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Does presence of top predator improve forest birds' survival and diversity? An ecological case study assessing umbrella conservational impact of tiger using carrion

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Abstract

After hunting, predators tend to leave a large amount of carrion behind. It is widely reported that this resource is commonly used by various species in the ecosystem and is essential for the survival of scavengers, particularly in winter. Although recent studies are focused on mammals, little is known about how this works with facultative scavenger birds, which may lead to a serious underestimation of the key role that top predators such as the Amur tiger (*Panthera tigris altaica*) play in ecosystems. Here, we conducted a field feeding experiment to quantitatively evaluate the effects of Amur tiger on avian scavengers by simulating their predation residue. The results show that the Corvidae is the main bird species that consumes carrion, while woodpeckers and some insectivorous songbirds also benefit from the remains that Amur tiger leaves behind. We assumed that in winter, if the daily energy demand for the six main scavenger birds completely relied on the predation residues of Amur tiger separately, the prey remains of one Amur tiger could feed about 28 crows, 49 azure-winged magpies, 61 Eurasian jays, 235 Eurasian nuthatches, 96 great spotted woodpeckers, or 385 willow tits. It means that the prey remains of top predators like Amur tiger may be an extremely important resource to avian scavengers and carrion could be a potential ecological indicator of Amur tiger keystone effect. This study provides experimental evidence from the field for the first time, and reveals the ecological mechanism of the role of keystone species of the Amur tiger, i.e., how to indirectly protect other animal groups in the forest ecosystem that have important ecological value for the biodiversity and the health of local forest vegetation through the protection of the Amur tiger.

Key words

Panthera tigris altaica, keystone species, ecological umbrella conservation, Avian scavenger, large predators, carrion provisioning

1. Introduction

Over hundreds of years, due to the increase in human activities and habitat destruction, the population of Amur tiger has significantly declined, and it has been listed as an endangered species by the International Union for Conservation of Nature (Seidensticker et al., 2010). It has been estimated that fewer than 600 individuals are distributed across Russia and northeastern China, and the effective population size in the Paektu Mountain area was estimated to be 11–14 individuals (Wang et al., 2018). Even though the Amur tiger is regarded as a key species, and top predators such as the Amur tiger have important ecological impacts on communities and ecosystems as key species (Estes et al., 2011; Miller et al., 2001). For a long time, a key question has been neglected, namely, what is the ecological mechanism by which top predators such as the Amur tiger acts as keystone species? Is there sufficient evidence to quantitatively evaluate and identify this ecological role?

Some scholars have proposed that keystone predators provide a food source to the scavenger community by leaving prey residue, thus regulating the richness and abundance of scavengers (Houston, 1978; Newton & Davis, 1982; Wilmers et al., 2003). However, field evidence on the impact of the Amur tiger as a keystone species on scavengers remains scarce, and research on the relevant mechanisms remains at a theoretical or cognitive level (Cho et al., 2013; Lu et al., 2001). Since Amur tiger is rare in quantity and hard to monitor, we could barely find detailed evidence on its kill in the wild. Therefore, the key role of Amur tiger and other top predators in the ecosystem has been seriously underestimated (Wilson & Wolkovich, 2011).

The Amur tiger generally hunts ungulates, such as the wild boar (*Sus Screfa*), the red deer (*Cervus elaphus*), and the roe deer (*Capreolus Capreolus*) (Gu et al., 2018; Teng et al., 2002). Like other predators, Amur tiger could store food and come back to the carcass multiple times to feed (Mark & Heiko, 2012). When food is abundant, they may tend to feed on a certain part of the prey rather than the whole. Therefore, there are lots of opportunities for avian scavengers to feed on the carrion during or after predators consuming their prey. Amur tiger normally eat about 65–75% of the edible portion of prey. Miller et al., (2013) evaluated the hunting rate and prey consumption of the Amur tiger. They found that they hunted once in every 6.5 days on average, and in winter, the hunting rate was 5.7 days/kill/tiger. The average daily amount of prey killed by the Amur tiger is 12.00 kg/day/tiger, and the average daily amount of food eaten in winter is about 10.30 kg/day/tiger. Thus, on average, each tiger leaves about 1.70 kg prey every day in winter, and the weight of the residual carrion over the whole winter (calculated over 3 months) reaches about 156 kg. Therefore, just as wolves in Yellowstone Park benefit scavengers by leaving deer carcasses, the predation residues of Amur tiger may provide an important source of food for scavengers in the ecosystem, particularly over the entire winter, when food is scarce (Beasley et al., 2015; Vucetich et al., 2004).

Carrion plays an important role in maintaining the biodiversity and biological processes in terrestrial ecosystems (Barton et al., 2013). More and more research has proven that carrion is an ecological resource for many kinds of animals, plants, and microbes (Sebastián-González et al., 2016; Towne, 2000; Wilson & Wolkovich, 2011; Yang, 2004). Newsome et al., (2021) pointed out that carrion could be used as an ecosystem indicator of food web. Its spatial distribution affects the survival, distribution, and movement of scavengers (Cortés-Avizanda et al., 2009). More importantly, most avian scavengers are facultative; that is, they also feed on other kinds of food, such as insects and seeds, which makes the food web more reticulate (McCann et al., 1998). Through scavenging, those facultative avian scavengers provide an important service for the ecosystem in balancing the nutrient chain, promoting the redistribution of ecosystem energy and nutrients, accelerating the removal of corpses and debris, controlling potential infectious diseases, and supporting the succession of forest vegetation (Cortés-Avizanda & Donázar, 2015; Inger et al., 2016; Li & Yin, 2004; Moreno-Opo et al., 2012). Therefore, we assume that carrion from Amur tiger could be an ecological indicator of its keystone effect, which benefits other species and the stability of ecosystem.

While the Amur tiger has a low population and that its cryptic and elusive behavior makes field observations on the species difficult, its predation residues can be simulated with the use of a feeding trial in the field to test the ecological mechanism of the Amur tiger on scavengers. This study was conducted in Taipinggou National Nature Reserve (TPGNR.), an Amur Tiger Reserve in northeastern China, where these tigers frequently appear (Fig. 1). The study area is in the Lesser Khingan, adjacent to the tiger habitat in the Jewish Autonomous Oblast of Russia, and it is an important corridor for Sino-Russian cross-border movement of the Amur tiger (Miquelle et al., 2016; Qi et al., 2021). To judge whether scavengers actively and selectively feed on Amur tiger's predation residues or randomly encounter them, as well as whether the beneficiaries of predation residues have species or group specificity, we compared the appearance of scavengers, whether they forage the food or not and their foraging/feeding behaviors among localities with feeding on meat (simulating the Amur tiger's hunting residues), feeding on vegetable food (control with different dietary habits), and no feeding (blank control without any food). First, we organized infrared camera data, identified every avian scavenger species that appeared in the photos and videos, and made records of the species and their behaviors. Then we further quantified the amount of carrion consumed by avian scavengers to quantitatively estimate the contribution of the tiger's predation residues to scavenger birds. We also investigated season as an influencing factor on scavenger behavior. We predicted that if the Amur tiger plays the role of a keystone species for scavenger birds, then the place where meat was left in this study (simulating the remains of animal carcasses left by Amur tiger) would produce a significant difference in the composition of scavenger groups relative to other feeding sites. Meat feeding sites would attract more scavenger birds, and avian scavengers would exhibit active scavenging behavior. This beneficial effect may be more significant in winter, because avian scavengers may count on carrion more when other food resources are scarce.

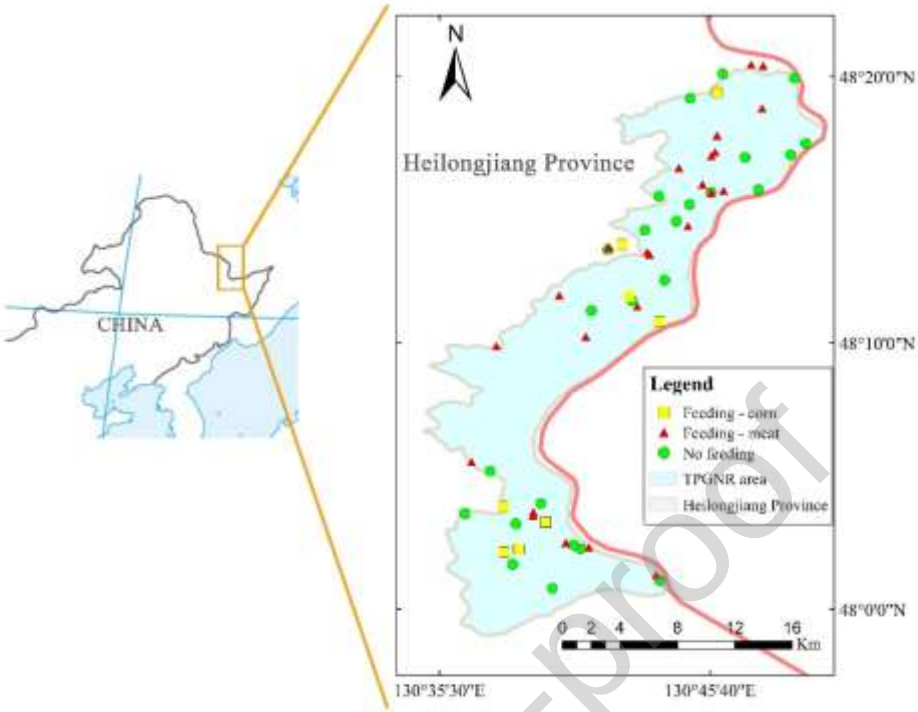

Fig. 1. Study area and setting of three feeding types of sampling points in the wild. The light blue area is the experimental research area: TPGNR. in Heilongjiang Province, Northeast China. The red line is the border between China and Russia. Red triangles represent the 25 meat feeding points, the yellow squares represent the 14 corn feeding points, and the green circles show the 26 non-feeding points. (Map source: http://bzdt.ch.mnr.gov.cn/index.html)

2. Methods

2.1. Study area and experimental design

The study area was TPGNR. in Heilongjiang Province, China (48°02′48″ to 48°20′19″ N, 130°31′12″ to 130°50′11″ E), located in the northern slope of Lesser Khingan, the low mountain mausoleum zone belonging to the continental monsoon climate of the northern temperate zone (Reserve, 2015). The reserve covers an area of 22,199 hectares, bordering Russia in the east. It is an important habitat for Amur tiger and it's also a Sino-Russian cross-border corridor (NEASPEC, 2018; Qi et al., 2021). The main prey of the Amur tiger in the reserve includes the wild boar, the roe deer, the red deer, and others (Yang, 2021). Field experiments were conducted from April 2018 to April 2021. A total of 65 different feeding sites were randomly set up and deployed infrared cameras in TPGNR. Three feeding types were included: 25 meat feeding sites (simulating the hunting remains of the Amur tiger), 14 vegetable feeding sites (corn), and 26 non-feeding sites (blank control). The Amur tiger has a wide range of activity (Rozhnov et al., 2011), so to avoid different habitat types interfering with the research results, the sampling points of those three feeding types basically covered the whole reserve, and different points were arranged randomly and adjacent to each other (Fig. 1). To explore whether there are seasonal differences in the role of the Amur tiger as a keystone species for scavenger birds, the study was carried out in different seasons. Drawing on local temperature changes throughout the year in the study area, a year was divided into cold season (October 20 to April 9) and warm season (April 10 to October 19) (Wang et al., 2014). The feeding experiment and data analysis were conducted during both seasons.

Considering the short keep time for wild meat in summer, this study used the roe deer, a small or medium-sized mammal, as a reference to simulate the predation residues of the Amur tiger. Judging the weight of the roe deer (25 kg) and the proportion of tiger consumption (65–75%), approximately 7 kg lamb was placed at each meat feeding site and fixed at a height of about 2 m from the ground with iron wire or thin rope to prevent scavengers from taking the meat out of the camera's range and to prevent feeding by mammalian scavengers. Corn was placed directly into food troughs in the study area or stacked on the ground, with approximately 20 kg each time. We installed a trigger infrared camera opposite each feeding point to record images and videos of animals and their behavior. The camera was fixed on a tree trunk 2–4 m from the feeding point, and the height was determined based on the food feeding height (Peers et al., 2021). The camera was set to capture color images during the day and black and white (infrared fill) images at night. The cameras were set to quickly take three photos after being triggered and then capture a 20 s video, with a triggering delay of 10 s. Maintenance of the camera was done every 2 months to rule out camera malfunctions and to replace the camera battery to ensure the camera's normal operation. When we found that the food we put in was missing, whether it was ingested or degraded or dragged away, we ended the experiment. If the food stays in the same place for more than 4 months, we may infer that it could not be found by scavengers. Under such circumstance, we also ended the experiment.

2.2. Analysis

Missing data from some infrared cameras due to equipment malfunctions, weather, or accidents were removed from the data analysis. Time intervals between photos or videos of the same species exceeding 5 min were taken as a new event. Events with an act of feeding on the food we put in were recorded as feeding events. All analyses were conducted in R 4.2.2 (R Core Team, 2022).

2.2.1. Main avian scavenger species and richness

We checked all photos and videos and extracted the following information from all experimental samples: date and time of shooting, identification of bird species captured, quantity, behavior type (whether forage or not), feeding frequency and feeding duration. To determine the relationship between the occurrence of scavenger birds and their feeding types, differences in species composition and behavioral parameters among the three feeding type samples were compared as follows. First, we calculated the number of occurrence events and feeding events (feeding meat or corn) of different species in different feeding types, then we used "origin" (OriginLab) to plot. We defined and calculated the occurrence and feeding rates for each species. The occurrence rate was defined as the ratio of the number of occurrences of each species to the total number of occurrences under a certain feeding type. The feeding rate was defined as the ratio of the number of feeding events of a given species to the total number of feeding events under a given feeding type. Next, we used the chi square test and correspondence analysis to compare the differences in species richness between different feeding types. We used the "corresp" function in the "MASS" package (Ripley et al., 2023) for correspondence analysis and used the plot function to evaluate the species composition under different feeding designs. Finally, we evaluated differences in the richness of scavenger birds in different seasons. Richness was represented by the number of bird species present in one trial. We used the Wilcoxon test function to conduct rank sum tests on three feeding types to evaluate the differences in bird richness in different seasons.

2.2.2. Amount of scavenging

The main scavenger birds in cold season were selected according to the feeding rate, and the average amount of food obtained by each individual in a single feeding event was estimated by the number of feeding times and the amount of food taken by birds per beak. We estimated the daily energy requirement for major scavenger birds from a previous study (Nagy, 2005). Finally, we calculated the proportion of energy obtained by scavenging to the main scavenger birds' daily energy needs.

We used the LME4 statistics package (Bates et al., 2023) to construct generalized linear mixed models (GLMM). We evaluated correlations among the feeding times of scavenger birds, species, and seasons using a log connection function with a Poisson distribution. We selected a negative binomial distribution to evaluate the correlations among the total time spent at feeding sites, feeding times, species, and seasons. Camera site was set as random effect of the model. The best models were selected using Akaike information criterion (AIC) values. We performed variance analysis on models using the ANOVA function in the car package (John Fox et al., 2023) and compared feeding frequency, residence time between scavenger species in cold season with the kwAllPairsNemenyiTest function in PMCMRplus package (Pohlert, 2022).

3. Results

Camera data that is damaged or missing were eliminated. For birds only, during the field feeding experiment, conducted from April 2018 to April 2021, 2184 events were observed, including 831 feeding events. Birds appeared in our feeding sites mainly included Corvidae, woodpeckers, and some small songbirds. Both the large-billed crow (*Corvus macrorhynchos*) and the carrion crow (*Corvus corone*) are distributed across the experimental sites, and their scavenging patterns are similar, which makes them difficult to be distinguished accurately with infrared photos and videos (Forbes et al., 2022). Therefore, both were classified as simply crow in this study. We choose six main avian scavengers to do the analysis, because the rest of these birds just appear occasionally.

As for mammals, the wild boar (*Sus scrofa ussuricus*) is the main species appeared in three kinds of experimental sites (120, 105, 112 events for meat, vegetable and none feeding sites respectively), and it's also the one fed most in vegetable feeding sites (51 feeding events). In meat feeding sites, the sable (*Martes zibellina*) fed most frequently (15 feeding events), after which is the Eurasian badger (*Meles meles*; 2 feeding events), the Asiatic black bear (*Ursus thibetanus*; 1 feeding events) and the Raccoon dog (*Nyctereutes procyonoides*; 1 feeding events).

3.1. Main avian scavenger species and richness

The bird species and feeding patterns that occurred for different feeding types and seasonal conditions were significantly different (Fig. 2). Among these scavenger species, only crows fed in flocks sometimes. The maximum number of crows can reach eight in a feeding event.

During warm season, the most common bird species at meat feeding sites was crow ($n_{\text{occurrence frequency}}$=277, occurrence rate 95.2%). The Eurasian jay (*Garrulus glandarius*) was the most common bird in vegetable feeding sites ($n_{\text{occurrence frequency}}$=94, occurrence rate 48.2%), followed by the Oriental turtle dove (*Streptopelia orientalis*) ($n_{\text{occurrence frequency}}$=56, occurrence rate 28.7%). At the non-feeding sites, the highest occurrence rate was seen for the Oriental turtle dove ($n_{\text{occurrence frequency}}$=21, occurrence rate 35%). In cold season, crows had the highest occurrence rate at meat feeding sites ($n_{\text{occurrence frequency}}$=532, occurrence rate 45.0%), followed by the Eurasian jay ($n_{\text{occurrence frequency}}$=376, occurrence rate 31.8%). The Eurasian jay had the highest occurrence rate at vegetable feeding sites ($n_{\text{occurrence frequency}}$=367, occurrence rate 59.7%). Crows had the highest occurrence rate at non-feeding sites ($n_{\text{occurrence frequency}}$=11, occurrence rate 31.4%). For occurrence statistics on all species, see Fig. 2(a).

Regardless of the season type, crows (in warm season $n_{\text{feeding event}}$=105, feeding rate 99.1%, in cold season $n_{\text{feeding event}}$=286, feeding rate 61.4%) and the Eurasian jay (in warm season $n_{\text{feeding event}}$=57, feeding rate 72.2%, in cold season $n_{feeding\ event}$=141, feeding rate 67.8%) had the highest feeding rates at meat and vegetable feeding sites, respectively. However, during cold season, a significant increase was seen in bird species feeding on carrion. In addition to the crow, the azure-winged magpie (*Cyanopica cyanus*) ($n_{feeding\ event}$=75, feeding rate 16.1%), Eurasian jay ($n_{feeding\ event}$=58, feeding rate 12.5%), and Eurasian nuthatch (*Sitta europaea*) ($n_{feeding\ event}$=37, feeding rate 7.9%) exhibited significant feeding behavior at meat feeding sites. For the feeding situation, see Fig. 2(b).

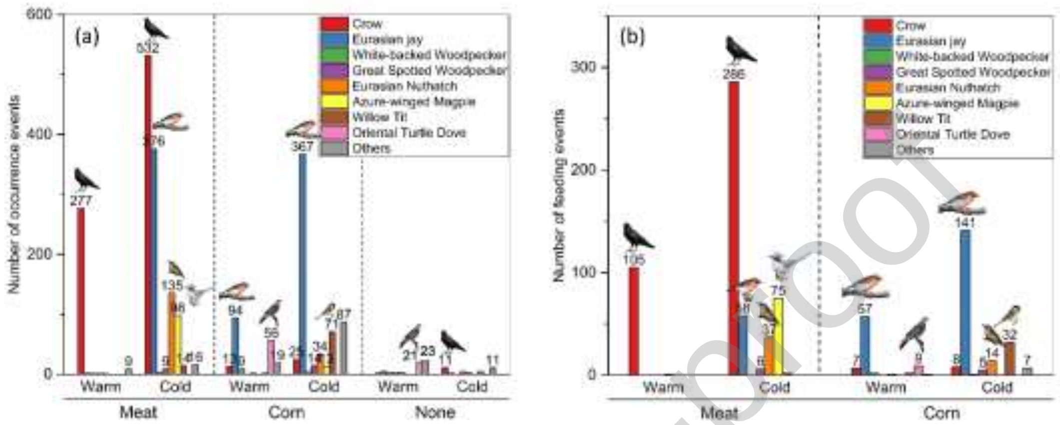

Fig. 2. Distribution of occurrences (a) and feeding events (b) of birds for different feeding types (meat, vegetable food, and no feeding) during warm season (April 10 to October 19) and cold season (October 20 to April 9) in all field experiments conducted in TPGNR. from April 2018 to April 2021. Species groups are shown in different colors, that is, red for crow, blue for Eurasian jay, green for white-backed woodpecker (*Dendrocopos leucotos*), purple for great spotted woodpecker (*Dendrocopos major*), orange for Eurasian nuthatch, yellow for azure-winged magpie, brown for willow tit (*Poecile montanus*), pink for Oriental turtle dove and grey for other species. The number of occurrence events refers to the number of events where the bird species was observed, and the number of feeding events refers to the number of events when bird feeding behavior was observed.

The results of correspondence analysis were consistent with above results, indicating significant differences in species composition for different feeding types and seasons (Fig. 3). In warm season, the distribution of species across the three feeding types was relatively directional, with the crow clearly tending to appear at meat feeding sites, and the Eurasian jay tending to visit vegetable feeding sites. In cold season, there was an increase in bird species appearing at meat feeding sites, including crows, azure-winged magpies, and Eurasian nuthatches. The number of bird species at non-feeding sites significantly decreased.

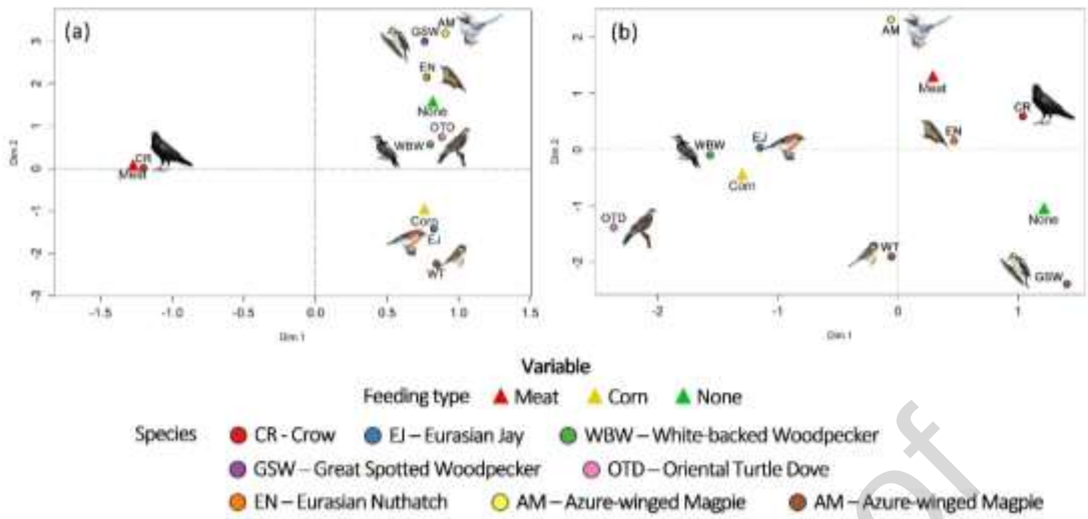

Fig. 3. The corresponding analysis results for avian scavengers at different feeding sites (meat, vegetable food, and no feeding) during (a) warm season (April 10 to October 19) and (b) cold season (October 20 to April 9) in field experiments conducted in the TPGNR. from April 2018 to April 2021. Feeding types are shown in triangle marks, and species groups were shown in circle marks. We use different color to distinguish different feeding types and species groups. See the legend for more details.

We also compared the occurrence and feeding rates of birds at different feeding types and seasons. The results of the Wilcoxon rank sum test (Fig. 4) showed significantly more bird species present and feeding at meat feeding sites during cold season than during warm season (T=1722.0, P=0.005). The average richness of birds during cold season at vegetable feeding sites was significantly higher than that during warm season (T=500.5, P=0.028), while the richness of birds at non-feeding sites was not significantly different between cold and warm seasons (T=358.0, P=0.270).

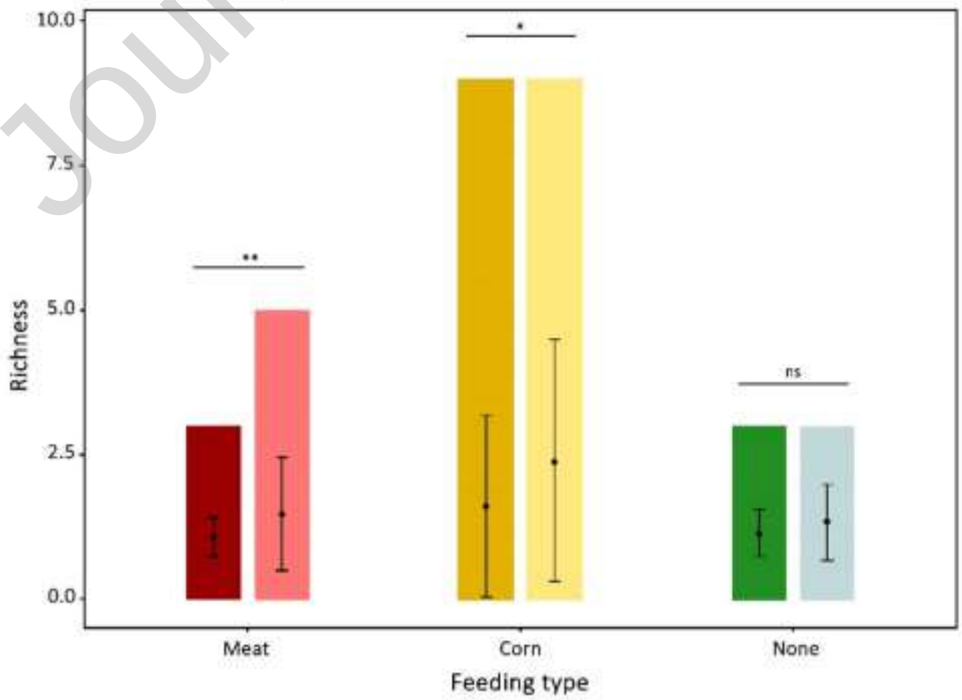

Fig. 4. Differences in bird species richness between warm season (April 10 to October 19) and cold season (October 20 to April 9) under three feeding types (meat, vegetable food, and no feeding). $^{**}P<0.01$, $^{*}P<0.05$, ns: not significant. The height of the column represents the maximum richness, the point at the center of the column represents the average, and the error bar corresponds to the 95% confidence intervals; dark columns represent the warm season, and light ones represent the cold season.

3.2. Birds benefit from carrion

The main scavenger birds in cold season were crows (feeding rate 61.4%), the azure-winged magpie (feeding rate 16.1%), the Eurasian jay (feeding rate 12.5%), the Eurasian nuthatch (feeding rate 7.9%), the great spotted woodpecker (feeding rate 1.3%), and the willow tit (feeding rate 0.4%).

According to Moreno-Opo et al., (2016), the crow consumes biomass at a rate of 1.15 g/peck. The corresponding data for the azure-winged magpie, Eurasian jay, Eurasian nuthatch, great spotted woodpecker, and willow tit were estimated from beak tip data provided in *Avifauna of China* (Zhao, 2001). From Nagy's research (Nagy, 2005), the daily energy requirements of the six bird species above were calculated (see Tab. S1 for body weight and beak data of the six bird species). We calculated the biomass of the six main scavenger birds consumed in a single feeding event and the proportion of their daily biomass requirements provided by the carrion amount of a single feeding event (Table 1).

Table 1. Results of the biomass acquired by six major species of avian scavengers in cold season (October 20 to April 9)

Species	Amount per peck (g/peck)	Average number of pecks per feeding event	Biomass acquired in a single feeding event (g)	Required daily energy (kJ/d)	Required daily biomass (g)	Percent of required daily biomass fulfilled per feeding event (%)
crow	1.15	29.4±69.7	33.8	732.9	59.6	56.7
azure-winged magpie	0.57	6.3±4.0	3.6	419.8	34.1	10.6
Eurasian jay	0.64	7.1±9.0	4.5	339.9	27.6	16.3
Eurasian nuthatch	0.33	5.5±3.2	1.8	88.8	7.2	25
great spotted woodpecker	0.57	7.0±2.8	4.0	216.3	17.6	22.7
willow tit	0.22	2.5±1.3	0.6	53.8	4.4	13.6

The energy values of mutton refer to the Nutritionix database (https://www.nutritionix.com/database).

During cold season, crows benefitted the most from a single scavenging event and could meet a larger share of the daily biomass demand, accounting for 56.7%. This was followed by the Eurasian nuthatch (25.0%), the great spotted woodpecker (22.7%), the Eurasian jay (16.3%), the willow tit (13.6%), and the azure-winged magpie (10.6%) (Fig. 5).

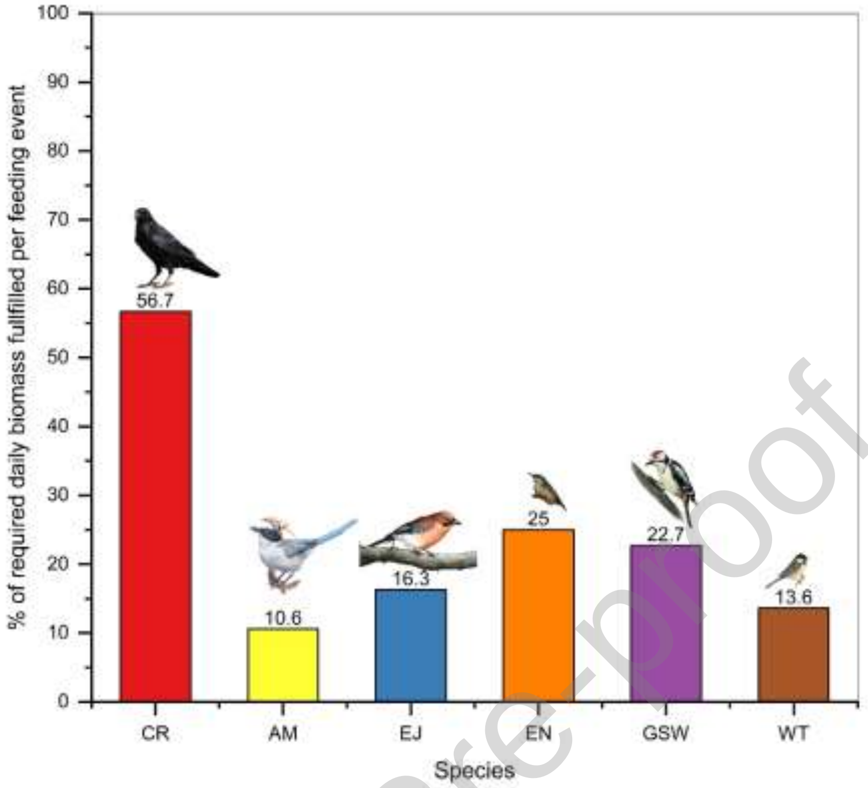

Fig. 5. Biomass obtained by six main scavenger birds in cold season (October 20 to April 9) in terms of the percentage of daily biomass demand in a single scavenging event. Species groups are shown in different colors, that is, red for crow, yellow for azure-winged magpie, blue for Eurasian jay, orange for Eurasian nuthatch, purple for great spotted woodpecker and brown for willow tit.

The GLMM model results (see Table S2-S4 and Fig. S1-S3) revealed a significant interaction between species and feeding frequency (χ^2=48.07, df=6, P<0.001), the total time spent by scavenger birds at meat feeding sites (χ^2=100.38, df=6, P<0.001), and the feeding time of scavenger birds (χ^2=50.59, df=6, P<0.001), respectively. All interactions with season ($\chi^2_{\text{feeding frequency}}$= 0.21, df= 1, P= 0.650; $\chi^2_{\text{total residence time}}$= 1.70, df= 1, P= 0.192; $\chi^2_{\text{feeding time}}$= 50.59, df= 6, P<0.001), or with both species and season ($\chi^2_{\text{feeding frequency}}$= 1.48, df=2, P=0.476; $\chi^2_{\text{total residence time}}$= 1.53, df= 2, P=0.465； $\chi^2_{\text{feeding time}}$= 4.90, df= 2, P=0.086) were not significant.

The results of Nemenyi's all pairs rank comparison test (Tab. S5) showed that the number of feeding times of crow was significantly higher than that of the Eurasian jay (q=6.95, P<0.001), the Eurasian nuthatch (q=5.46, P=0.002), and the willow tit (q=4.63, P=0.014). Crows had a significantly longer residence time than the Eurasian jay (q=5.93, P<0.001), Eurasian nuthatch (q=10.53, P<0.001), and the willow tit (q=5.11, P=0.004). The residence time of the Eurasian jay was significantly longer than that of the Eurasian nuthatch (q=5.86, P<0.001). The residence time of the azure-winged magpie was significantly longer than that of the Eurasian nuthatch (q=5.10, P= 0.004). The number of feeding events for crow was significantly more than that of the Eurasian jay (q=7.70, P<0.001), the Eurasian nuthatch (q=8.72, P<0.001), and the willow tit (q=4.81, P=0.009). The number of feeding events of the azure-winged magpie was significantly higher than that of the Eurasian nuthatch (q=4.46, P=0.020). There were no significant differences in other cases.

4. Discussion

Previous studies have found that the predation residues of top predators, such as wolves and cougars, are widely used by vertebrate scavengers (Kaczensky & Christoph, 2005; Mark & Heiko, 2012), but few studies have identified the beneficial effects of the Amur tiger and other big cats in the northern forest ecosystem on scavengers. In this study, a field feeding experiment was conducted to quantitatively demonstrate the mechanism of the benefit of top predators on local forest scavengers through simulating the predation residues of the Amur tiger in the field. The experimental results were in line with our prediction, i.e., the predation residue of the Amur tiger is an important food source for local forest scavenger birds, and this beneficial effect is larger in winter. We proved that the existence of Amur tiger can benefit the survival of facultative scavenger birds in forests, which indirectly plays a positive ecological role in local biodiversity.

Our study also confirmed that crows tend to be the largest beneficiaries among avian scavengers. Most studies on scavengers note the scavenging activity of crows, reflecting their representative role as facultative scavenger birds (Cortés-Avizanda & Donázar, 2015; Vucetich et al., 2004). In Tasmania, the decrease in the population of the main scavenger mammal, the Tasmanian devil, resulted in an increased population of the main avian beneficiary, the raven (Calum & Christopher, 2018). Inger *et al*., (2016) proposed that, although there are many other scavengers in ecosystems, crows largely dominate. Similarly, in this study, crows were found to be the largest beneficiaries of Amur tiger's hunting remnants. In both warm and cold season, crows consistently appeared at meat feeding sites but rarely at vegetable feeding sites (Fig. 2), indicating that they selectively search for and feed on carrion rather than appearing at feeding sites at random. This study also validated the seasonal differences in scavenging activities. The general view of previous research is that during winter, due to the low temperature, slow decomposition rates, and the limited availability of food for vertebrates, carrion resources are particularly important for facultative scavengers (Beasley et al., 2015; Selva et al., 2005). In winter, carrion may account for half of raven's daily food (Temple, 1974). In our study, the hunting residues provided 56.7% of the food required for winter survival of crows. In addition, the number of bird species that appeared at meat feeding sites and exhibited scavenging behavior during cold season was significantly higher than during warm season. Besides crows, the carrion resources were obtained in cold season by other birds, such as the Eurasian jay, the azure-winged magpie, woodpeckers (the great spotted woodpecker, the white-backed woodpecker, and others), and small songbirds, such as the Eurasian nuthatch and the willow tit. Woodpeckers and small songbirds' scavenging behavior are mentioned in several previous studies (Leonard & Pauli, 2019; Selva et al., 2005). This study both verified scavenging behavior in birds and quantified it. Our results showed that carrion resources provided by top predators such as Amur tiger have high ecological value for the survival and diversity of local resident birds over the long winter in high-latitude areas.

Following previous research, we estimated that the Amur tiger could leave about 156 kg residual carrion over the course of an entire 3-month winter (Miller et al., 2013). Assuming that in winter, the daily energy demand for the six main scavenger birds, namely, of crows, the azure-winged magpie, the Eurasian jay, the Eurasian nuthatch, the great spotted woodpecker, and the willow tit, completely relied on the predation residues of Amur tiger separately, the prey remains of one Amur tiger could feed about 28 crows, 49 azure-winged magpies, 61 Eurasian jays, 235 Eurasian nuthatches, 96 great spotted woodpeckers, or 385 willow tits, respectively. It should be noted that, in this study, we focused on avian scavengers only, while mammals' feeding behavior could have an impact on the results. In the meat feeding sites, the main mammal scavenger was the sable (15 feeding events). And the Asiatic black bear could consume all the meat in just one feeding event by which the actual number of birds that can rely on the predation residues of Amur tiger in winter should be lower than our results. These birds, particularly small songbirds, struggle to survive through winter. For example, to survive, the tits need to find an item of food every 3 s every day during winter (Gibb, 1960). These bird species that benefit from Amur tiger's predation residues and survive the cold winter have a key impact on forest health and ecosystem biodiversity maintenance that cannot be ignored.

Crows benefit the most. And as a facultative scavenger bird, they have important ecological significance in accelerating the removal of dead bodies, reducing the risk for disease outbreaks, increasing the necessary connections in the food web, and promoting the energy flow of the ecosystem (Beasley et al., 2015). At the same time, as a predator, crows may play an important ecological role in controlling invasive pests. For example, in Japan, crows effectively control the population density of the invasive apple snail *Pomacea canaliculata* (Architaenioglossa Ampullariidae) (Uehara et al., 2021). In the crow diet, insects (accounting for about 33% of the total) and seeds of trees such as junipers are also included (Nelson, 1934; Tyrrell, 1945). The prey species of crows varies greatly in different seasons. In late summer and autumn, terrestrial invertebrate residues are more common in crow feces. In late autumn, they eat more berries, and in October and December, they eat more rodents (Marquiss & Booth, 1986). Their feeding on insects and invertebrates may have an impact on the prevention and control of forest diseases and pests, their feeding on fruits and seeds is conducive to helping seeds of trees to spread, and their feeding on rodents can prevent them from damaging tree bark (Spengler, 2012). The other five bird species tracked also have important ecological value for forest health. For example, woodpeckers are indicators of forest conditions, and their abundance is correlated with the abundance of all forest birds (Drever & Martin, 2010). The predation of caterpillars by carnivorous birds such as the azure-winged magpie and tits limits leaf damage (Gunnarsson et al., 2018). A pair of tits can prey on 150,000 to 200,000 caterpillars during the breeding season (Török, 1998). The Amur tiger plays a huge ecological role in the prevention and control of forest pests, forest health, and the maintenance of forest ecosystem biodiversity by benefiting these scavenger birds.

It has been reported that large birds of preys could forage carrion too (Orr et al., 2019), but we didn't find any raptors eating the meat in our experiment, though *Aquila chrysaetos* and *Buteo buteo* appeared one and two times respectively. The reasons may be that carrion occupy only a small part of their diet, and other factors are hard to explain why the raptors in this research didn't eat the meat, e.g., availability of alternative food sources, eagle's age and the ability to hunt, and the competition tensity for carrion (Margalida et al., 2017). In this study, we used corn and meat to simulate the prey residues instead of carrion left by Amur tiger, but carrion or dead animal bodies which are much closer to the reality are more recommendated in future research.

In general, our research reveals the beneficial effects of the Amur tiger on birds from an idealized perspective. We identified the mechanisms by which the Amur tiger, a keystone species, affects the forest ecosystem through a field experiment. That is, the tiger provides benefits for scavenger birds through its predation residues. And it also makes carrion a potential indicator of Amur tiger's ecological role. Therefore, the significance of protection for top predators is not only to save large endangered species such as the Amur tiger but also to indirectly protect many other species with important ecological functions facilitated through the beneficial role of Amur tiger, maintaining the stability and health of the forest ecosystem. This study also illustrates the important ecological value of Amur tiger conservation in relation to interspecific relationships.

CRediT authorship contribution statement

Zhifeng Ding, Atul Kathait and Xiaoying Xing: Conceptualization, Data curation, Methodology, Formal analysis, Funding acquisition, Supervision, Project administration. **Zhiyu Chen, Chunying Wang and Ying Zheng:** Data acquisition, Data curation. **Jiao Sun**: Validation, Visualization. **Jiao Sun, Zhifeng Ding, Atul Kathait and Xiaoying Xing**: Writing – original draft, Writing – review & editing.

Declaration of competing interest

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

Data availability

The analysis and data visualization performed in R software are available in a Fig-share repository (https://doi.org/10.6084/m9.figshare.23691057).

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Competing interests

The authors declare no competing interests.

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Declaration of interests

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