Intensive hunting fundamentally changes human-wildlife relationships (#74673)

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Intensive hunting fundamentally changes human-wildlife relationships

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Wildlife alter their behaviors in a trade-off between consuming food and fear of becoming food themselves. The risk allocation hypothesis posits that variation in the scale, intensity and longevity of predation threats can influence the magnitude of antipredator behavioral responses. Hunting by humans represents a threat to wildlife thought to be perceived similar to those of a top predator, although hunting intensity and duration varys widely around the world. Here we evaluate the effects of hunting pressure on wildlife by comparing how two communities of mammals under different management schemes differ in their relative abundance and response to humans. Using camera traps to survey wildlife across disturbance levels (yards, farms, forests) in similar landscapes in southern Germany and southeastern USA, we tested the prediction of the risk allocation hypothesis: that the higher intensity and longevity of hunting in Germany (year round vs 3 months, 4x higher harvest/km^2) would reduce relative abundance of hunted species and result in a larger fear-based response to humans (i.e., more spatial and temporal avoidance). We further evaluated how changes in animal abundance and behavior would result in potential changes to ecological impacts (i.e., herbivory and predation). We found that hunted species were relatively less abundant in Germany and less associated with humans on the landscape (i.e., yards and urban areas), but did not avoid humans temporally in hunted areas while hunted species in the USA showed the opposite pattern. These results are consistent with the risk allocation hypothesis where we would expect more spatial avoidance in response to threats of longer duration (i.e., year-round hunting in Germany vs. 3-month duration in USA) and less spatial avoidance but more temporal avoidance for threats of shorter duration. The expected ecological impacts of mammals in all three habitats were quite different between countries, most strikingly due to the decreases in the relative abundance of hunted species in Germany, particularly deer, with no proportional increase in unhunted species, resulting in American yards facing the potential for 25x more herbivory than German yards. Our results suggest that the duration and intensity of managed hunting can have strong and predictable effects on animal abundance and behavior, with corresponding changes in the ecological impacts of wildlife. This shows that hunting can be an effective tool for reducing wildlife conflict due to overabundance but may require more intensive harvest than is seen in much of North America.

Title: Intensive hunting fundamentally changes human-wildlife relationships

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Abstract

Wildlife alter their behaviors in a trade-off between consuming food and fear of becoming food themselves. The risk allocation hypothesis posits that variation in the scale, intensity and longevity of predation threats can influence the magnitude of antipredator behavioral responses. Hunting by humans represents a threat to wildlife thought to be perceived similar to those of a top predator, although hunting intensity and duration varys widely around the world. Here we evaluate the effects of hunting pressure on wildlife by comparing how two communities of mammals under different management schemes differ in their relative abundance and response to humans. Using camera traps to survey wildlife across disturbance levels (yards, farms, forests) in similar landscapes in southern Germany and southeastern USA, we tested the prediction of the risk allocation hypothesis: that the higher intensity and longevity of hunting in Germany (year round vs 3 months, 4x higher harvest/km^2) would reduce relative abundance of hunted species and result in a larger fear-based response to humans (i.e., more spatial and temporal avoidance). We further evaluated how changes in animal abundance and behavior would result in potential changes to ecological impacts (i.e., herbivory and predation). We found that hunted species were relatively less abundant in Germany and less associated with humans on the landscape (i.e., yards and urban areas), but did not avoid humans temporally in hunted areas while hunted species in the USA showed the opposite pattern. These results are consistent with the risk allocation hypothesis where we would expect more spatial avoidance in response to threats of longer duration (i.e., year-round hunting in Germany vs. 3-month duration in USA) and less spatial avoidance but more temporal avoidance for threats of shorter duration. The expected ecological impacts of mammals in all three habitats were quite different between countries, most strikingly due to the decreases in the relative abundance of hunted species in Germany, particularly deer, with no proportional increase in unhunted species, resulting in American yards facing the potential for 25x more herbivory than German yards. Our results suggest that the duration and intensity of managed hunting can have strong and predictable effects on animal abundance and behavior, with corresponding changes in the ecological impacts of wildlife. This

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Keywords: Antipredator behavior, ecological impacts; Europe; hunting pressure; landscape of fear; North America; relative abundance; risk allocation.

Introduction

All prey species must balance the trade-off between consuming resources and becoming resources for their predators such that the mere risk of predation can shape how prey behave (Miller & Schmitz 2019). These consumptive and non-consumptive effects of predation are collectively termed the "landscape of fear", an inherently spatial concept describing elements on the landscape that an animal may perceive as high risk (i.e., predation) relative to reward (i.e., food; Laundré *et al.* 2010). However, fear is a simultaneous spatial and temporal concept where animals may change their antipredator behaviors relative to the temporal scale and intensity of threats, a hypothesis termed the "risk allocation hypothesis" (Lima & Bednekoff 1999). According to this hypothesis, an animal will increase antipredator behavior, thereby reducing foraging, proportionally to the severity of the perceived threat. Taking both the spatial and temporal concepts of fear-based responses together, we can learn about how species perceive risk by comparing spatial movement and temporal activity patterns with different potential risk factors (Dröge *et al.* 2017). For example, elk in Yellowstone National Park, USA spatially avoid habitats with the highest wolf predation risk, including high-quality habitats (Creel *et al.* 2005). However, where predation risk is lower, elk continue to use high-quality high-risk habitats, but do so when wolves are least active during the day (Kohl *et al.* 2018). Thus, the form of threat, scale, predictability and longevity are all factors that shape how wildlife species respond to risks both temporally and spatially.

Humans represent a threat to wildlife which can be perceived as a top predator (Cromsigt *et al.* 2013). Numerous studies have shown wildlife altering their behaviors in response to human activities by changing their vigilance (Ciuti *et al.* 2012), movement rates (Proffitt *et al.* 2009), flight responses (Chassagneux *et al.* 2019) and activity patterns (Parsons *et al.* 2016). However, not all humans are wildlife predators, and some animal populations have habituated to lose their fear of humans (Wheat & Wilmers 2016). Given that prey species can rapidly change antipredator behaviors in response to changes in risk (Relyea 2003), we predict that variation in how humans hunt wildlife should affect the behavior and space use of those species.

The nature of human hunting varies greatly by region and species with regulations affecting the level of threat (firearms vs. archery or trapping), location (hunting grounds), seasonality, longevity and intensity (bag limits; the number of individual animals a hunter can harvest) of hunting pressure. For example, in Central Europe (hereafter "Europe"), hunting occurs year-round for most species, with hunting grounds being privately-owned lands, managed locally (Bubenik 1989). By contrast, hunting in the United States and Canada (hereafter "North America") is restricted to shorter seasons with hunting grounds being a combination of public lands managed at the state or provincial levels and private lands (McShea 2012). Bag limits also differ between the two systems with North America limiting bags by individual hunter and Europe limiting bags at the state level by species, or by property, with many properties imposing no limits (Adams & Hamilton 2011). The result is a more sustained and intensive hunting pressure in most of Europe compared to a more temporally and spatially heterogeneous hunting effort in North America. Exactly how these differences in hunting regulations and pressures affect the abundance and behavior of wildlife populations is poorly understood but has implications for ecosystem health and human-wildlife interactions. Indeed, although using hunting regulations to shape animal behavior has been suggested for wildlife managment (Cromsigt et al 2013), ~~there have been relatively~~ few studies comparing the effect of different hunting practices on wildlife behavior (e.g., Little *et al.* 2016).

Here we use camera traps run in two areas with similar ecologies, but different hunting regimes, to evaulate how hunting affects the degree to which animals fear humans. Specifically, we use spatio-temporal data on wildlife distribution across a range of human development to test predictions of the landscape of fear and risk allocation hypothesis. Finally, to evaulate the ecological consequences of these changes, we estimate the ecological roles of mammals at both sites. To improve our inference that any differences we observe are associated with hunting, we chose two landscapes similar in climate and land cover proportions but with different hunting systems: Baden-Württemberg (BW) in southern Germany and North Carolina (NC) in southeast USA. The spatial intensity of hunting is much higher in BW with 4.71 European roe deer (*Capreolus capreolus;* hereafter "roe deer") harvested/km^2 compared to 0.78 white-tailed deer (*Odocoileus virginianus*) harvested/km^2 in NC in 2018. Furthermore, hunting in NC occurs only during short seasons (e.g. 3 months for deer, Table 1) but is longer-lasting in BW (year round; Table 1). Based on these differences, we make three predictions: 1) abundance: the more intensive hunting pressure in Germany will result in hunted species being relatively less abundant than in the USA, 2) spatio-temporal risk allocation: the more intense and sustained hunting pressure of Germany will necessitate a larger fear-based response to humans (i.e., high spatial avoidance) whereas the low-intensity, short-term hunting pressure in America will allow wildlife to maintain space with humans, instead avoiding them temporally where necessary, and

3) ecological impacts: the lower relative abundance and use of human-dominated habitats for hunted species in Germany will be related to the reduced potential for herbivory and/or predation when scaled by body size and diet.

Materials & Methods

Study sites

In Germany, we sampled sites around the city of Konstanz (pop 84,911), BW. Our study covered an approximate area of 60,000km^2 surrounding the city (Fig. 1) where the landscape was 25.9% forested, 16.8% urban and 30.7% agricultural landcover with an average population density of 259 people/km^2. In the United States we focused on a similar sized area (50,000km^2) from Raleigh, NC (pop 464,485) to the east (Fig. 1), that was 41.4% forested, 9.1% urban and 29% agricultural landcover with an average population density of 103 people/km^2. The climates of the two sites were similar (BW=coastal, NC= humid subtropical; Kottek *et al.* 2006) with similar mean annual precipitation (1195mm BW, 1218mm NC; Fick & Hijmans 2017) but with higher mean annual temperatures in NC (7.5C BW, 15.6C NC; Fick & Hijmans 2017). Both areas had similar levels of gross primary productivity (13083 kg C/square meter BW, 13418 NC in 2015; Hobi *et al.* 2017) with rolling hills (BW mean elevation = 136m, NC = 146m) of mixed deciduous and coniferous forests fragmented by similar levels of agriculture and urban development. Thus, our two study landscapes were broadly similar with the biggest differences being: 1) the amount forest cover was higher in NC (41% vs 26%), 2) human population density was higher in BW (259 vs. 102/km^2), 3) average temperature was higher in NC (15.6 vs 7.5C) and 4) the German landscape featured small, densely settled villages while the American landscape had one larger city with more dispersed housing across rural areas. As much as possible, our statistical analysis controlled for these differences to strengthen inference related to the different hunting systems.

Our study focused on the big game species which are both largest and most heavily managed (i.e., bag and season limits) and/or heavily hunted in each region, hereafter referred to as “hunted” species (Table 1). In BW these are roe deer and wild boar (*Sus scrofa*; hereafter “boar”), both having long hunting seasons with no bag limits (Table 1). In NC these are white-tailed deer, American black bear (*Ursus americanus*; hereafter “bear”) and wild turkey (*Meleagris gallopavo;* hereafter “turkey”), all of which have short hunting seasons (1-3 months) and strict bag limits (Table 1). Though different in size (roe deer are smaller), roe deer and white-tailed deer are ecologically similar with similar diets (Vangilder *et al.* 1982; Tixier & Duncan 1996), habitat preferences (Williamson & Hirth 1985; Tufto *et al.* 1996) and ability to live close to humans (Etter *et al.* 2002; Wevers *et al.* 2020). However, deer competitors are absent from NC but present in BW (European fallow deer (*Dama dama*) and sika deer (*Cervus nippon*)), though far less common and unlikely to broadly compete with roe deer (Burbaiteė & Csányi 2009). Additionally, large carnivores capable of preying upon deer, especially fawns, are absent from BW but present in NC (coyote (*Canis latrans*), bobcat (*Lynx rufus*) and bear; Boone 2019).

Field data collection

We used a consistent camera trapping protocol between sites (BW and NC) to facilitate comparisons. For each site, trained citizen science volunteers (see Parsons *et al.* 2018 for details) or staff deployed unbaited camera traps across each study region (Fig. 1). We sampled 242 sites in NC and 233 in BW, with camera placement stratified between hunted and unhunted areas as well as residential yards, forest fragments and agricultural fields (> 0.02km^2; Table S1). Information on whether a site allowed hunting came directly from the property owner. In Germany, all hunted areas were forests with no samples from hunted yards or open areas, while in NC some forests, fields and rural yards were hunted (Table S1). We used Reconyx (RC55, PC800, and PC900, Reconyx, Inc. Holmen, WI, USA) and Bushnell (Trophy Cam HD, Bushnell Outdoor Products, Overland Park, KS, USA) camera traps attached to trees at approximately 40cm above the ground. Trigger sensitivity was set to high for all cameras and we verified that both brands of camera had similar trigger speeds (<0.5s). Cameras were left undisturbed for 3-4 weeks and then moved to a new location (at least 200m apart), with sampling taking place over several overlapping seasons and years (2018-2020 Germany, 2013-2019 NC). Cameras recorded multiple photographs per trigger, re-triggering immediately if the animal was still in view. We grouped consecutive photos into one sequence if they were <60 seconds apart (Parsons *et al.* 2016), and used these sequences as independent records, counting detections by sequence, not individual photos. Initial species identifications were made by volunteers or staff using customized software (eMammal.org) and all were subsequently reviewed for accuracy before being archived at the Smithsonian Digital Repository. Detection rates for each species at each camera site were calculated as the count/days camera ran, considering groups as a single detection.

Relative abundance

We used a generalized linear regression with a log link, offset for how many days each camera ran, and term for extrapoisson variation, to assess predictors of species detection rates as a measure of relative abundance. We assessed relative abundance for both hunted and unhunted species for which we had >100 detections (n=10 BW, 9 NC; Table S2). We modeled variation in counts using six covariates (Table S3). To account for differences in the amount of forest and human population between the two sites, we used predictors for the percent urban and percent forested landcover in a 1km radius (Jung *et al.* 2020), and their interaction. To account for differences in the pattern of urban areas across the landscape between BW and NC, we added covariates representing the size (km^2) of the closest urban area and the distance (km) to that urban area. We used 0/1 indicators for whether a site was a residential yard and whether a site was hunted, respectively.

We fit models in JAGS (Plummer 2003) via rjags (Plummer 2016) in R (v3.6.1; R Development Core Team 2008). We based inference on posterior samples generated from three Markov chains, using trace plots to determine adequate burn-in. All models converged (Gelman *et al.* 2014) by running for 50,000 iterations following 3,000 iterations of burn-in, thinning every 10 iterations.

Inferring fear

Although experimental manipulation provides the strongest evidence for fear-based responses, many past studies have inferred fear from observational data (e.g., Wooster *et al.* 2021). Fear response can manifest in many ways, including increased vigilance and avoidance of high risk areas and/or high risk times (Palmer *et al.* 2017). Here, we inferred “fear” by using a multispecies occupancy model with continuous-time detection process (Kellner *et al.* 2021) to assess the extent to which wildlife species were using human-dominated habitats and co-occuring with humans, spatially and temporally, while accounting for imperfect detection. We modeled variation in occupancy for each species for which we had at least 100 detections (Table

S2) using the same six covariates used for our relative abundance models (Table S3). We modeled detection intensity using two covariates (Table S3): the time latency from a human detection to the next detection of the target wildlife species, used to measure how wildlife responded temporally to humans, and a 0/1 indicator of whether hunting was allowed at the site. We diagnosed correlations in covariates using a Pearson correlation matrix ensuring correlation <0.60. All covariates were centered and scaled prior to analysis. We fit models in R by minimizing the negative log-likelihood using “optim” (R Development Core Team 2008), with a log-likelihood function implemented in C++ (see Kellner *et al.* 2021 for model code).

Ecological impacts

To assess the relative potential for ecological impacts of each species *s* we first adjusted the relative abundance to account for larger species being detected over a larger area (Rowcliffe *et al.* 2011). To relate this to ecological impact, we multiplied by the amount of time spent in front of the camera and the number of animals present, in the case of animal groups.

$$d_{sj} = \frac{\left(\frac{n_{sj}}{D_j}\right) * t_{sj} * g_{sj}}{A_{sj}} \qquad \text{Equation 1.1}$$

where d_{sj} is the scaled activity of species *s* on camera *j*, n_{sj} is the total count of species *s* on camera *j*, D_j is the total number of days camera *j* ran, and A_{sj} is the estimated detection area of camera *j,* given the body size of species *s*, following the estimation procedure of Rowcliffe *et al.* (2011). t_{sj} is the average amount of time species *s* spent in front of camera *j* in seconds and g_{sj} is the average group size of species *s* on camera *j*.

We calculated the relative ecological impact of each species, specific to three trophic levels (plants, invertebrates, vertebrates), by accounting for their metabolically active mass and diet (Table S4) with the ecological impact of species *s* on trophic level *v* given by:

$$I_{sv} = M_s * p_{sv} * \overline{d}_s \qquad \text{Equation 1.2}$$

where M_s is the average amount of metabolically active tissue in species *s,* p_{sv} is the percent of the diet of species *s* made up of items from trophic level *v* and $\overline{d}_s$ is the average scaled species activity (d_{sj}) for species *s* from Equation 1.1.

Results

Over 7,469 and 5,221 trap nights in BW and NC, we detected mammals and terrestrial birds >80g a total of 640 and 704 times representing 16 and 20 species, respectively. Hunted species were relatively less abundant with lower occupancy in BW compared to the NC, consistent with the reported 4x greater intensity of harvest in 2018 for BW compared to NC (Table 1, Fig. S1).

Spatial risk allocation

Both sites had a suite of species, hunted and unhunted, that were detected at high levels of urbanization and near human dwellings (Figs. 2, 3, Table S5). Most species in both countries showed no significant spatial relationship with humans at the site-level except gray fox (*Urocyon cinereoargenteus*) and eastern cottontail (*Sylvilagus floridanus*) in NC and red fox and Eurasian badger (*Meles meles*) in BW which were more likely to use the same sites as humans (Fig. 4,

Table S2). Coyotes in NC were less likely to use the same sites as humans, but only in larger urban areas (Table S2).

Hunted species were relatively less abundant at high levels of urbanization for both sites, with the difference being greater in BW (Fig. 2). Relative abundance for hunted species in NC was similar between habitat types (yard, forest, open), while hunted species in BW were much less likely to be detected in yards than unhunted species (Fig. 3; Table S6). This result was mirrored in our occupancy analyses which showed negative relationships with most hunted species in yards and urban areas, especially for BW (Fig. 4, Table S5).

Temporal risk allocation

Despite few species showing any spatial relationship with humans at the site-level, most species (80% (n=8) in BW, 56% (n=5) in NC) showed temporal avoidance of humans (Table S2). Hunted species often showed more temporal avoidance of humans in areas where they were hunted, where most other species temporally avoided humans regardless of hunting (Appendices 2, 7). White-tailed deer showed evidence of temporal avoidance of humans in hunted areas but not unhunted areas while roe deer showed the opposite pattern (Figs. 4, S2). Bears showed evidence of temporal attraction to humans in unhunted areas, but not hunted areas (Figs. 4, S2). Turkeys showed evidence of temporal avoidance of humans, but predominantly in unhunted areas (Figs. 4, S2). Boars temporally avoided humans in both hunted and unhunted areas, but slightly more in hunted areas (Figs. 4, S2).

Potential ecological impacts

Due to the high relative abundance of white-tailed deer in NC, potential rates of herbivory were much higher compared to BW. Most striking were the several orders of magnitude lower herbivory rates in yards than forests or open areas in BW due to a lack of roe deer in yards (Fig. 3). Potential predation rates were higher in BW, especially in yards, due to high red fox (*Vulpes vulpes*) relative abundance while rates in NC were lower and similar across habitats (Fig. 3). Potential predation rates on invertebrates were similar between the countries, being highest in forests in NC and lowest in forests in BW (Fig. 3). Potential ecological impacts in BW across all diet types were much lower in forests that were hunted, while in NC hunted areas had similar or higher potential ecological impacts compared to unhunted areas (Fig. 3).

Discussion

While it seems obvious that increased hunting pressure would affect how animals respond to humans on the landscape, ours is the first study to quantify this by directly comparing the effects of two different wildlife management schemes across a range of human disturbance. Although most of the mammal species are different between the sites, their range of ecological roles are analogous, and the two sites are similar in climate, topography, and land cover. We found several lines of support for the prediction that the more intensive, long-lasting hunting system of Germany contributes to lower relative abundance and differences in risk allocation of hunted species, particularly deer. Although the relative abundance of roe deer in BW appeared to be lowered by intensive hunting, other non-hunted herbivores did not compensate by increasing relative abundance, resulting in lower potential ecological impacts in terms of herbivory in BW hunted areas but not in NC, where hunting does not appear as effective at reducing the relative abundance of white-tailed deer.

Relative abundance

Our prediction that the higher hunting intensity of BW would result in hunted species being relatively less abundant than in the USA was supported. Hunted species had substantially higher occupancy and relative abundance in NC than in BW, suggesting that a more intensive hunting regime may reduce the relative abundance of hunted species and restrict spatial distributions. This also suggests that the presence of deer predators in the NC system did not substantially bias our relative abundance results, consistent with Bragina *et al.* (2019). The high relative abundance of deer in NC is typical of the eastern portion of the USA where adult deer face little population control from natural predators (Bragina *et al.* 2019). We found no difference in the relative abundance of unhunted species between the countries, however we note that such a comparison is made difficult by common species with no clear analog in the other country (e.g., stone marten (*Martes foina*) in BW).

Risk allocation

All hunted species showed evidence of spatial avoidance of human modifications to the landscape (i.e., urbanization, yards), with no such avoidance for unhunted species. Our prediction that hunted German wildlife would show more spatial avoidance of humans than hunted American wildlife was supported, with hunted species in BW being relatively less abundant in yards and urban areas that species in NC. This result is consistent with the risk allocation hypothesis which predicts more spatial avoidance in response to threats of higher intensity and longer duration (i.e., year-round hunting vs. 3-month duration), especially in landscapes with smaller, scattered urban areas that can be easily avoided, as we find in BW. The wide suburban sprawl of NC may necessitate a higher level of habituation for hunted species to navigate the landscape and that, along with a lower hunting intensity, shorter duration and common hunting prohibitions in cities and towns, may allow wildlife to maintain activities at a site while avoiding threats temporally. This prediction was supported by our temporal analysis where hunted species in NC showed little spatial avoidance of humans, but more temporal avoidance of humans in hunted areas, especially for the most heavily hunted species: white-tailed deer. However, in BW, heavily hunted roe deer and wild boar showed no temporal avoidance of humans in hunted areas. These results, taken with the spatial avoidance of humans displayed by roe deer, suggest that they are selecting sites with few humans. Indeed, detection rates of humans in forests in BW were low (BW = mean 0.09 people/day, NC = mean 0.21 people/day), making temporal avoidance less necessary. Further study of the fine-scale spatiotemporal dynamics of humans and deer in both countries will help improve our understanding of fear-based responses of wildlife to consumptive recreation.

Potential ecological impacts

Comparing just hunted and unhunted forests showed stark differences in the potential ecological implications of the two wildlife management systems due to difference in relative abundance. German hunted forests had lower mammal relative abundances and thus lower potential predation and herbivory rates. However, hunting in American forests was associated with only marginal declines in expected herbivory, consistent with past studies (Kays *et al.* 2016). Deer browsing in both countries can be high and has profound effects on forest health and regeneration (Stromayer & Warren 1997). In Germany, managers often take a “trees before animals” approach that promotes deer hunting as a means of enhancing tree growth (Rooney

2001). This approach can successfully foster forest regeneration (e.g., Schmit *et al.* 2020) but is dependent on how successfully deer populations can be controlled. Our results suggest that the hunting system of BW is better suited to fostering forest regeneration than in NC where hunting was not associated with a strong reduction in herbivore relative abundance.

In American forests, hunting was associated with increases in predator relative abundance. Given that NC hunters killed over 100,000 predators in 2018 (Table 1), this finding of higher predator relative abundance in hunted forests in NC is non-intuitive. However, light levels of hunting have been shown to increase local predator abundance through increased immigration rates (Gese 2005) and the potential for increased reproductive output supported by scavenging of carcasses (Mateo-Tomás *et al.* 2015). This suggests potential indirect community-level effects of hunting through altered social systems and/or productivity of non-target species.

There were striking differences in the relative abundance of red foxes, one of only two species to occur at both sites. Red foxes are less common in NC and must contend with a variety of competitors (i.e., raccoon, gray fox, bobcat, coyote), unlike BW where competitors are rare. The lack of competition, an innate ability to exploit urban habitats (Bateman & Fleming 2012) and decades of successful rabies vaccination schemes in BW (Storch *et al.* 2005) may benefit red fox populations. We found lower prey relative abundance in BW compared to NC yards which could be a result of higher red fox relative abundances and/or differences in the amount of food and cover present in German yards compared to American yards. Indeed, German and American yards differ substantially in their size, fencing and vegetation, with German yards tending to be smaller, fenced and highly manicured where American yards tend to be larger and unfenced with more tree cover and natural brush which may support small mammal populations.

Study limitations

Our study has some limitations on the interpretation of whether the changes in behavior and relative abundance of hunted animals we observed were caused by the differences in hunting regimes, or by other differences between the countries. The two countries differ not only in hunting style but also in landscape, human population density and yard structure which, although we took into account as much as possible, could nevertheless have affected our results. The ecology of each species could also have influenced our results, including the selection of habitats based on forage quality, presence of conspecifics or population demographic factors (e.g., age structure, density-dependence). While we were unable to account for these factors in the present study, we suggest that further research into their effect on fear-based responses is warranted. Finally, population-specific adaptation should be considered when extending our results to other areas. For example, boars in urban Berlin, where it is difficult or imposible to hunt them, use more urban landscape than in our study area (Stillfried *et al.* 2017) which could lead to different fear-based responses to humans. This highlights the need for broader study of wildlife and hunting systems to improve our understanding of how hunting practices and human disturbance interact to affect the distribution, abundance and behavior of wildlife populations.

Conclusions

Our results suggest that the more intensive hunting system typical of Germany is associated with lower relative abundance but that the duration of hunting and spatial pattern of humans on the landscape was associated with different fear responses to humans compared to the USA. We noted more spatial avoidance of humans and human structures on the landscape in BW that in NC which should reduce the potential for human-wildlife interactions in an increasingly urban landscape. We found no evidence that unhunted species increase activity or abundance to compensate for declines in their hunted competitors, resulting in ecological benefits in terms of less damage due to herbivory with potential benefits to forest regeneration. Our results show that hunting is a tool that can help reduce potential ecological and social impacts by changing wildlife abundance and behavior, especially in and around urban areas, and suggests that increasing the intensity of hunting pressure results in more fear of humans. Striking a balance between hunting regimes that effectively regulate wildlife populations and the public's willingness to tolerate and participate in hunting activities will be important to wildlife management as the world continues to urbanize.

Acknowledgements

We thank Gregor Wolf for help in the field and in identifying species in Germany. We are indepted to all citizen science volunteers for their support of this project.

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Tables and Figures

Figure 1: Camera trap locations set within and around two cities: Raleigh, NC, USA and Konstanz, BW, Germany. We sampled 242 sites in NC and 233 in BW, stratified by urbanized habitat and forest fragments, residential yards and open areas. Cameras ran for 3-weeks, placed in Germany between 2018-2020 and the USA between 2013 and 2019. Basemaps © 2021 Esri.

Figure 2: Relative abundance (detection rate: count/day) for mammal species detected on cameras run in Germany and the USA compared between two levels of urbanization, low (<40% urbanized in a 1km radius) and high (>40% urbanized in a 1km radius) and two habitat types (residential yards and not yards (i.e., forest fragments, open areas)). Data are taken from 242 sites in NC and 233 in BW. An (*) denotes heavily hunted species. Bars show standard error. Hunted species were relatively less abundant at high urbanization but the difference was much greater for German species. Relative abundance for hunted species in the USA were similar between habitat types, while relative abundance for hunted species in Germany was generally lower in residential yards.

Figure 3: Relative potential for ecological impact based on relative abundance, body mass and diet for species captured on camera traps in Germany and the USA. Herbivores are colored in shades of green, carnivores in pinks and omnivores in blues. We noted an order of magnitude difference in herbivory in yards and open areas in Germany, but similar rates in the USA and in German forests. Potential rates of herbivory were higher in the USA than in Germany for all habitats. Potential predation rates on invertebrates were similar between the countries, being highest in forests in the USA and lowest in forests in Germany. Potential predation rates on

vertebrates were higher in Germany, especially in yards, due predominantly to red foxes. Hunting in forested areas reduced the potential ecological impact of mammals across diet types in Germany but increased or did not substantially change it in the USA.

Figure 4: Infographic showing main spatial and temporal relationships with humans for four heavily hunted species. The position of each species along the color bar indicates the degree of avoidance (red) or attraction (green) to people and their infrastructure. Shown left to right on the "Humans at a site" bar are roe deer and boar in Germany and white-tailed deer and black bear in the USA. Data are taken from camera traps, with 242 sites sampled in NC and 233 in BW. Detailed model results in Table S2 and Table S5. Animal silhouettes are available online under a CC BY license.

Figure 1

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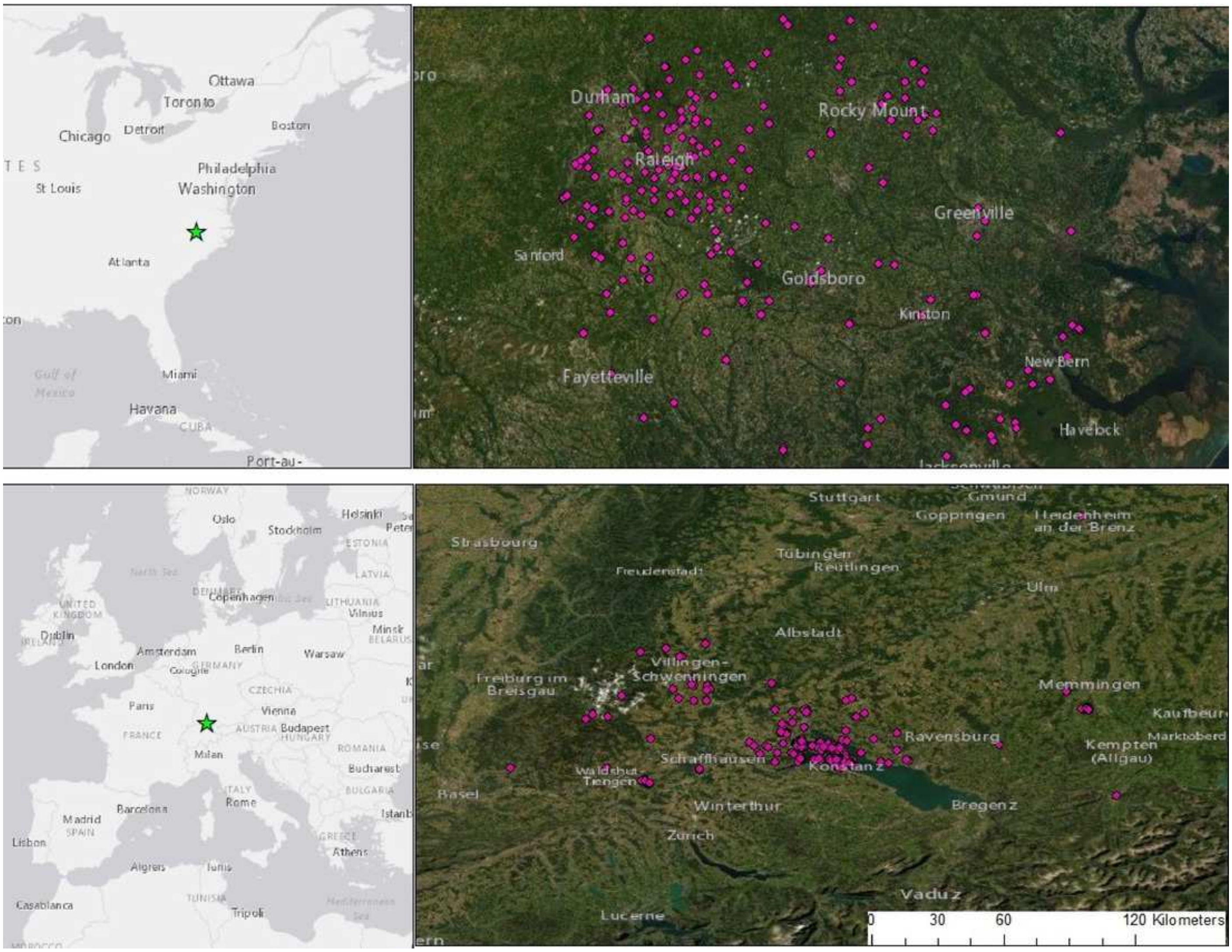

Figure 2

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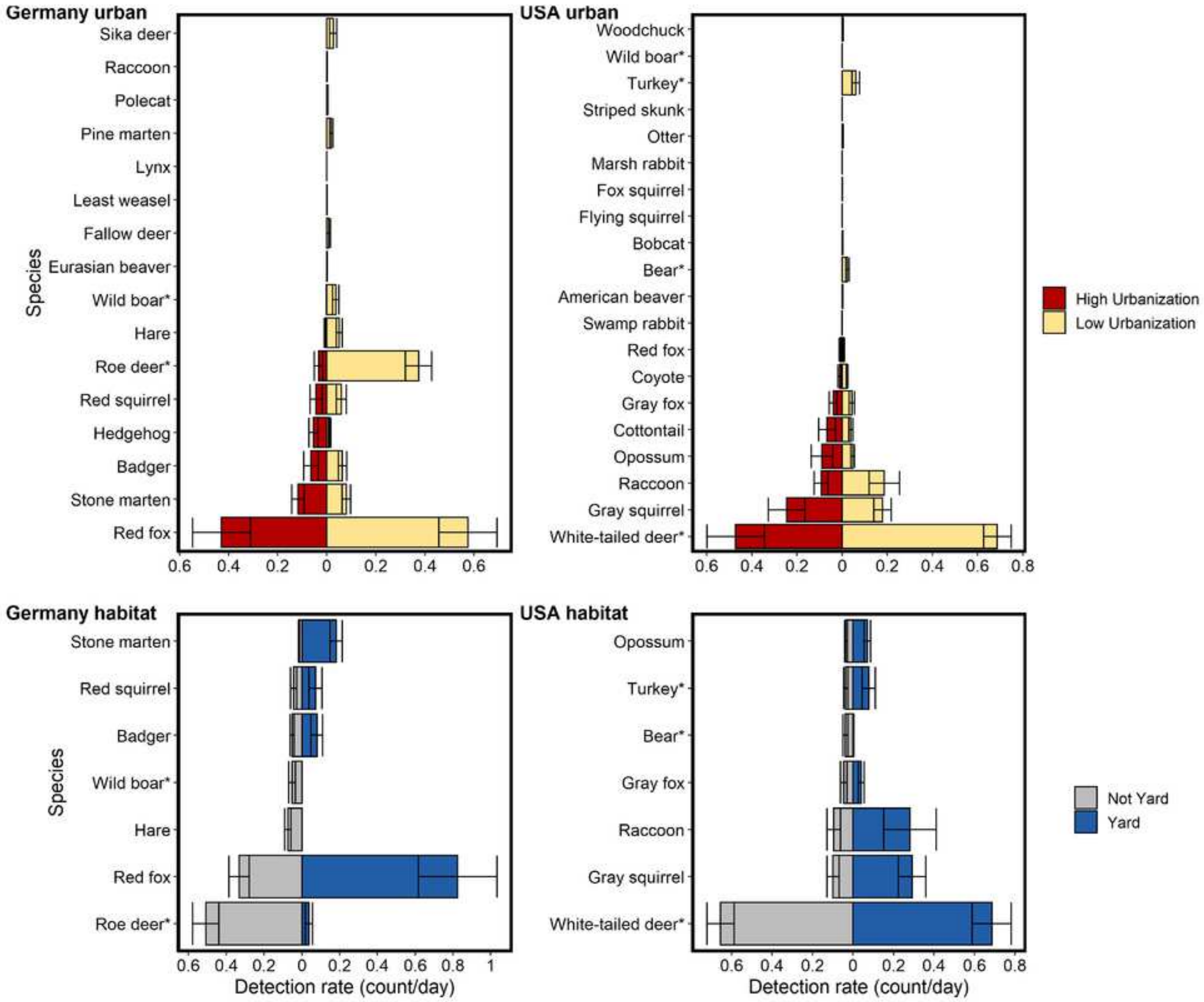
Germany urban
Sika deer
Raccoon
Polecat
Pine marten
Lynx
Least weasel
Fallow deer
Eurasian beaver
Wild boar*
Hare
Roe deer*
Red squirrel
Hedgehog
Badger
Stone marten
Red fox
Species
0.6 0.4 0.2 0 0.2 0.4 0.6
USA urban
Woodchuck
Wild boar*
Turkey*
Striped skunk
Otter
Marsh rabbit
Fox squirrel
Flying squirrel
Bobcat
Bear*
American beaver
Swamp rabbit
Red fox
Coyote
Gray fox
Cottontail
Opossum
Raccoon
Gray squirrel
White-tailed deer*
0.6 0.4 0.2 0 0.2 0.4 0.6 0.8
🟥 High Urbanization
🟨 Low Urbanization
Germany habitat
Stone marten
Red squirrel
Badger
Wild boar*
Hare
Red fox
Roe deer*
Species
0.6 0.4 0.2 0 0.2 0.4 0.6 0.8 1
Detection rate (count/day)
USA habitat
Opossum
Turkey*
Bear*
Gray fox
Raccoon
Gray squirrel
White-tailed deer*
0.6 0.4 0.2 0 0.2 0.4 0.6 0.8
Detection rate (count/day)
⬜ Not Yard
🟦 Yard

Figure 3

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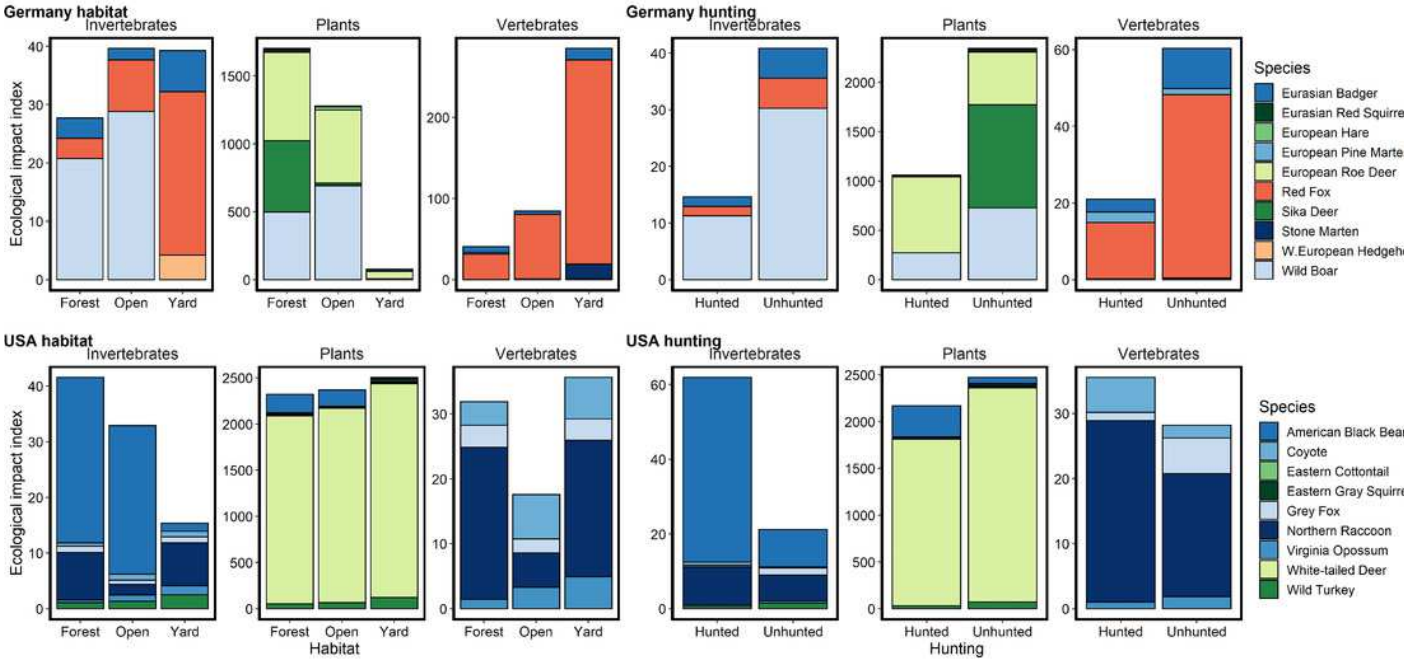
Germany habitat
Invertebrates
Plants
Vertebrates
Germany hunting
Invertebrates
Plants
Vertebrates
Ecological impact index
0
10
20
30
40
0
500
1000
1500
0
100
200
0
500
1000
1500
2000
0
20
40
60
Forest
Open
Yard
Hunted
Unhunted
Species
Eurasian Badger
Eurasian Red Squirre
European Hare
European Pine Marte
European Roe Deer
Red Fox
Sika Deer
Stone Marten
W.European Hedgeh
Wild Boar
USA habitat
Invertebrates
Plants
Vertebrates
USA hunting
Invertebrates
Plants
Vertebrates
Ecological impact index
2500
Habitat
Hunting
Species
American Black Bear
Coyote
Eastern Cottontail
Eastern Gray Squirre
Grey Fox
Northern Raccoon
Virginia Opossum
White-tailed Deer
Wild Turkey

Figure 4

Figure 4: Infographic showing main spatial and temporal relationships with humans for four heavily hunted species.

The position of each species along the color bar indicates the degree of avoidance (red) or attraction (green) to people and their infrastructure. Shown left to right on the “Humans at a site” bar are roe deer and boar in Germany and white-tailed deer and black bear in the USA. Data are taken from camera traps, with 242 sites sampled in NC and 233 in BW. Detailed model results in Table S2 and Table S5. Animal silhouettes are available online under a CC BY license.

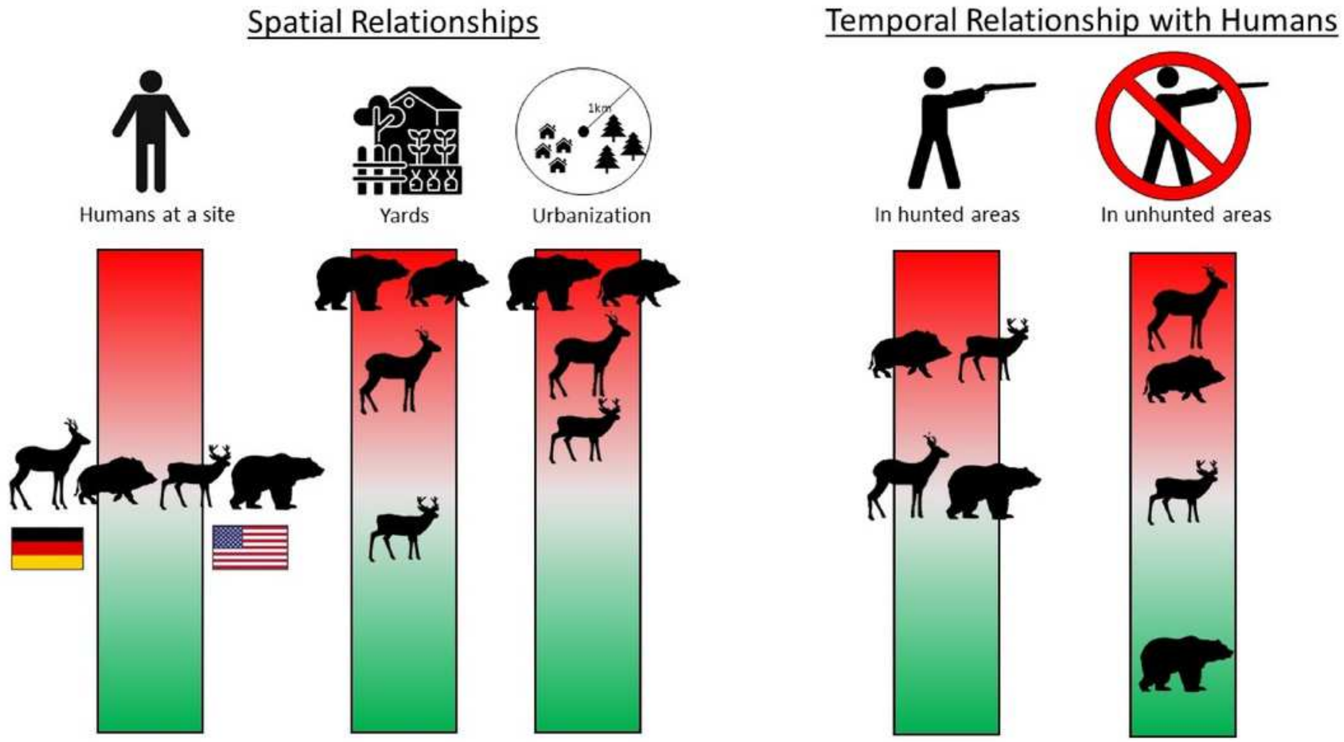
Spatial Relationships
Temporal Relationship with Humans
Humans at a site
Yards
1km
Urbanization
In hunted areas
In unhunted areas

Table 1(on next page)

Table 1: Hunted species in North Carolina (NC), USA and Baden-Württemberg (BW), Germany with associated bag limits, seasons lengths and annual bag for the region.

Data for NC and BW are taken from the North Carolina Wildlife Resources Commission[1] and the Jagdbericht Baden-Württemberg für das Jagdjahr 2018/2019[2], respectively. Bags are calibrated by average body mass to show the kg hunted (in 2018) for each species. Germany has requirements for minimum and maximum numbers of hunted animals, but no bag limit per hunter.

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Species	Country	Season bag limit	Season length (months)	2018 statewide harvest	Body size (kg)	kg hunted
Heavily managed and hunted						
White-tailed deer	NC, USA	6	3	178,554[1]	68	12,141,668
Bear	NC, USA	1	1	3,476[1]	181	629,156
Turkey	NC, USA	3	1	26,423[1]	9	237,806
European roe deer	BW, Germany	None	9	168,401[2]	27	4,546,827
Boar	BW, Germany	None	Year round	47,864[2]*	70	3,350,480
Hunted but not heavily managed (i.e., no bag limits imposed, longer seasons)						
Raccoon	NC, USA	None	4	65,353	6.8	444,400
E. gray squirrel	NC, USA	None	4	219,207	1.8	394,573
Coyote	NC, USA	None	Year round	31,808	12	381,700
E. cottontail	NC, USA	None	4	402,214	0.5	201,107
Bobcat	NC, USA	None	4	921	14	12,889
Red/gray fox	NC, USA	None	Year round	1,977	4.5	8,895
E. fox squirrel	NC, USA	None	3	2,931	1	2,931
Eurasian hare	BW, Germany	None	3	6,422	3	19,266
Red fox	BW, Germany	None	8	52,836	11	581,196

[1] NCWRC

[2] Berichte der Wildforschungsstelle (2020)

*2018 was a particularly bad hunting year for boar in BW. In 2017, a total of 78,628 individuals were hunted.