into the GLMs as an offset.

To analyze preferences of growth stages for crop consumption per species category, we used data on the number of damaged fields per species category, study area, crop type and stage of growth of each crop type. We also included the length of each growth stage per crop type in the analysis (Appendix B, Table 2 in Supplementary material). We only used data of crops consumed by wildlife species. We assumed zero damage per sampling unit

Table 1 Number of crop damage events per species category and percentage of the total number of crop damage events per region in four study areas (*SL* South Luangwa/Zambia, *TA* Tarangire/Tamzania, *BA* Bardia/Nepal, *MA* Manas/India) from 2009 to 2014

	SL	TA[j]	BA	MA
Elephant[a]	1036 (85.5%)	6 (6.1%)	455 (63.6%)	474 (95.2%)
Rhino[b]	–	–	102 (14.3%)	11 (2.2%)
Hippo[c]	71 (5.9%)	0	–	–
Buffalo[d]	3 (0.2%)	8 (8.1%)	–	1 (0.2%)
Zebra[e]	0	46 (46.5%)	–	–
Antelopes/deer[f]	0	12 (12.1%)	67 (9.4%)	0
Boars/hogs[g]	51 (4.2%)	24 (24.2%)	89 (12.4%)	12 (2.4%)
Primates[h]	44 (3.6%)	1 (1.0%)	1 (0.1%)	0
Porcupine[i]	7 (0.6%)	2 (2.0%)	1 (0.1%)	0

In cases where species did not cause any damage, though present in the study area, zero (0) was indicated and in cases where species were not present in a study area this was indicated with a dash (–)

[a]SL and TA *Loxodonta africana*, BA and MA *Elephas maximus*

[b]BA and MA greater one-horned rhino (*Rhinoceros unicornis*)

[c]SL and TA *Hippopotamus amphibius*

[d]SL and TA African buffalo (*Syncerus caffer*) and MA Wild water buffalo (*Bubalus arnee*)

[e]SL Crawshay's zebra (*Equus quagga crawshayi*), TA Burchell's zebra (*Equus quagga burchellii*)

[f]TA common eland (*Taurotragus oryx*) and impala (*Aepyceros melampus*), BA blue bull (*Boselaphus tragocamelus*) and spotted deer (*Axis axis*)

[g]SL bushpig (*Potamochoerus larvatus*), TA bushpig (*Phacochoerus africanus*) and warthog, BA and MA wild boar (*Sus scrofa*)

[h]SL vervet monkey (*Chlorocebus pygerythrus*) and baboon (*Papio cynocephalus*), TA vervet monkey, BA common langur (*Semnopithecus entellus*)

[i]SL cape porcupine (*Hystrix africaeaustralis*), TA crested porcupine (*Hystrix cristata*), BA and MA Indian porcupine (*Hystrix indica*)

[j]Damage numbers for TA refer to the years 2010 and 2011 only

Table 2 Summary of results on crop damage caused by eight species categories in all four study areas from 2009 to 2014

Species category	Number of damaged crop types	Most consumed crop types	Preferred stage of growth for consumption
Elephant	16	Rice, maize, wheat	Harvested and mature
Rhino	7	Wheat	Intermediate
Hippo	3	Maize	No preference
Buffalo	3	Maize	No preference
Zebra	2	Maize	Harvested and mature
Antelopes/deer	7	Lentil, wheat	Intermediate
Boars/hogs	9	Maize, potato	harvested
Primates	5	Maize	No preference

(i.e., combination of study area, year, crop type, and growth stage) when no damage was reported, but at least one damage claim for the particular crop in the particular study area existed. We also used a quasipoisson distribution (with a log-link function), accounting for overdispersion in the data.

We investigated the cause of the type of destruction (feeding or trampling) by a GLM using a binomial distribution (with logit-link function), to understand crop preferences of the species categories. Thus, we summarized the numbers of fields damaged by feeding versus fields damaged by trampling only, per species, study area, and crop type. We grouped staple crops (wheat, maize, rice) and compared them to crops which are farmed as cash crops or nutritional supplements (betel nut, cotton, lentil, mustard, vegetables). Each best model was chosen by downward model selection (Appendix C in Supplementary material). For all *p* value calculations we conducted a Holm-correction for multiple comparisons if necessary.

Results

In this study we analyzed 2524 crop damage events, encompassing 6236 individual victims/farms (SL: 2.79 ± 2.89; TA: 1.09 ± 0.32, BA: 2.67 ± 3.01, MA: 1.69 ± 1.07 victims/crop damage event) to determine factors that are associated with crop damages by wildlife. The crop damage events were distributed throughout the farming areas of the study sites (Fig. 1). In SL and TA, where agricultural areas are interspersed with natural habitats, crop damage occurred in farmlands much further away from the border of the national parks compared to BA and MA, where scarcely any natural habitat were found outside the National Parks. Here, crop damage occurred up to a distance of 5–7 km from the national park boundary.

Most frequent crop consumers

In three out of four study areas (SL, BA, MA), the greatest number of damage events was caused by elephants (Table 1), in contrast, zebra were mostly involved in crop damage (46.5%) in TA. Boars/hogs were involved in crop damage in all four study areas, ranking second in terms of frequency in TA and MA, and third in SL and BA. Hippos and rhinos ranked second in terms of frequency of crop damage in SL and BA, respectively, whereas rhinos ranked third in MA, and antelopes/deer ranked third in TA. With only six cases of crop damage (6.1%) within the study period of 2 years in TA elephants ranked number six of the crop consuming species.

Seasonality of crop consumption

In three out of four study areas (SL, BA, MA), the DS is the season with the fewest crop damage events (Fig. 2a). In TA, a total of only two crop damage events were observed during the DS, and none during the IS, while 94 crop damage events occurred in the RS. Overall, the number of crop damage events were found to be significantly different between DS and RS ($\chi^2 = 32.157$; $p < 0.001$) as well as between DS and IS ($\chi^2 = 27.988$; $p < 0.001$). Between RS and IS, however, there was no significant difference in crop damage numbers ($\chi^2 = 0.472$; $p = 0.49$). The lowest number of crop damage events in the DS also applied at the species level (Fig. 2b). Nearly all eight wildlife species categories showed the lowest

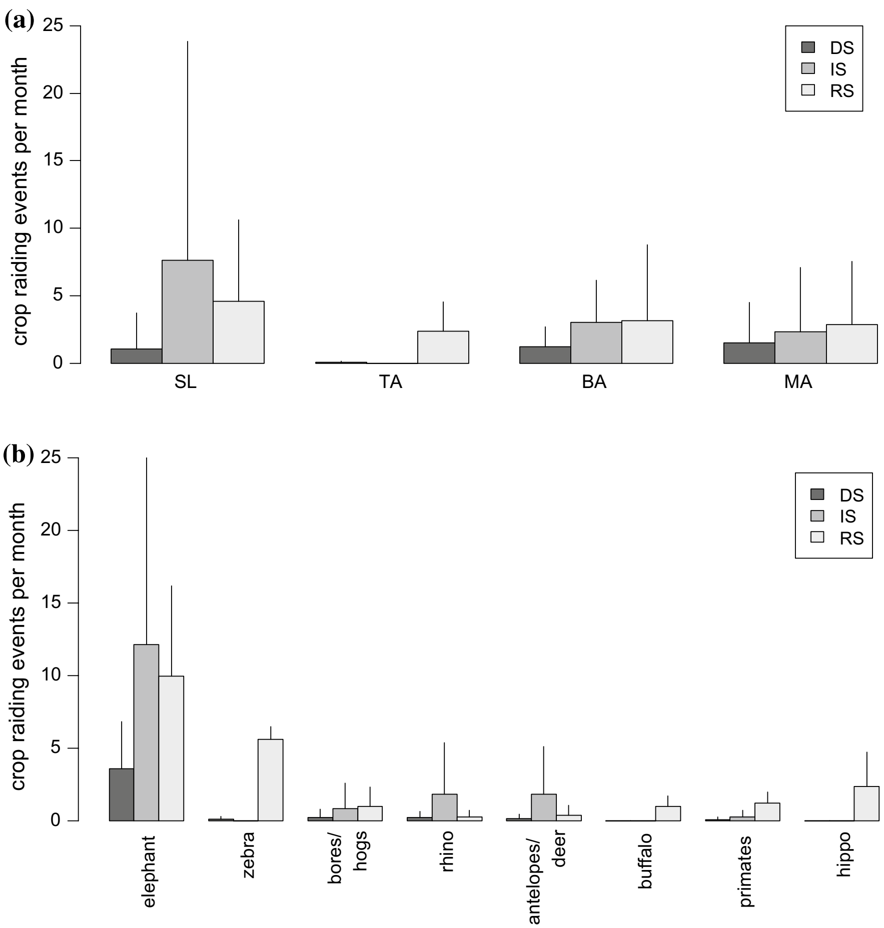

Fig. 2 Mean number of crop damage events per month for dry (DS), intermediate (IS) and rainy season (RS) per **a** study site and **b** per species category. Standard deviation is illustrated by whiskers

number of damage events per month during the DS. Zebra was an exception with one crop damage event during the DS compared to none during the IS and 45 during the RS.

Influence of growth stage of crops on crop consumption

By analyzing the effect of the phenology of crop types on the number of damaged fields by specific wildlife species categories, it was shown that elephants (Fig. 3a) damaged fields with harvested crops (laid out for drying on fields) as well as mature crops significantly (p = 0.025) more frequently than fields with crops at an intermediate growth stage; whilst seed/seedlings were the least damaged. Additionally, zebra caused the highest number of damage by feeding on harvested and mature crop fields (p = 0.011) (Fig. 3b). Boars/hogs damaged more harvested crops, compared to fields with crops at intermediate or seed/seedling growth stages, at a significantly higher frequency (p = 0.021) (Fig. 3c). In contrast, rhinos and antelopes/deer fed on crops at an intermediate growth stage significantly

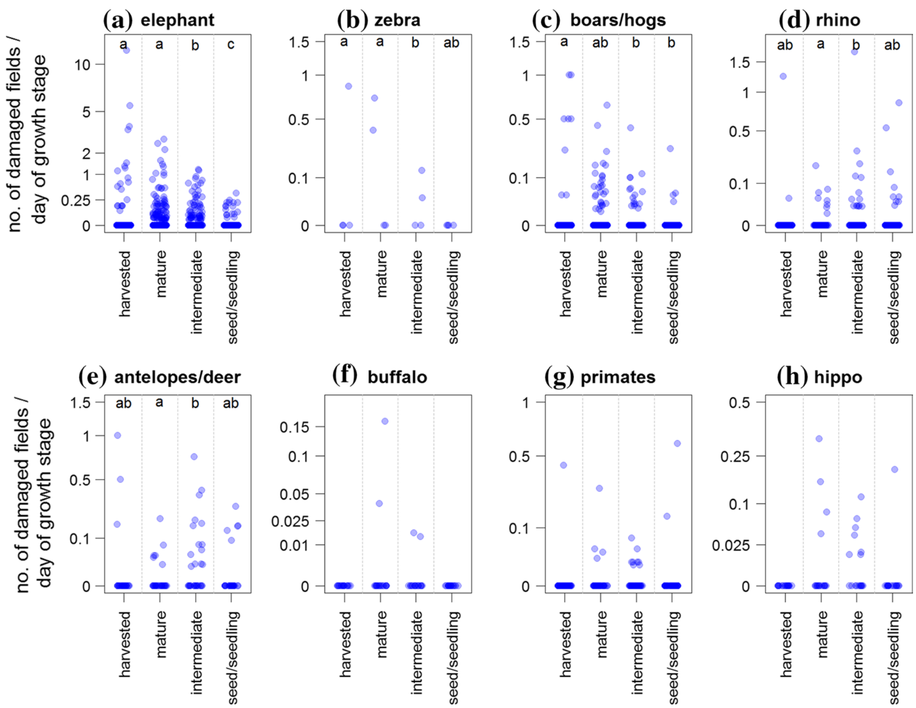

Fig. 3 Mean number of fields damaged per phenology stage by different wildlife species categories. Length of growth stage is accounted for: each dot shows the number of damaged fields in a respective growth stage for one crop type, region and year per day of growth stage. For better visibility y-axis is square root transformed. Different lower case letters on top of each column indicate a statistical difference between the groups

($p = 0.003$) more often than on fields with mature crops (Fig. 3d, e). Buffalo did not consume any crops at the seed/seedling and harvested stages of growth (Fig. 3f). For primates and hippos, the stage of growth had no significant impact on the incidence of crop damage (Figs. 3g, 4h). For exact χ^2- and p-values, see Appendix B, Table 3 in Supplementary material.

Crop preferences of wildlife species

We further analyzed the difference in the proportions of damage types (crop consumption versus trampling only) for different crop types by each species (Fig. 4). With 16 different types of crops, elephants damaged the widest variety of crops compared to all other species ($n = 2319$ damaged fields, 87.9% consumed, 12.1% trampled only). Elephants damaged fields containing staple crops (maize, rice, wheat) (89.5% consumed, 10.5% trampled) significantly more often through feeding than through trampling, compared to those containing cash crops and nutritional supplements (betel nut, cotton, lentil, mustard, vegetables) (72.6% consumed, 27.4% trampled) ($\chi^2 = 49.284$, $p < 0.001$).

Rhinos damaged fields with seven different crop types ($n = 240$ damaged fields, 95.8% consumed, 4.2% trampled only). Wheat fields were damaged at a significantly higher proportion through feeding than through trampling (99.5% consumed, 0.5%

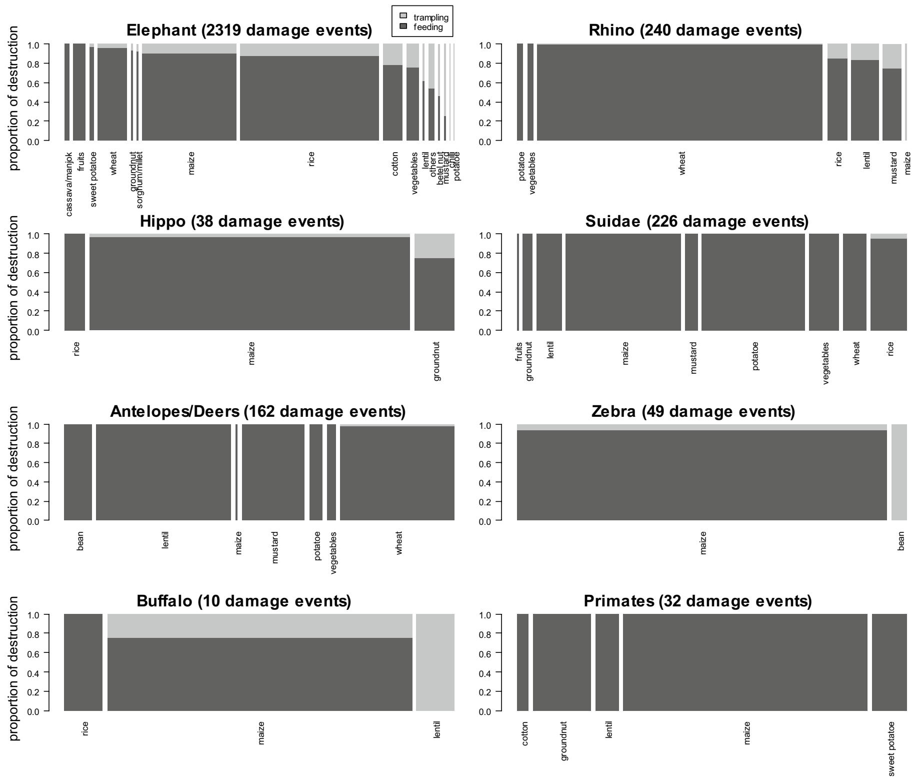

Fig. 4 Proportions of damage through feeding (black color) or trampling (without feeding) (grey color) per crop type by eight species categories. Each bar indicates one crop type. The bars are ordered from highest to lowest proportion of feeding. The width of each bar indicates the proportion of damaged crop type per species category

trampled only), compared to lentil and mustard fields, which were trampled to a higher proportion (80.0% consumed, 20.0% trampled only) (χ^2 = 12.357, p < 0.001). Rice was damaged to a higher proportion (15.4%) through trampling by rhinos than was wheat (0.5%). Detailed analysis for the type of crop destruction by elephant and rhino is given in Appendix C in Supplementary material.

Hippos damaged maize, rice and groundnuts although there was no statistical evidence that the type of crop had an influence on the type of damage (n = 38, 94.7% consumed, 5.3% trampled). Buffalo damaged fields containing rice, maize and lentils (n = 10, 70.0% consumed, 30.0% trampled), whereas zebra damaged maize and beans fields (n = 49, 89.8% consumed, 10.2% trampled). It was observed that buffalo trampled lentils and that zebra trampled beans preferentially, although both animals did not feed on the respective crops. As boars/hogs (n = 226 on 9 crop types, 99.6% consumed, 0.4% trampled), antelopes/deer (n = 162 on 7 crop types, 99.4% consumed, 0.6% trampled) and primates (n = 32 on 5 crop types, 100% consumed) hardly caused any damage through trampling without feeding a difference in preferences could not be determined.

Discussion

The damage of farm crops by wildlife species is one of the most frequently mentioned causes of HWC (Hill and Wallace 2012). Through comparing observations of four areas prone to crop damage by wildlife species, we gained insight on the seasonality of crop damage, species preferences on crop maturity and preferences of crop types (Table 2).

General findings

Due to their sheer size and the potentially great amount of food intake within a short period, elephants are likely to be perceived as the most severe crop pests (Naughton-Treves and Treves 2005). On the other hand, the less visible damage caused by smaller herbivores (antelopes/deer, primates, hogs/boars), as well as a greater difficulty in species identification, may cause underreporting for other species (Gubbi 2012). Although the assessment of crop damage by wildlife species was standardized throughout the four study areas, it is likely that the HWC officers were not able to obtain information on all crop damage events. If damage events were not noticed by the victims themselves or were not perceived as problematic, reports may have been missed. However, predictive models appeared to be robust to the underreporting of damage events, if underreporting was not spatially biased and damage events occur in non-random patterns (Snow et al. 2015).

Seasonality has been mentioned as an important factor in influencing crop consumption by wildlife species (Lahm 1996; Linkie et al. 2007; Webber et al. 2011). In all four study areas farming of the main staple crops (maize for SL/TA, rice for BA/MA) started with the onset of rains and harvest started after the rains had stopped (IS). After this, vegetables (SL, TA, BA, MA), maize, wheat, lentils, mustard (BA, MA) were farmed in the intermediate and DS. Fruits (banana, mango and pawpaw) were available throughout all seasons (SL, TA, BA, MA). Natural food sources for herbivores, however, were limited in the peak DS in the natural habitat (Lakshminarayanan et al. 2016; Van Aarde et al. 2008). Although crop damage by all eight wildlife species categories occurred throughout the year in the study areas, they were significantly less during the DS, but high during times when the main staple crops were cultivated (RS/IS).

The preference of food sources to herbivores can be determined by the degree of consumption and avoidance (Iason and Villalba 2006). As large and heavy wildlife species move through farms with different available crop types, they can cause damage either by crop consumption (accompanied with trampling as well) or by trampling only, without the consumption of crops. Through the comparison of the proportions of crops that have been consumed (and thereby may, to some extent, have also been trampled) to crops that have been trampled only, without any signs of consumption, we inferred that various crop types are less or more attractive to wildlife species. A similar approach to determine the attractiveness of crop types to wild elephants, was used in an experimental design in Zambia (Gross et al. 2016) and Nepal (Gross et al. 2017a). In those studies significant differences between the attractiveness of staple crops, such as maize (Zambia) and rice (Nepal) compared to crops containing antifeedants (e.g., lemon grass, ginger, mint or basil), were determined.

Characteristics of crop damage by African and Asian elephants

African and Asian elephants are regarded as important pest mammals in farms close to national parks or within other protected areas (i.e., buffer zone, Game Management Area), which have the objective of preserving these threatened species (Hoare 2000; Schmutterer et al. 1969; Sukumar 2006; Thirgood et al. 2005). The data collected and analyzed in this study underlines the importance of damage by elephants in three out of four study areas (SL, BA, MA). In TA, however, elephants caused only a few crop damage events, although this species is present in the area and damage to crops has been described for villages 10–20 km further north of the study area (Pittiglio et al. 2014). Particularly in the rainy season, when maize and other attractive crops are planted, elephants disperse into larger areas (Shrader et al. 2012; Van Aarde et al. 2008), travelling long distances to exploit nutritious food sources (Thouless 1995). The seasonal presence of elephants was, therefore, expected on the farms of TA. As a main elephant migration route is located in our study area, connecting the Tarangire National Park and a wet season dispersal area (Pittiglio et al. 2012), elephants may have passed the farms of TA before crop growth had started and returned after the harvest, thus explaining the low elephant crop damage incidence. Another reason may be due to the guarding practices by the Maasai people, who are famous for their martial lifestyle and cultivation of warrior status (Hazzah et al. 2009), as the elephants can distinguish different ethnic groups by smell and vision avoiding those that are associated with danger (Bates et al. 2007).

The temporal distribution of crop damage by elephants has been found to vary, depending on the habitat; in African forest habitats most crop damage occurs during the dry season (Chiyo et al. 2005), whereas in savannah habitats the late wet season was identified as the main time for crop damage (Osborn 2004). During those seasons the nutritional value of the natural forage (moisture and crude protein content) is thought to be less than that of planted crops. The coincidence with the time of crop ripening, however, makes it difficult to determine whether the decline of the nutritional value of the forage or the availability of highly nutritious crops triggers crop damage behavior (Webber et al. 2011). In this study it is shown that elephants clearly preferred harvested and mature crops to crops at other stages of growth; the riper a crop became, the more frequently it was damaged. Due to multiple factors that can influence the movement and behavior of species (Chiyo and Cochrane 2005; Songhurst et al. 2015), we cannot determine what exactly affects elephants to move onto farms to consume crops. For the development of strategies to reduce crop losses, however, it is important to understand that maturing crops and harvested crops laid out for drying are especially susceptible to damage by elephants. Furthermore, this study took into consideration crop damage on fields, only. Post-harvest losses and search for food in villages by elephants however follow a different seasonal pattern (Gross et al. 2017b).

In our study elephants mainly fed on staple crops, damaging them less through trampling only (without consumption) than crops such as cotton, vegetables, lentils, betel nut or mustard. For this reason a higher attractiveness can be attributed to maize and rice for elephants. However, the less attractive crops were still damaged by feeding to some extent; even cotton, which is in some cases seen as a potential buffer crop unpalatable to elephants (Gubbi 2012; Rode et al. 2006), has been consumed in 78.1% ($n = 138$) of all observed cotton damage cases. Whether some of these crops could be used as less attractive buffer crops, e.g. due to a lower feeding quality index than natural forage or chemical defense, needs to be determined through chemical analysis and experimental approaches, taking into consideration long term learning effects.

Crop preferences of rhinos in Asia

Although the black rhino (*Diceros bicornis*) was formerly found in TA and SL, this species has been hunted to extinction in both areas in the late 1980s to early 1990s (Emslie and Brooks 1999). For this reason rhinos were observed as crop damaging species only in the Asian study areas.

The natural diet of the greater one-horned rhino is mainly made up of tall grasses, especially during the rainy season (Laurie 1982), whilst browse contributes to their diet in a smaller quantity, mainly in the dry season, when grasses are less available and less nutritious (Pradhan et al. 2008). In contrast to elephants, rhinos preferred feeding on crops at younger and fresh green growth stages (intermediate and seed/seedling). Although the main staple crop farmed in the Asian study sites was rice, rhinos showed a stronger preference for feeding on wheat. We therefore suggest that wheat was the most attractive crop for rhinos in the Asian study areas. This finding is supported by an earlier interview-based study on farmers' perceptions of crop losses due to wildlife in Bardia/Nepal, where wheat and lentils were identified as the most damaged crops by rhinos (Studsrod and Wegge 1995).

Crop damage by hippo

Due to the preference of short grasses by hippos (Owen-Smith 1988; Snyder 2015), a greater number of damage events on fields at the seed/seedling and intermediate stages of growth could have been expected. A majority of damage to crops at an early growth stage was reported in a study on crop damage by hippos in Ruaha/Tanzania (Kendall 2011). However, in our study, no preference for a certain growth stage of crops was observed. Hippos have long been described as selective grazers, feeding especially on stoloniferous grasses (C_4 grasses) and coping well with very low feeding levels (Field 1970). More recent studies showed that they do not only consume C_4 grasses, but also C_3 plants (Boisserie et al. 2005). Later it was found that some individual hippos even fed purely on C_3 plants (Cerling et al. 2008). In our study, hippos consumed maize (a C_4 plant), rice, and groundnuts (both C_3 plants). This corresponds with observations from Ruaha/Tanzana, where maize and rice were described as the most damaged crop by hippos (Kendall 2011). The increase of C_3 plants in hippo diets, as described by Cerling et al. (2008), may be due to an increase of C_3 crop availability to hippos through an expansion of agricultural fields in the vicinity of hippo habitats.

The role of zebra and buffalo for crop damage

As obligate grazers (Cerling et al. 2008), zebra and buffalo have only consumed crops belonging to the family of *Gramineae* (maize and rice), but not dicotyledonous plants (beans, lentils), even though they were found to pass through these fields (trampling 100%). As with most herbivores, zebra and buffalo disperse further away from water sources in the rainy season (Ogutu et al. 2014), when staple crops are planted. Zebra mainly caused damage in TA in the rainy season, during which the density of this migratory species is highest in the Simanjiro plains of the study area, due to breeding (Rija and Hassan 2011). Zebra were previously mentioned as a crop damaging species in this area (Lewis et al. 2016; Pittiglio et al. 2014), but do not play a major role in crop damage in other zebra habitats (SL). In Kenya, however, zebra is ranked fourth as a problem wildlife species, after antelopes, elephants and primates (Naughton-Treves and Treves 2005). Similar to elephants, zebra showed a clear preference for mature and harvested crops, as they are able to feed on fibrous and coarse plant materials, such as husks and stems (Owaga 1975). Highly nutritious, mature and harvested maize seems to be an attractive crop for zebra to feed on during the late rainy season. Crop damage by buffalo was not frequent in our study areas, and no preference for any growth stage was determined.

The role of antelopes/deer for crop damage

All four antelope/deer species (of TA and BA) assembled under this group are mixed feeders, feeding on browse and grasses to varying proportions, where browse is consumed during the dry season and freshly re-growing grasses are consumed during the rainy season (Cerling et al. 2003; Khan 1994). Coinciding with their grazing preferences during the rainy season, these species preferred visiting farms with crops at green and soft intermediate growth stages. In total, they fed on a variety of seven crop types, but trampling alone scarcely ever occurred. The moderately sized impala and spotted deer are relatively light in weight (< 100 kg), therefore, these were unlikely to cause damage through trampling. In contrast, the heavier blue bull (up to 300 kg) and eland (up to 1000 kg) were more likely to have caused damage by trampling.

The role of boars/hogs for crop damage

Boars/hogs were implicated in crop damage within all four study areas. Wild boars and bushpigs are opportunistic feeders (Ballari and Barrios-García 2014; Breytenbach and Skinner 1982), consuming browse, grasses, roots, barks, larvae and even scavenge. Warthogs, in contrast, are selective grazers (Botha and Stock 2005), consuming mainly grasses and small amounts of forbs during the rainy season, whilst feeding on underground plant parts during the dry season. The generalist diet, especially of boars, is reflected in the variety of nine different crop types consumed in this study. Similarly, in Sumatra, it was found that wild boars seemed to consume whatever was available to them (Linkie et al. 2007). Warthogs, however, only caused damage through feeding on maize. Furthermore, boars/hogs show destructive feeding habits through digging up the soil in search for food, causing damage patterns which are difficult to distinguish from feeding (Barrios-Garcia and Ballari 2012). The high proportion of destruction through feeding, in contrast to trampling, could also be a result of this behavior. Boars/hogs show a preference for harvested crops. Similar observations in Sumatra on *S. scrofa* suggest that crop consumption might be determined by the seasonal ripening of crops (Linkie et al. 2007). Boars/hogs are important crop pests in many Asian, African and European countries (Herrero et al. 2006; Keuling et al. 2016; Linkie et al. 2007; Nyirenda et al. 2011), but due to their low conservation status (IUCN Red List Least Concern) (Cumming 2008; Oliver and Leus 2008; Seydack 2016) they receive little attention by nature conservationists, especially in their original regions of occurrence. From a farmers perspective the family of *Suidae* however should not be neglected when developing measures to manage HWC.

Crop damage by primates

In our study the highest number of crop damage events by primates was found in fields with seed/seedlings and harvested crops. The type of damage that this group causes to crops, i.e. at a very early stage of growth, agrees with findings from Uganda, where a high rate of primate damage was observed just after seedling or even while seeding was being carried out (Wallace 2010). Earlier studies observed crop damage by primates throughout the year with a climax during the time of crop ripening (Hill 2000). To reduce crop losses, the protection of crops in areas prone to primates seems especially important during the seeding and post-harvest stages. The high nutritional value of food can induce primates to crop raid (Taylor et al. 2016), so the choice for mature crops and seeds seems obvious. Seeds on freshly prepared fields are easily accessible and easy to collect by primates and great damage can be caused within a short time; the same applies to harvested crops, which are laid out for drying. Due to the light body weight of primates, damage through trampling does not occur.

Conclusion

Crop consumption by wildlife species has been described as part of an optimal foraging strategy (Sukumar 1990). The high nutritional value, palatability and ease of handling during foraging makes crops highly attractive for consumption (Biru and Bekele 2012). In this study for the first time crop damage patterns caused by different large herbivores were compared throughout study areas on two different continents. We have shown that in all four study areas the growth stage of the crops influences the frequency of damage by various wildlife species. This has a strong relevance for the management of HWCs, especially for the timing of appropriate conflict mitigation strategies. Our results indicate that in general, crops are most attractive to elephants, zebra and boars/hogs when they are harvested and laid out for drying on the fields. Enhancing crop protection during this fairly short period of a few days/weeks could strongly decrease a substantial number of crop damage events. For staple crops, such as rice or maize, the time of maturing (a time span that lasts only 1–3 months of crop production) is also highly sensitive. Focusing on the installment of effective crop protection measures during this specific period bears the potential to decrease crop damage in a timely and cost effective manner.

In areas where greater one-horned rhino are present, crop protection measures need to be in place at the early stage of farming. At a later stage, when crops are maturing, protection measures could be lowered, but need to be enforced again during the time after harvest, when crops are laid out for drying in the fields. In African wildlife areas populated by hippos, such as close to entry points at rivers (Kendall 2011) or at hippo pools, measures for crop protection need to be taken from an early stage of growth onwards. Also, in the case of primates, mitigation strategies to prevent damage have to be implemented at an early stage of farming.

Factors such as habitat fragmentation, degradation of habitat quality, loss of forest cover or laxity in management of physical barriers are causes for HWC (Fall and Jackson 2002; Gubbi 2012; Sukumar 1990). However, with the results of this study we emphasize that the attractiveness of crops planted in the vicinity of, or even within, natural wildlife habitats has to be included in this list and has to be taken more seriously in HWC management. Highly nutritional staple crops will always bear a high attractiveness to wildlife species. Even when protected by fences, chili smoke or human guarding, crops such as maize, rice and wheat will be susceptible to crop damage (Gross et al. 2017c; Karidozo and Osborn 2005). For this reason, we emphasize the necessity to consider the presence of large herbivores as another ecological factor, when selecting crops for farming in areas where people and large herbivores coexist. Recommendations for crop selection also need to be included in the local land-use planning of buffer zones and Game Management Areas. As long as the attractiveness of crops is not reduced, crop protection will continue to have high labor and financial costs. Choosing crops with a lower nutritional value than wild forage could disable the trigger for crop damaging behavior. Accordingly, the replacement of staple crops by alternate cash crops less attractive to wildlife species (Gross et al. 2016, 2017a; Rode et al. 2006), should be incorporated more strictly into management strategies and land use planning of protected areas in which people and wildlife coexist. For a sustainable implementation of effective buffer zones more research is needed on their placement and dimensions as well as long-term effects on different species.

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