Effects of free-ranging livestock on sympatric herbivores at fine spatiotemporal scales

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Received: 9 August 2020 / Accepted: 26 February 2021 / Published online: 16 March 2021 © The Author(s), under exclusive licence to Springer Nature B.V. 2021

Abstract

**Context** Livestock grazing is one of the most widespread types of anthropogenic land use, even occurs in many protected areas and has become a threat to wildlife worldwide. Understanding livestock-wildlife interactions is crucial for rare large carnivores conservation. In China, free-ranging cattle within forests degrade the habitat of the tigers (*Panthera tigris*) and leopards (*Panthera pardus*), but quantitative assessments of how livestock affect the spatial and temporal use by the major ungulate prey of the two endangered felids are very limited.

**Objectives** This study aimed to examine the interactions of several sympatric wildlife species with livestock at a fine spatiotemporal scale in a human-dominated forest landscape.

**Methods** Based on a large-scale camera-trapping data across the China-Russia border, we used N-mixture models, two-species occupancy models and activity pattern overlap to understand the effects of cattle grazing on three ungulate species (sika deer *Cervus nippon*, wild boars *Sus scrofa* and roe deer *Capreolus pygargus*).

**Results** Spatially, with cattle activity increasing, wild boar and roe deer had different degrees of decline in the intensity of habitat use. Sika deer were displaced as more cattle encroached on forest habitat. Temporally, in the presence of cattle, wild boar and sika deer decreased their activities in the day. In addition, three wild ungulates trend to exhibit lower spatiotemporal overlap with cattle at shared camera sites.

**Conclusions** Our study shows that wildlife species may reduce the probability of habitat use by spatial avoidance and changing the daily activity patterns. We underscore that fine-scale (i.e. camera-site level) spatiotemporal avoidance is likely a key component of co-occurrence between livestock and the sympatry of competing ungulates inhabiting forest ecosystems. Given prey were depressed, efforts to minimize the livestock disturbance on these species need to be considered to ensure their sustained recoveries.
Keywords Camera trap · Wildlife-livestock interactions · N-mixture model · Activity pattern · Spatiotemporal overlap · Northeast China

Introduction

Livestock grazing covers nearly a quarter of the land surface of the planet (Robinson et al. 2014). As one of the most widespread types of land use (Díaz et al. 2007), livestock grazing generally is thought as detrimental to wildlife, although facilitation may occur as well (Ondadi et al. 2011; Schieltz and Rubenstein 2016). If not properly managed, grazing by domestic livestock could constitute a threat to native fauna by competing for limited space and resources (Dettemmaier et al. 2017; Filazzola et al. 2020). Livestock grazing can intensify pressure on local wildlife, as it may alter their temporal activity patterns and decrease their spatial distribution, habitat use and food availability (Madhusudan 2004; Herfindal et al. 2017; Pudyatmoko 2017; Filazzola et al. 2020). Livestock grazing can intensify pressure on local wildlife, as it may alter their temporal activity patterns and decrease their spatial distribution, habitat use and food availability (Madhusudan 2004; Herfindal et al. 2017; Pudyatmoko 2017; Filazzola et al. 2020). Livestock grazing can intensify pressure on local wildlife, as it may alter their temporal activity patterns and decrease their spatial distribution, habitat use and food availability (Madhusudan 2004; Herfindal et al. 2017; Pudyatmoko 2017; Filazzola et al. 2020). Livestock grazing can intensify pressure on local wildlife, as it may alter their temporal activity patterns and decrease their spatial distribution, habitat use and food availability (Madhusudan 2004; Herfindal et al. 2017; Pudyatmoko 2017; Filazzola et al. 2020). Livestock grazing can intensify pressure on local wildlife, as it may alter their temporal activity patterns and decrease their spatial distribution, habitat use and food availability (Madhusudan 2004; Herfindal et al. 2017; Pudyatmoko 2017; Filazzola et al. 2020).

Large wild herbivores are particularly susceptible to the impacts of livestock through interference competition and changes in forage quantity and quality in many ecosystems (Stewart et al. 2002; Schieltz and Rubenstein 2016; Lahkar et al. 2020). This, in turn, could be a major constraint on the population performance of large and threatened carnivores via trophic cascades (Filazzola et al. 2020). In the temperate mixed-forests of northeast Asia, for example, sympatric carnivore species such as the endangered Amur tiger (Panthera tigris altaica) and Amur leopard (Panthera pardus orientalis) and their prey face threats from free-ranging cattle grazing (Wang et al. 2016). Due to poor management practices and law enforcement, villagers graze their livestock even in the reserve. Currently, the husbandry of free-ranging cattle in the forest is one of the greatest factors in habitat destruction. Cattle can reduce the plant biomass in the shrub-herb layer by ~24% in summer in Northeast China (Wang et al. 2019). Wild ungulate densities are reduced due to competition with livestock for forage and snaring by local villagers (Zhou and Zhang 2011; Wang et al. 2016). The combination of cattle grazing and other human activities is restricting the expansion of tigers and leopards further into China (Wang et al. 2016, 2018). Due to depressed prey availability, tigers and leopards also prey on livestock, which causes further conflicts with humans (Soh et al. 2014). In seeking to create a protected area for tigers and leopards, the Chinese government recently created a large national park (ca. 15,000 km²) along the China-Russia border. Management department plans to shift forest management away from livestock grazing to restore habitat for declining populations of tigers and leopards, while also providing important ecological services to support human livelihoods (McLaughlin 2016).

Here, we present a fine-scale (i.e. camera sites) analysis of the spatiotemporal use patterns of large wild ungulates in response to cattle grazing in Northeast China using data from a large-scale camera-trap study. We investigated the livestock-ungulate interactions in combination with environmental factors using N-mixture and co-occurrence models that account for imperfect detection (MacKenzie et al. 2004; Royle 2004). We focus on three main ungulate prey species (sika deer Cervus nippon, wild boars Sus scrofa and roe deer Capreolus pygargus) because (1) they collectively account for 92% of the tiger diet (21%, 49% and...
22%, respectively) and 87% of the leopard diet (50%, 18% and 19%, respectively) (Sugimoto et al. 2016), (2) the effect of livestock grazing on biodiversity are greatest for trophic levels directly dependent on plants, such as wild herbivores (Filazzola et al. 2020). This research tested three hypotheses. First, spatially, we hypothesized that all wild ungulates would demonstrate a decreased abundance and habitat use as cattle abundance increased, but the magnitude of the impact of livestock will vary among the species. Specifically, we predicted that sika deer may show lower tolerance of livestock disturbance than wild boar and roe deer as sika deer is sensitive to human activities in this area (Xiao et al. 2018). Second, wild ungulates will show temporal avoidance of cattle. Finally, we consider spatiotemporal avoidance, whereby ungulate species might not avoid a site used by cattle altogether (i.e., complete spatial avoidance), but rather avoids a given site for some period of time after it is visited by cattle. This research can help to refine strategies for conserving tigers, leopards and their natural prey in China.

Methods

Study area

We conducted our research in the eastern part of Northeast Tiger Leopard National Park. The park was established in 2016 and located in the northern portion of the Changbai Mountains in Jilin Province, China, adjacent to southwestern Primorsky Krai, Russia, to the east and North Korea to the southwest. The approximately 5000-km² study area includes three natural reserves (Hunchun, Wangqing and Laoyeling) established earlier and forms the core of a potential recovery landscape for tigers and leopards in China (Hebblewhite et al. 2012; Wang et al. 2016). Recent study suggest that tiger and leopard density are comparatively low (0.20–0.27 adult tigers and 0.30–0.42 adult leopards/100 km², respectively) in the area (Wang et al. 2017, 2018). Elevations range from 5 to 1477 m. The climate is characterized as a temperate continental monsoon with an average annual temperature of 5.60 °C (± 1.30 °C) and a frost-free period of 110–160 days/yr. The annual average precipitation was 618 mm (± 68 mm) during 1990–2010, with the most precipitation occurring in the summer from June to August. Forest cover is more than 92% and the majority of forests have been converted into secondary deciduous forests over the past 5 decades (Li et al. 2009).

Like many of the natural reserves in China, the park was created after farmers began settling there. Within the park over 62,300 people reside in 130 villages, and rely on crop cultivation, gathering of non-timber forest products and livestock husbandry for their livelihoods. Livestock is essential to sustain the livelihood of local people and for the rural development of the region. There appears to be 25,000–65,000 each year that graze most part of the year in the study area during the past 10 year (Wang et al. 2016). Grazing can begin at various times in early April and extend to middle November. Over 90% of the cattle-owners already keep their cattle at night in the intricate network of wire or electric fences distributed across the forests, unlike in neighboring small villages in Russia where livestock are herded back into barns at night. When food is scarce in winter, cattle are stall-fed in the village. Cattle weigh more than 300 kg, which much greater than three wild ungulates (wild boar, roe deer and sika deer) with body size ranging 30–110 kg (Dou et al. 2019).

Camera trap survey

Camera trapping was conducted continuously from August 2013 to July 2014 (Fig. S1). We established 3.6 × 3.6 km grids to guide the placement of 356 camera trap sites throughout the study area. We deployed at least one camera per grid cell and excluded any non-forest habitat within all grids; on average, adjacent camera sites were 2.36 km apart. We maximized detection probability by placing cameras at sites where wildlife and livestock were likely to travel (e.g., along ridges, valley bottoms, trails, forest roads and near scent-marked trees). We deployed unbaited cameras (LTL 6210, Shenzhen, China) along forest roads (n = 199 sites) and game trails (n = 157 sites), where they were fastened to trees approximately 40–80 cm above the ground and programmed to take videos 24 h/day with a 1-min interval between consecutive 15 s videos. Sensitivity, flash brightness, and ISO settings were all standardized. We visited...
each camera 3–5 times a year to download photos and check the batteries.

**Covariates**

We considered a suite of abiotic and biotic covariates that could potentially influence the spatial distribution of the three wild ungulates and cattle in this area (Table 1). Specifically, we considered elevation, topographic position index (TPI; e.g., finer-scale depressions or ridges) (De Reu et al. 2013), percent tree cover (PTC), the nearest distance to the Russian border, cattle encounter rates and anthropogenic activity. We also tested for a quadratic effect of elevation and TPI assuming the three ungulates prefer intermediate levels of these covariates. TPI was calculated using a circular neighborhood with a 1-km radius from the Shuttle Radar Topography Mission (SRTM) 30-m digital elevation model. The PTC was derived for each camera site from the Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (product MOD44B) of the study area. We used distance to the Russian border (e.g., the boundary of leopard land national park in Russia) as a measure of the effect of the source wildlife populations on wild ungulate occurrence. For the spatial measures of anthropogenic activity, we calculated the nearest distance to settlements and roads as well as encounter rates of humans (i.e., people on foot) and vehicles at each camera-trap site. All distance covariates were calculated in ArcMap 10.1 (ESRI Inc., Redlands, CA, USA) for each camera site.

To understand species interactions, we considered the cattle encounter rate (i.e., a quantitative measure of grazing intensity) or presence/absence (0/1) as predictors of the activity of the three ungulates. Given that sika deer outcompete roe deer (Aramilev 2009), we added sika deer to the roe deer models. We calculated encounter rates for tigers, leopards, wild boar, sika deer, roe deer, cattle, and humans and vehicles at each camera-trap station as the number of detections per 100 camera-trap days using a 30-min period of independence per animal or vehicles for the entire grazing period (from April to November) (O’Brien et al. 2003).

We used camera days (i.e. number of days camera traps were active during each sampling occasion) as a measure of effort to model the baseline detection probability. The risk of predation may shape behavior of fearful prey and alter animal’s detection rates (Say-Sallaz et al. 2019). We therefore included two predation risk factors (tiger and leopard activity) in the detection model. We also allowed for detection probabilities to vary by different occasions and treated it as a categorical covariate with 30-day intervals.

We tested for collinearity among covariates using two methods. First, a variance inflation factor (VIF), which measures multicollinearity among variables, was calculated for all covariates and those with a VIF < 3 were retained in the model. Then, Pearson’s correlation coefficients (r) were calculated to further exclude highly correlated variables with a |r| > 0.7 (Dormann et al. 2013). All continuous covariates were scaled to a mean of 0 and a standard deviation of 1 prior to the analyses.

**Habitat use modelling**

Under the assumption that detections were fully explained by the covariates and the population was closure (Barker et al. 2017), we used N-mixture models (Royle 2004) to assess the relative effects of abiotic and biotic covariates on the spatial use of the three wild ungulates and cattle at each camera site using grazing season of camera trap data (from April to November). Binomial N-mixture models allow separate estimation and modeling of relative abundance (or the intensity of spatial use) from replicated counts of unmarked individuals under imperfect detection, therefore the models have proven very useful and widely used (Keever et al. 2017; Kery 2018). Because camera trap designs are considered “plotless designs”, N-mixture models have been used to estimate activity rates from spatially and temporally replicated counts of unmarked animals while accounting for imperfect detection (Shamoon et al. 2017b). Thus, for each camera site, we used 30-day as the temporal sampling unit (i.e., survey occasion) and accumulated encounters within each occasion as counts (Xiao et al. 2018). The number of encounters, which was considered a measure of activity rate, indicated whether a site was more or less likely to be visited by animals (Rowcliffe et al. 2008; Shamoon et al. 2017a), so we also used the encounter index as an indicator of the intensity of habitat use by the three ungulates based on the assumption that habitat conditions are directly related to the number of times that a location is visited by the species (Boyce and McDonald 1999). For
Table 1  Covariates used for N-mixture models to model habitat use by wild boar, roe deer and sika deer along the China-Russia border

| Covariate (abbreviation) | Description                                                                 | Observed range of values | Data source                                                                 | Component expected to influence |
|--------------------------|------------------------------------------------------------------------------|--------------------------|----------------------------------------------------------------------------|---------------------------------|
| Elevation                | Numeric (m), elevation of point generated from 30-m DEM                      | 152–1349                 | Shuttle Radar Topography Mission (SRTM) 1 Arc-Second Global a               | Abundance                       |
| Topographic position index (TPI) | Numeric, the difference between the elevation of a central pixel and the mean of its surrounding cells. Negative values represent valley bottoms | -70–109                  | Calculated from elevation grids                                            | Abundance                       |
| Percent tree cover (PTC) | Numeric, percent of pixel that is covered by trees (%)                      | 22–70                    | MODIS/Terra Vegetation Continuous Fields Yearly 250 m (MOD44B) b            | Abundance                       |
| Distance to border (Dist.border) | Numeric (km), distance from camera to the nearest border                  | 0.019–48.21              | Calculated from local geographic information dataset                        | Abundance                       |
| Distance to settlement (Dist.settlement) | Numeric (km), distance from camera to the nearest settlement       | 0.33–14.89               | Calculated from local geographic information dataset                        | Abundance                       |
| Distance to road (Dist.road) | Numeric (km), distance from camera to the nearest road                     | 0–7.30                   | Calculated from local geographic information dataset                        | Abundance                       |
| Human presence (Human)   | Numeric, encounter rate of people on foot (detections /100 trap-days)       | 0–140.48                 | Camera trap                                                                | Abundance                       |
| Vehicles                 | Numeric, encounter rate of vehicles (detections /100 trap-days)             | 0–282.97                 | Camera trap                                                                | Abundance                       |
| Sika deer                | Numeric, encounter rate of sika deer (detections /100 trap-days)            | 0–28.92                  | Camera trap                                                                | Abundance                       |
| Cattle                   | Numeric, encounter rate of cattle (detections /100 trap-days)               | 0–258.33                 | Camera trap                                                                | Abundance                       |
| Cattle presence (Cattle.pres) | Categorical, cattle presence/absence in camera site (0/1)          | Indicators of each category (1 or 0) | Camera trap                                                                | Abundance                       |
| Tiger                    | Numeric, encounter rate of tigers (detections /100 trap-days)               | 0–10.72                  | Camera trap                                                                | Detection                       |
| Leopard                  | Numeric, encounter rate of leopards (detections /100 trap-days)             | 0–5.29                   | Camera trap                                                                | Detection                       |
| Days                     | Numeric, total days each camera was in operation during each sampling occasion | 0–31                    | Camera trap                                                                | Detection                       |
| Time                     | 30-day interval (categorical)                                              | -                        | Camera trap                                                                | Detection                       |

aSRTM dataset (https://doi.org/10.5066/F7PR7TFT)

bMODIS vegetation continuous cover/fields (https://lpdaac.usgs.gov/products/mod44bv006/)
example, if an animal forages or shelters in an area, it will be photographed for longer periods of time and thus, have higher encounter rates.

We began our modelling procedure by using the monthly encounter rates at each camera trap to build N-mixture models for each species with all covariates (hereafter, ENV model). In this step, we removed covariates that were not significant for any species using a stepwise selection procedure, and we then established two additional models for each wild ungulate species. We added cattle encounter information (hereafter, cattle.num model) and the presence or absence of cattle (hereafter cattle.pres model) into the first model to test levels of tolerance to cattle disturbance. For each ungulate, we determined the most supported model using AIC (Burnham and Anderson 2012). We used computationally efficient graphical checks and overdispersion measures to assess the goodness-of-fit of N-mixture models using the R package nmixgof (Knape et al. 2018). The coefficient estimates of the final model were considered significant if their 95% CIs did not include zero. We used a zero-inflated Poisson variant of the N-mixture since there were many zeroes in the data, which provided a better fit to the data compared to a Poisson variant as determined by a likelihood ratio test (LRT) (Zuur et al. 2012). All N-mixture models were fit using the R package unmarked (Fiske and Chandler 2011).

Deer and wild boar in our study area are highly sedentary, with no detectable seasonal movement patterns (Hojnowski et al. 2012), we thus reported the result of N-mixture models using grazing season data which reflecting the influences of long-term livestock husbandry practices on the intensity of habitat use by the three ungulates.

Spatia co-occurrence

We investigated the potential co-occurrence between the cattle and the three ungulates by fitting two-species habitat occupancy models to the camera-trapping data from the study area. We used conditional parameterization to estimate each parameter (Table S1) (Richmond et al. 2010) and assumed that the occupancy and detection of the three ungulates (subordinate species B) were dependent on the presence or absence of the cattle (dominant species A). As we assessed fine-scale space use, we interpreted occupancy as the probability of the use of a camera site. We aggregated 2-week survey periods into a single sampling occasion and constructed detection histories for cattle and the three ungulates for each camera site, resulting in 18 temporal replicates. We include the detection and occupancy variables from the most supported N-mixture models to construct the co-occurrence models, which reduce the likelihood that species interactions is confused with differential habitat selection. We estimate and compare (1) the probability of wild ungulate occupancy (B) where cattle are present (A) ($psiBA$) versus where cattle are absent (a) ($psiBa$); and (2) the probability of wild ungulate detection (B) where both ungulates and cattle (A) are present ($rBA$) versus where cattle are absent ($pB$) for each site.

We estimated a species interaction factor (henceforth, SIF) for each species combination and considered SIF < 1.0 to be evidence of apparent spatial segregation (e.g. occur together less often than expected if independent), SIF > 1.0 to be apparent spatial overlap (e.g. occur together more often than expected if independent), and SIF = 1.0 to be evidence of site-use independence. We implemented the model in the programme PRESENCE 11.8 (Hines 2017).

Daily activity patterns

All detections were used to create 24-h activity patterns by ignoring the calendar date for each species. We used kernel density estimation and trigonometric sum distribution to estimate the probability density functions of the activity patterns (i.e., density of activity) for each animal. We estimated the overlap coefficient ($\Delta$) using the R package overlap (Ridout and Linkie 2009) to assess activity pattern overlap between cattle and each wild ungulate species during the grazing season (Ridout and Linkie 2009; Meredith and Ridout 2017). We also tested whether a species changed activity patterns by grouping records according the presence and absence of cattle and then assessed the overlap. The coefficient ranges from 0 (no overlap) to 1 (complete overlap) with a low degree of overlap indicating temporal avoidance. We tested for statistical differences in activity using the non-parametric Mardia–Watson–Wheeler test for homogeneity, which tests for differences in the mean angle or variance of two samples. To account for the continuous changes of sun’s position throughout the year in northern latitudes, we therefore transformed
clock time to sun time, with 06:00 representing sunrise and 18:00 sunset (‘sunTime’ function in overlap package in R). We obtained 95% confidence intervals for Δ for every pairwise species using 10,000 bootstrapped samples. Lashley et al. (2018) recommend at least 100 detections of a targeted species were collected before estimating activity pattern from camera trap data; in this study, all species detections exceeded the detection threshold.

Spatiotemporal interactions

Following Karanth et al. (2017), we used multiresponse permutation procedures to assess spatiotemporal segregation between cattle and each wild ungulate, which is conditional on the observed space use and temporal activity patterns of the focal species. At camera sites where both cattle and each ungulate co-occurred, we calculated the minimum cattle encounter time for each ungulate and then generated expected statistical distributions of times-to-encounter by randomly assigning encounter times to camera-trap locations in 1000 simulations. We compared the median observed time-to-encounter with a random simulated expected distribution; a larger observed time-to-encounter than expected (assuming species independence) reflects species segregation while a smaller value implies species aggregation. Spatiotemporal niche analyses were conducted separately in 2013 (from August to November) and in 2014 (from April to July).

Results

We recorded 1631 independent detections of wild boar, 3559 independent detections of roe deer, and 1166 independent detections of sika deer over 114,854 trapping-days from August 2013 to July 2014 (Table S1). Wild boar and roe deer were photographed at 84% and 92% of the camera sites respectively, while sika deer were only photographed at 40% of the stations (Fig. 1a-c). We observed a total of 3110 cattle detections with approximately 30% of all stations having cattle presence (Fig. 1d). Tigers (n = 356 detections) and leopards (n = 362 detections) were photographed at 21% and 31% of all stations, respectively (Fig. 1e, f).

Habit use modelling

There is evidence that the zero-inflated Poisson variant of N-mixture model is significantly superior to the Poisson variant (LRT: L = 100.92, p < 0.001 for wild boar; L = 83.00, p < 0.001 for roe deer; L = 61.07, p < 0.001 for sika deer; L = 275.02, p < 0.001 for cattle). All covariates were retained because no collinearity was detected (VIF < 3.0 and r < 0.7) (Table S3), and including the cattle interactions improved the N-mixture model performance for each species (Table 2). Introducing the cattle encounter rates to the habitat use model (cattle.num) better predicted wild boar and roe deer encounters than the simple presence/absence of cattle (cattle.pres), while the opposite was found for sika deer encounters. As expected, the cattle spatial activity had a significant negative correlation with wild boar and roe deer encounters, while the presence of cattle correlated negatively with sika deer encounters (Fig. 2 and Table S4).

Wild boars were detected more often at intermediate elevations (with preference peaking at ca. 600 m a.s.l.), farther from roads, closer to settlements, and they preferred valleys and flat slopes (Fig. 2a and Fig. S3). Roe deer were found at higher elevations and farther from roads, and they preferred ridges and avoided sika deer and humans (Fig. 2b and Fig. S4). Sika deer activity was predicted to be at lower elevations and farther from settlements, and they tended to avoid vehicles but preferred flat to moderate slopes, dirt roads and lower forest coverage (Fig. 2c and Fig. S5). In addition, sika deer were detected more often closer to the border (< 10 km), reflecting more suitable habitats across the China-Russia border (also see Fig. 1c). Cattle used lower elevations and valley bottoms and were closer to settlements (Fig. 2d and Fig. S6). They also occurred where there was higher percent tree cover and did not avoid people on foot or vehicles.

The detection probabilities of the three ungulates and domestic cattle depended on camera trap effort. Roe deer and sika deer were more likely to be detected at locations with lower tiger and leopard presence, but wild boar were associated with lower tiger presence and higher leopard presence. Cattle were more likely to be detected at locations with lower tiger activities. Although overdispersion metrics for the top model for wild boar (c-hat = 1.16), roe deer (c-hat = 1.06), sika deer (c-hat = 1.83) and cattle (c-hat = 1.26) suggested
a slight high-dispersion, we did not find strong spatial patterns in the site-sum randomized-quantile residuals of the N-mixture model for each species (Fig. S2).

**Spatial co-occurrence**

Wild boar or roe deer showed little relationship in co-occurrence with cattle ($SIF = 1.07 \pm 0.04$ SE and $0.99 \pm 0.03$ SE, respectively, Table 3). However, cattle and sika deer exhibited lower levels of spatial co-occurrence in habitat use (i.e., apparent spatial avoidance, $SIF = 0.87 \pm 0.05$ SE) with sika deer occupancy being higher at sites where cattle were absent ($psiBa = 0.41 \pm 0.03$ SE) compared to where they were presence ($psiBA = 0.34 \pm 0.01$ SE). The probability of detecting wild boar did not differ between areas occupied by cattle ($rBA = 0.19 \pm 0.01$ SE) and cattle-free areas ($pB = 0.20 \pm 0.01$ SE) (Table 3). The probability of detecting roe deer and sika deer was lower in areas occupied by cattle ($rBA = 0.27 \pm 0.01$ SE and $0.18 \pm 0.02$ SE, respectively) than in cattle-free areas ($pB = 0.33 \pm 0.01$ SE and $0.24 \pm 0.01$ SE, respectively).
### Table 2  N-mixture model for interactions of sika deer, roe deer and wild boar with livestock along the China-Russia border

|                  | Wild boar       | Roe deer        | Sika deer       |
|------------------|-----------------|-----------------|-----------------|
|                  | Cattle.num | ENV | Cattle.pres | Intercept-only | Cattle.num | Cattle.pres | ENV | Intercept-only | Cattle.pres | Cattle.num | ENV | Intercept-only |
| Elevation        | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| Elevation²       | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| TPI              | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| TPI²             | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| PTC              | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| Dist.settlement  | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| Dist.road        | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| Dist.border      | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| Human            | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| Vehicles         | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| Sika deer        | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| Cattle           | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |
| Cattle.pres      | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● | ● ● ● ● ● ● ● ● ● |

|   | K   | AIC  | ΔAIC | wi   |
|---|-----|------|------|------|
| Wild boar | 12  | 7706.76 | 0 | 1.00 |
|         | 11  | 7724.40 | 17.65 | 0.99 |
|         | 12  | 7725.65 | 18.88 | 0.01 |
|         | 2   | 7947.99 | 241.23 | 0.00 |
| Roe deer | 13  | 12,365.00 | 0 | 0.99 |
|         | 13  | 12,374.03 | 9.02 | 0.01 |
|         | 11  | 12,384.00 | 18.51 | 0.00 |
|         | 2   | 12,951.93 | 586.91 | 0.00 |
| Sika deer | 15  | 4555.37 | 0 | 0.79 |
|         | 15  | 4558.60 | 3.23 | 0.16 |
|         | 14  | 4560.90 | 5.55 | 0.05 |
|         | 2   | 5772.54 | 1217.17 | 0.00 |

All models use the same detection covariates (time + days + tiger + leopard). See Table 1 for variable definitions and abbreviations. Black points represent the covariates included in the corresponding model.

K is the number of parameters, ΔAIC the difference in AIC relative to the best model, wi Akaïke weight that indicates the relative support for each model.
Daily activity patterns

The three ungulates exhibited high diurnal and crepuscular activity. The diurnal cattle showed a statistically significant different activity patterns with the ungulates (all \( p < 0.001 \)), although had a high degree of overlap in daily activity with wild boar (\( \Delta = 0.70, 95\% \ CI = 0.69–0.72 \)), roe deer (\( \Delta = 0.74, 95\% \ CI = 0.71–0.75 \)) and sika deer (\( \Delta = 0.80, 95\% \ CI = 0.77–0.83 \)) (Fig. 3). Wild boar (\( w = 0.65, p < 0.001 \)) and sika deer (\( w = 0.37, p < 0.01 \)) noticeably decreased diurnal activities at sites with cattle presence, respectively (Fig. 4). In contrast, roe deer did not change their activity patterns at sites with cattle presence (\( w = 0.17, p > 0.05 \)), but showed the higher crepuscular activity at sites with cattle absence.

Spatiotemporal interactions

When spatiotemporal overlap occurred, we examined the times-to-encounter between the three ungulates and cattle to test for behavioural avoidance. The proportion of independent detections recorded in the sites where cattle were absent exceeded 70% among three ungulates (Table S5),
and sika deer and cattle co-occurred at the fewest camera sites. The median observed minimum time-to-encounter (ranging from 6.86 to 16.94 days) was significantly greater than the randomly generated time-to-encounter (ranging from 4.10 to 6.72 days) in both years, suggesting fine-scale (i.e., exact same point locations) behavioural avoidance (Fig. 5 and Table S5).

**Discussion**

Our study combined large-scale camera-trap data and multiple spatiotemporal methods to assess the drivers of fine-scale spatiotemporal variation in habitat use by three ungulate species along the China-Russia border. We highlight that current practices of livestock grazing within the park influence the spatial and...
temporal behaviour of these animals with unmeasured, but likely negative effects on fitness. Further, we underscore that fine-scale spatial, temporal or combined spatiotemporal avoidance is likely a key component of co-occurrence between livestock and the sympatry of competing ungulates inhabiting temperate forest ecosystems. This will greatly improve our understanding of species interactions in a livestock-dominated landscape, which compose a contributing disturbance to global biodiversity.

Not surprisingly, habitat use by the three ungulates was influenced by topography, human disturbance and land management practices (i.e., grazing). The N-mixture models revealed some separation by all ungulates along the elevation gradient with sika deer responding positively to lower elevations, followed by wild boar, which selected intermediate elevations, and roe deer, which selected higher elevations. The three ungulates also exhibited different responses to TPI. Thus, topographic features may reduce resource competition and promote co-occurrence among sympatric ungulates in our study area. Due to their tendency to be active during the daytime, the three ungulates avoided roads, vehicles and other areas with people. Elsewhere in Asia, ungulates have been documented to exhibit similar behavioural responses when

Fig. 5 Spatiotemporal interactions, as indicated by times-to-encounter, between cattle and wild boar, roe deer and sika deer generated from multi-response permutation procedures along the China-Russia border. The vertical lines represent the median minimum time-to-encounter between two species, while the area under the curve shows randomly simulated times-to-encounter. The $p$-values, representing the proportions of randomly generated times-to-encounter values that are greater than the observed times-to-encounter, are given for each year.
inhabiting areas with anthropogenic disturbance. In the Russian Far East, the three ungulates strongly avoided areas with high road densities, and sika deer were found far from settlements (Hebblewhite et al. 2014). The relative abundance of wild ungulates declined with the number of villages in the vicinity and increased with the distance to the nearest village in the Himalayan mid-hill landscapes of Nepal (Paudel and Kindlmann 2012). We noted that wild boar thrive near settlements, which likely reflects their preference for agricultural lands along the edges of human developments (Apollonio et al. 2010).

Our results demonstrate the importance of biotic interactions in shaping distribution patterns and potential range limits. Although species distribution modelling is widely applied in conservation (Romero et al. 2016), most studies exclude species interactions (Wisz et al. 2013), so our results contribute to the low but growing recognition of the influence of biotic interaction on distribution patterns. For example, the marked negative influence of sika deer on the use of camera sites by roe deer suggested that sika deer might cause roe deer to move into areas that they do not use (e.g., higher elevations, Fig. 2), perhaps leading to ecological niche differentiation. This was consistent with a study by Aramilev (2009) which found sika deer occupy roe deer habitats in the Russian Far East and cause roe deer shift to mid-mountain elevations. In particular, the cattle-ungulate interactions provided additional explanatory power and improved model performance for all ungulate species (see Table 2). The best model for each ungulate incorporated cattle interaction (either presence or number of encounters), but ecological differences between wild ungulates resulted in different behavioural responses, supporting the first research hypotheses.

Wild boar and roe deer are highly flexible species that thrive in human-dominated landscapes, and they are now common throughout much of the region (their naïve occupancy was > 80%). Cattle used lower elevations than wild boar and roe deer, and both wild ungulates noticeably reduced their habitat use at low elevations and valley bottoms as more cattle were encountered, suggesting that cattle could compel these two wild species to shift to higher elevations. This was consistent with the findings of Stewart et al. (2002), who demonstrated substantial resource partitioning in the elevations used by elk (Cervus elaphus nelsoni), mule deer (Odocoileus hemionus) and cattle. In brief, wild boar and roe deer physically distance themselves from cattle herds but do not abandon the habitat; they apparently exhibited fine-scale behavioural avoidance (see Fig. 5). Similarly, Madhusudan (2004) reported that wild boar, a non-ruminant generalist, did not strongly respond to livestock activities in a tropical Indian wildlife reserve.

For sika deer, the best model included the presence/absence of cattle instead of livestock encounter rates, so as expected, sika deer may be less tolerant of disturbance from livestock than the other two ungulates. The existing levels of grazing by livestock could be high enough to alter the habitat preference of sika deer, irrespective of the intensity. The two-species occupancy model further validated this idea that cattle occupy the resources and limit sika deer dispersal to the west of the border (spatial exclusion, see Fig. 1 and Table 3). Food availability and energy requirements could influence their diet and further impact their interactions. Cattle and sika deer mainly feeding by grazing, roe deer are browsers, while wild boar feed through browsing, grazing or rooting (Bollari and Barrios-Garcia 2014). For sika deer and cattle, we speculated that spatial exclusion might be a result of the similar food habit, which mitigated the interspecific competition but blocked the dispersal of sika deer to the habitat inland China.

This evidence of negative interactions among cattle and ungulates supports research showing that livestock may be displacing large ungulates, particularly grazing ruminants, or altering their niches in areas of overlap (Madhusudan 2004; Hibert et al. 2010; Dave and Jhala 2011). Long-term livestock grazing lowered chital density by 62% compared to livestock-free areas in the Gir Forest of India (Dave and Jhala 2011). Similar avoidance patterns were also observed in landscapes in the north-western United States, where elk were displaced by the presence of cattle (Stewart et al. 2002). In summary, we revealed divergent responses of the three ungulates to livestock activities. Madhusudan (2004) suggested that feeding ecology and digestive strategies could play an important role in determining livestock impacts on wild herbivores. In our study area, additional work regarding the diet and foraging behaviour of domestic and wild herbivores is needed to improve our understanding of their co-occurrence relationships.

Temporal activity patterns are a key component of species’ niches (Schoener 1974) and the sympathy of
competing wildlife is often facilitated by segregation along this temporal niche axis (Kronfeld-Schor and Dayan 2003). The data observed in this study also offer marginal support for behaviour-mediated segregation between wild ungulates and livestock (hypothesis 2 and 3). For example, the three species showed some shifts in their temporal niche in response to the presence of cattle. Specifically, our result revealed that wild boar and sika deer decreased their use of the cattle’s diurnal temporal niche following cattle presence, and roe deer showed a more pronounced peak at sunrise and sunset, suggesting release from exploitation competition with cattle. Similarly, Lahkar et al. (2020) found that the temporal activity of several ungulates were more nocturnal in response to livestock and human disturbances. In contrast, Pudyatmoko (2017) found that some ungulate species even altered their activities from diurnal to nocturnal in the presence of livestock (for lessening the interaction with livestock). In general, however, such extreme competition-induced shifts in activity are rare (Kronfeld-Schor and Dayan 2003). Our analysis revealed that three ungulates used also fine-scale spatio-temporal avoidance behaviors to reduce encounters with cattle. This finding suggests that behavioural avoidance is likely an important feature of co-occurrence between competitors. Similar avoidance behaviors were also observed between large carnivores (Karanth et al. 2017).

Conclusions and management recommendations

Overall, our study documents the effects of livestock-mediated disturbances on the ungulate species in several ways along the China-Russia border, such as by decreased habitat use, spatial avoidance or changing the daily activity pattern of animals. The primary goal of Northeast Tiger Leopard National Park is to protect the diversity of mammalian species, especially the prey and carnivore communities. This study showed that the animal most affected by livestock was sika deer, the dominant prey in the diet of tigers and leopards (Kerley et al. 2015; Sugimoto et al. 2016). Given that availability of ungulate prey is crucial to the persistence of any tiger and leopard population (especially large-bodied deer for tigers) (Karanth et al. 2004; Hayward et al. 2012; Li et al. 2019), the results of this study have conservation implications in terms of assessing the cascading effects of cattle grazing through a multispecies perspective (Filizzola et al. 2020). Tigers and leopards are now showing a trend towards expanding their range into China (Wang et al. 2015; Ning et al. 2019) but with distribution still spotty and overall numbers low (Vitkalova et al. 2018; Wang et al. 2018). At this juncture, solving the free-ranging livestock problem should be key priority in the new era of conservation.

Based on our camera-trapping data and field surveys, currently, villagers continue to rely on the park land to graze their livestock for subsistence in 2020. Thus, we suggest that the local government implement policies related to progressively controlling cattle for recovering wild ungulates while simultaneously addressing the economic needs of local communities to ensure the long-term success of tiger and leopard conservation. A conservative intervention in our study area might be to convert free-ranging livestock to stall feeding, which could reduce the impacts on the forest and conflicts between wildlife and humans. The more progressive intervention would be to ban livestock and redirect ranchers to an ecosystem service project. If it is not feasible to ban all free-range livestock grazing in the study area, we suggest only allowing cattle to enter the forest after the birth peak in spring and early summer and to move cattle to stalls in the village at night. These interventions to reduce livestock grazing may rapidly benefit wild herbivores that have been competitively suppressed, as has been observed in India (Madhusudan 2004). The above actions would require better collaboration among different government departments to effectively implement the policy, the establishment of a corresponding monitoring and evaluation system, and a functional law enforcement regime to facilitate the protection of the landscapes that wild ungulate as well as their predators inhabit (Johnson et al. 2016).

Acknowledgements We thank Daniel Eacker and the anonymous referees for their comments and suggestions that greatly improved our manuscript. This work was supported by the National Key Research and Development Program (2016YFC0500106) and grants from the National Natural Science Foundation of China (31971539, 31270567, 31700469). This project was carried out with the approval of Chinese National Forestry and grassland Administration and Northeast Tiger Leopard National Park. Non-invasive camera-trapping technology did not involve direct contact with animals. All study was in accordance with the guidelines approved by The American Society of Mammalologists.
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