



Evidence for interspecific modulation of carcass consumption among facultative scavengers in Asian temperate forest

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ABSTRACT

Interspecific interactions are one of the key drivers that can determine community structure through the complex energy dynamics in food webs. Top-down regulation by large mammals on other species is well documented, but is still limited to a few species in scavenging communities that compete for limited and ephemeral animal carcasses. In this study, we examined the effects of large scavengers (Asian black bear, *Ursus thibetanus* and wild boar, *Sus scrofa*) and seasons (summer and autumn) on carrion consumption. Specifically, we analyzed how large scavenger and season affected the visitation and duration of feeding on carcasses by other omnivorous scavengers (both each other and smaller mesocarnivores) in a temperate forest ecosystem in Japan. We found that bears and wild boars appear to have a competitive relationship by limiting each other's visitation to the carcasses. We also found that these large scavengers had limiting effects on the carrion consumption by mesocarnivores, suggesting that large scavengers not only reduce the available carrion largely but also create a landscape of fear for mesocarnivores. In addition, we found that the potential probability of visitation for large scavengers was associated with season. This suggests that top-down regulation from large scavengers to mesocarnivores may change with season, especially in omnivorous communities in temperate regions with varying seasonal abundance of different food sources. These complex interspecific interactions between scavengers among different seasons can contribute to maintaining and structuring the food web in this system.

1. Introduction

Species interactions are important drivers for determining the structure of ecological communities, including complex energetic flows (Prugh and Sivy, 2020). One of the major determinants of interspecific interactions is food web dynamics (e.g., predation, competition, coexistence), and understanding interspecific interactions in communities can provide important insights for evaluating not only the ecological role of individual species but also the functioning of communities (Hooper et al., 2005; Sebastián-González et al., 2020). Large carnivores with high trophic level can have important ecological roles through top-down regulation (Ripple et al., 2014). For example, apex carnivores can reduce the abundance and distribution of mesocarnivores by killing them or changing their behavior by instilling fear (Ritchie and Johnson,

2009), but also increase abundance of some subordinate carnivores through cascading effects (Levi and Wilmers, 2012). These interspecific interactions with large mammalian species have been well documented – especially among carnivores because of their influences at the community level, but there is also increasing interest in these dynamics among scavenging communities.

The vertebrate scavenging communities that form at ephemeral animal carcasses have important ecological functions in food web dynamics. For example, the number of energy transfer links that vertebrate scavenging builds from carcasses is greater than those built by direct predation, and these numerous energy flow paths contribute to the stabilization of food webs (Wilson and Wolkovich, 2011). Furthermore, scavenging dynamics strongly contribute to the maintenance of food web dynamics by regulating energy transfer links in the predator-prey

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interactions (Focardi et al., 2017; Moleón et al., 2014). In particular, facultative scavengers that opportunistically utilize carcasses comprise the majority of terrestrial vertebrate scavengers and build numerous energy flow pathways (DeVault et al., 2003; Selva and Fortuna, 2007; Wilson and Wolkovich, 2011). One important factor driving these complex scavenging dynamics is interspecific interactions (Sebastián-González et al., 2016; Selva and Fortuna, 2007). Interactions among scavengers can not only increase access to carrion for some species, but also decrease it for others (e.g., Allen et al., 2015; Panda et al., 2022). These direct effects on carrion consumption for each scavenger species also likely indirectly relate to population and community functioning. Previous studies of the effects by large scavengers on carrion consumption of other species have been limited to species such as wolves (*Canis lupus*), pumas (*Puma concolor*), American black bears (*Ursus americanus*), brown bears (*Ursus arctos*), striped hyenas (*Hyaena hyaena*), spotted hyenas (*Crocuta crocuta*) (e.g., Selva et al., 2003; Krofel et al., 2012; Allen et al., 2015; Balme et al., 2017; Panda et al., 2022), and there is a need to explore variation in their effects across more species, given the ubiquity of scavenging across ecosystems.

The Japanese temperate forest ecosystem, located in East Asia, has Asian black bears (*Ursus thibetanus*; hereafter bears) and wild boars (*Sus scrofa*) as large scavengers. Previous studies have shown that bears (American black bears and brown bears) are dominant scavengers that monopolize carrion and also take prey from other large carnivores (Allen et al., 2015; Krofel and Jerina, 2016). Wild boars also sometimes compete with large carnivores and steal from their kills (Focardi et al., 2017). These are the only two large scavengers that have the potential to influence the carrion consumption of other scavenger species, because there are no large carnivores that kill adult ungulates in this system. Considering their kleptoparasitic ability and comparable body sizes, Asian black bears and wild boars may have a competitive relationship for the limited carrion resources. Furthermore, large scavengers provide competition (suppression) and coexistence (facilitation) interactions to mesocarnivores (Allen et al., 2015; Selva et al., 2003; Sivy et al., 2017; Turner et al., 2017). For example, large scavengers not only directly limit carrion consumption by excluding other carnivores (Allen et al., 2015; Panda et al., 2022), but also facilitate carcass utilization by opening the thick skin of ungulate carcasses (Selva et al., 2003). Asian black bears feed on carcasses longer per visit than wild boars (Inagaki et al., 2020), and the suppressive effect on carcass consumption of mesocarnivores may be stronger and the facilitating effect weaker in carcasses with bears present than in carcasses with wild boars present. Examining the effects of large scavengers on carrion consumption by other species is an important step in evaluating interspecific interactions, but the relationship between bears and wild boars and mesocarnivores is understudied.

In addition to the interspecific effects, season is likely to be a key factor in carrion consumption for scavengers in the Japanese temperate forest system. The food habits of most scavengers, including bears and wild boars, are omnivorous and mainly consume plant matter (Inagaki et al., 2020). Hence the importance of carrion for food resources of omnivores may shift seasonally due to availability of food resources and climatic conditions (Pereira et al., 2014). For example, seasonal changes in plant resources may affect scavenging frequency in omnivorous scavengers (Inagaki et al., 2020). For some species, carrion is an alternative food resource when other food resources are scarce (Allen et al., 2021; Needham et al., 2014; Selva et al., 2005). Furthermore, interspecific competition among vertebrate scavengers decreases as climate warms seasonally (in regions with distinct seasonal changes) because invertebrate and microbe activities increase, thereby accelerating the decomposition rate of carrion and decreasing carcass persistence times (DeVault and Rhodes, 2002; Ray et al., 2014). Thus, seasonal changes may be a driver in determining the structure of scavenging dynamics. Therefore, examining how carcass consumption for omnivorous scavengers may be determined by interspecific effects and season provide understanding the scavenging mechanisms in omnivorous community.

In this study, we aimed to evaluate how the effects of large scavengers and season are related in the carrion consumption for large scavengers and mesocarnivores in a Japanese temperate forest ecosystem. We used a two-step approach to analyze 1) number of visits per carcass and 2) mean feeding time per carcass as the consumption of carrion. We tested number of visits by bears to carcasses, number of visits by wild boars to carcasses, and seasons (summer and autumn) affected the carrion consumption for each scavenger. We compared seasons in summer (June to August) and autumn (September to November) for three reasons; 1) the forest canopy is closed in both seasons, and mammalian scavengers are primary, and carcass utilization by avian scavengers is limited (Inagaki et al., 2020), 2) Asian black bears that hibernate in winter are active during both of these seasons, and 3) the phenology of woody plant bearing fruits and hard masts and of insects consumed by mammalian scavengers changes between summer and autumn (Koike et al., 2012; Koike et al., 2011). Specifically, we expected;

- (1) Carrion consumption for each scavenger would vary with season.
- (2) Bears and wild boars would limit carrion consumption for each other.
- (3) Bears and wild boars would have species-specific limitation or facilitation effects on carrion consumption by mesocarnivores.

2. Material and methods

2.1. Study area

The study was conducted as part of a larger scavenging study (see Inagaki et al., 2020, 2022) in the forest of Nikko City, Tochigi Prefecture on central Honshu, Japan (approximately 1150 km²; 36°36'N–37°05'N, 139°19'E–139°51'E) during 2016 and 2017. The study area include lowland and mountains with elevation of 300 to 1300 m but similar environments. The climate is temperate with mean daily temperature and mean annual rainfall in summer of 21.5 °C (14.3 °C to 22.7 °C) and 782.5 mm, and in autumn of 13.8 °C (3.9 °C to 22.5 °C) and 602.3 mm (Imaichi Meteorological Station, 36°43'N, 139°40'E). The habitat throughout the study area is generally composed of deciduous broad-leaved forests (mainly of *Quercus* in tree layer and *Rhododendron* in shrub layer), conifer plantation forests (*Cryptomeria japonica* and *Chamaecyparis obtusa*), and patchy mixed forests. Although there is understory vegetation that is dominated by bamboo grasses, the presence or absence of understory vegetation has been previously found to have no effect on detection of large carcasses by scavenger species (Inagaki et al., 2022).

Large ungulates including sika deer (*Cervus nippon*; hereafter deer), Japanese serow (*Capricornis crispus*), and wild boar inhabit the area, but there are no large carnivores that can regularly kill adult ungulates. Large omnivorous mammals that scavenge from deer carcasses include Asian black bear (mean weight of 36 kg for females and 62 kg for males), wild boar (mean weight of 50 kg for females and 100 kg for males), both of which have similar body weight ranges (Inagaki et al., 2020; Ohdachi et al., 2009). Bears primarily feed on plant, fruits, insects, and hard mast (Koike, 2010) but are also known to be a dominant scavenger at deer carcasses (Inagaki et al., 2020). Wild boars also primarily feed on bulbs, roots, aerial parts of plants, fruits and seeds (Ohdachi et al., 2009), but are less frequent scavengers than bears in our study area (Inagaki et al., 2020). Mesocarnivores that scavenge from deer carcasses include red fox (*Vulpes vulpes*; hereafter fox; mean weight of 5.1 kg for males and 4.4 kg for females), raccoon dog (*Nyctereutes procyonoides*; mean weight of 4.1 kg), masked palm civet (*Paguma larvata*; mean weight of 3.0 kg), and Japanese marten (*Martes melampus*; hereafter marten; mean weight of 1.6 kg for males and 1.0 kg for females) (Inagaki et al., 2020; Ohdachi et al., 2009). See supporting information in Inagaki et al. (2022) for the relative densities of these scavenger species.

2.2. Data collection

From June to November, we placed 55 deer carcasses (ranging from newborn to adult) that had not been scavenged in the closed canopy forest (Table S1). We recorded the weight of each deer carcass in 10-kg increments. To record scavenging behaviors for each scavenger, we set camera traps (Ltl-Acorn 6210) at the deer carcasses. We programmed the camera traps to record 30 s of video at each motion with a pause of a 30 s refractory period before the next motion (see Inagaki et al. (2020) for further details). We used the data until >80% of the deer carcass including bones and skins had been consumed. In some instances, the camera trap did not record all of the data until the carcass was completely consumed due to being destroyed by bears or malfunctioning. We used the available data in these cases ($n = 9$, Table S1), because malfunctions happened towards the end of carrion being available and most scavenging occurs when carcasses are fresher. The duration of these use data was defined as the carrion period (Table S1). We excluded one carcass (ID: 1719; Table S1) from our analyses because it was not visited by mammalian scavengers.

From the video recordings, we calculated the two indices we used as proxies for species-specific scavenging processes: (1) number of visits per carcass and (2) mean feeding time per carcass. We considered individuals of the same species that were recorded within 30 min of each to be the same individual and lumped these detections together as one visit. In the case of simultaneous visits by multiple individuals of the same species, we determined visits for each individual. We considered it zero if scavengers did not visit carcasses. We also calculated the mean feeding time of each scavenger per carcass that summed feeding counts that documented whether or not the scavengers feeding on carcasses every 3 s of the video, because the range of feeding time [seconds] per visit was very wide. We considered it zero if scavengers did not feed (e.g., only smelling the carcass or exploring around the carcass).

2.3. Permits of carcass handling

We obtained deer carcasses from vehicle collisions or culling efforts for prevent overabundance and agricultural or ecological damage. Culling efforts included shooting operations or captured by snare traps. In the case of snare traps, captured deer were euthanized by electrocution or shooting quickly after capturing. These methods were most minimizes pain and distress in accordance with the “Welfare and Management of Animals Act” (Ministry of the Environment) and “Specified Wildlife Conservation and Management Plan” (Tochigi Prefecture). We handled deer carcasses according to the guidelines of the American Society of Mammalogists (Sikes and Animal Care and Use Committee of the American Society of Mammalogists, 2016) and the guidelines for animal research set forth by the The Mammalogical Society of Japan (2009).

2.4. Statistical analyses

We analyzed five species (Asian black bears, wild boars, raccoon dogs, red foxes, and Japanese martens), but excluded masked palm civets because we only observed a total of 7 visits and 136 unique feeding counts which were not sufficient samples for analyses. We performed all analyses with R program version 4.1.1 (R Core Team, 2021).

We estimated the relationship between number of visits for each scavenger and predictor variables (i.e., the effects of bear and wild boars, and season) by using zero-inflated regression models for each species because our data has large number of zeros and did not adequately fit a standard distribution (i.e., overdispersion). We used zero-inflated Poisson (ZIP) regression with the glmmTMB package (Brooks et al., 2017), which enable examination of the influences of independent variables simultaneously on count response and the probability of zero count (Zuur et al., 2009). We considered that zeros of our data included random zeros (i.e., the sampling variability) and

structural zeros (Blasco-Moreno et al., 2019). The structural zeros included effects of carrion consumption or landscape of fear by large scavengers (i.e., unable to visit due to the presence of bears or wild boars) and seasonal factors. In the models, we used three variables: (1) bear: number of visits of bears for each carcass, (2) wild boar: number of visits of wild boars for each carcass, and (3) season: summer (June to August) and autumn (September to November), as the independent variables in both count and zero-inflated components. We also used an offset for carrion period [day] each carcass because we assumed the longer a carcass remained the larger the number of visits as well as the higher carrion detection or various feeding preferences would be.

We estimated the relationship between mean feeding time for each scavenger and predictor variables by using generalized liner models (GLM) for each species. We used Gamma distribution with a log link, and to add 0.1 to the dependent variable (i.e., mean feeding time) for each model to fit the distribution because the mean feeding times included zeros. In the models, we used three variables: (1) bear (2) wild boar (3) season as the independent variables and an offset for carcass weight [kg] each carcass assuming the larger a carcass remained increased the mean feeding times. We detected no significant multicollinearity for independent variables in the models ($VIF \leq 1.15$; Dormann et al., 2013).

To determine the best explanatory models for each species, we compared models using Akaike information criterion (AICc) and Akaike weights (w_i) following an information theoretic approach (Burnham and Anderson, 2002). First, we selected top models from AICc differences (Δ_i) scores <2 of the highest ranked model (i.e., best model) using dredge function of the MuMIn package. Second, we fitted model averaging with the MuMIn package to estimate parameters (coefficients) and compare the effect of independent variables. The ZIP models included a count part model and zero-inflated part model, and we compared both part models of effects.

3. Results

We recorded 1727 total visits to deer carcasses by the five omnivorous scavengers in the 414 total days of monitoring deer carcasses (Table S1). Of the 54 deer carcasses, we documented bears visiting 18 and 16 deer carcasses in summer and autumn (and did not visit 5 and 15 of the carcasses in summer and autumn, respectively). Wild boars visited 4 and 15 deer carcasses in summer and autumn (and did not visit 19 and 16 of the carcasses in summer and autumn, respectively; Fig. 1). The mean number of visits per carcass was highest for raccoon dogs (8.74 visits) and lowest for wild boars (1.48 visits; Table 1). The mean total feeding time per carcass was longest for raccoon dogs (1047.84 ± 1565.05 unique feeding counts) and shortest for Japanese martens (174.96 ± 255.73 unique feeding counts; Table 1). In contrast, the mean feeding time per visit was longest for Japanese martens (60.31 ± 94.98 unique feeding counts) and shortest for raccoon dogs (21.76 ± 56.22 unique feeding counts; Table 1).

3.1. Asian black bear

We recorded 366 visits and 21,037 unique feeding counts of bears. We found five top models for the number of visits (Table 2). The variables in the best model included wild boar ($\beta_{\text{count}} = -0.08$) in the count model and season in the zero-inflated model ($\beta_{\text{zero-inflated}} = 1.24$; Table 2). The result of model averaging showed that the top variable in the count model was presence of wild boar ($\Sigma_w = 0.90$) and that the top variable in the zero-inflated model was season ($\Sigma_w = 0.64$). Parameter estimates of model averaging showed that the number of visits decreased by a factor of 0.93 ($\beta_{\text{count}} = -0.08$) for each additional visit of wild boars, and autumn increased the probability of not visiting by a factor of 3.3 ($\beta_{\text{zero-inflated}} = 1.19$) compared to summer (Table 3, Fig. 2).

We found two top models for the mean feeding time, but the second model was null model (Table 4). The variables in the best model included wild boar ($\beta = -0.16$). The results of model averaging showed

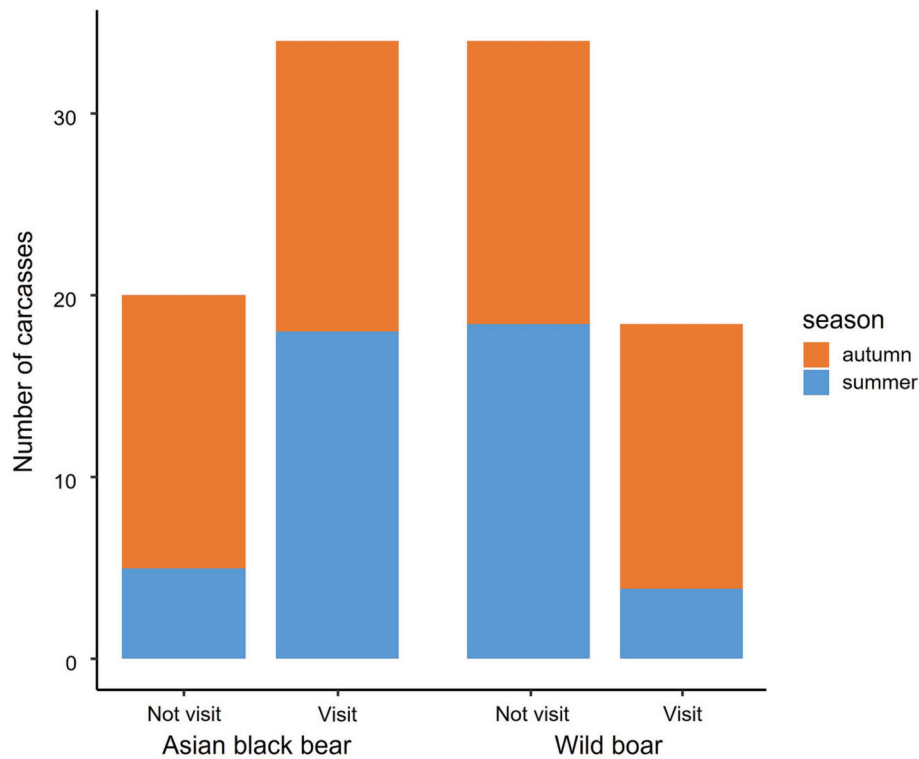


Fig. 1. The number of deer carcasses that were visited or not by bears and wild boars within each season.

Table 1

Mean number of visits (min to max) and mean total feeding time ± SD per carcass, and mean feeding time ± SD per visit for each species.

| Species | Mean number of visits (min-max) | Mean total feeding time ± SD | Mean feeding time ± SD |
|------------------|---------------------------------|------------------------------|------------------------|
| Asian black bear | 6.04 (0–34) | 618.74 ±646.66 | 57.48 ±120.27 |
| Wild boar | 1.48 (0–15) | 304.74 ±442.15 | 26.10 ±69.92 |
| Raccoon dog | 8.74 (0–34) | 1047.84 ±1565.05 | 21.76 ±56.22 |
| Red fox | 2.15 (0–17) | 154.10 ±296.74 | 48.63 ±126.41 |
| Japanese marten | 3.07 (0–30) | 174.96 ±255.73 | 60.31 ±94.98 |

that the top variable in the models was wild boar ($\Sigma_w = 0.56$), and the mean feeding times decreased by a factor of 0.85 ($\beta = -0.16$) for each additional visit of wild boars (Table 5, Fig. 2).

3.2. Wild boar

We recorded 96 visits and 5790 unique feeding counts of wild boars. We found three top models for the number of visits (Table 2). The variables in the best model included bear ($\beta_{\text{count}} = -0.05$) and season ($\beta_{\text{count}} = 1.25$) in the count model and no variable in the zero-inflated model (Table 2). The results of model averaging showed that the top variable in the count model was visits of bears ($\Sigma_w = 0.91$) and that the top variable in the zero-inflated model was season ($\Sigma_w = 0.49$). Parameter estimates of model averaging showed that the number of visits decreased by a factor of 0.95 ($\beta_{\text{count}} = -0.05$) for each additional visit of wild boars, and in autumn decreased the probability of not visiting by a factor of 0.28 ($\beta_{\text{zero-inflated}} = -1.28$) compared to summer (Table 3, Fig. 2). We found only one null model for the top model of the mean feeding time (Table 4).

Table 2

Top models for number of visits for each scavenger species using zero-inflated poisson regression. We ranked the models based on Akaike information criterion with small sample bias adjustment (AICc). We show models with AICc difference (Δ_i) of <2 from the best model (see Table S2 for all models). w_i shows the model AICc weights.

| Species | Variable | | AICc | Δ_i | w_i |
|------------------|---------------------------|---------------------------|--------|------------|-------|
| | count model | zero-inflation model | | | |
| Asian black bear | wild boar | season | 402.73 | 0.00 | 0.24 |
| | wild boar + season | season | 403.58 | 0.86 | 0.15 |
| | wild boar | wild boar + season | 404.13 | 1.40 | 0.12 |
| | wild boar | wild boar | 404.49 | 1.76 | 0.10 |
| Wild boar | bear + season | | 188.24 | 0.00 | 0.32 |
| | bear + season | season | 189.30 | 1.06 | 0.19 |
| | bear | season | 189.74 | 1.50 | 0.15 |
| | bear + wild boar + season | | 558.34 | 0.00 | 0.29 |
| Raccoon dog | bear + wild boar + season | bear | 559.73 | 1.39 | 0.15 |
| Red fox | bear | wild boar + season | 228.74 | 0.00 | 0.21 |
| | bear | bear + wild boar + season | 230.43 | 1.69 | 0.09 |
| | bear + season | bear | 250.09 | 0.00 | 0.11 |
| | bear + season | bear | 250.23 | 0.14 | 0.10 |
| Japanese marten | bear + season | bear + season | 250.59 | 0.50 | 0.08 |
| | bear + season | season | 250.61 | 0.51 | 0.08 |
| | bear + season | wild boar | 250.99 | 0.90 | 0.07 |
| | bear + season | bear + wild boar | 251.40 | 1.30 | 0.05 |
| | bear + wild boar + season | bear | 251.87 | 1.78 | 0.04 |
| | bear + wild boar + season | | 251.97 | 1.88 | 0.04 |

Table 3

Parameter estimates (coefficient and standard error: SE) and model-averaged weights (Σ_w) of models explaining visit process for each scavenger. Each model includes two parts models; count model and zero-inflated model. The top variables of each part model shown in bold.

| Species | Part model | Variable | Coefficient | SE | w |
|------------------|----------------|----------------------|--------------|-------------|-------------|
| Asian black bear | Count | Intercept | 0.34 | 0.07 | |
| | | Wild boar | -0.08 | 0.03 | 0.90 |
| | | Season (autumn) | -0.15 | 0.12 | 0.43 |
| | Zero-inflation | Intercept | -1.13 | 0.56 | |
| | | Season (autumn) | 1.19 | 0.64 | 0.64 |
| Wild boar | Count | Intercept | -1.38 | 0.66 | |
| | | Bear | -0.05 | 0.02 | 0.91 |
| | Zero-inflation | Intercept | 0.59 | 0.79 | |
| | | Season (autumn) | -1.28 | 0.80 | 0.49 |
| Raccoon dog | Count | Intercept | 0.26 | 0.10 | |
| | | Bear | -0.03 | 0.01 | 1.00 |
| | | Wild boar | -0.03 | 0.01 | 0.78 |
| | Zero-inflation | Intercept | -1.72 | 0.46 | |
| | | Bear | 0.05 | 0.04 | 0.33 |
| | | Season (autumn) | 0.35 | 0.11 | 0.97 |
| Red fox | Count | Intercept | -0.11 | 0.11 | |
| | | Bear | -0.08 | 0.02 | 1.00 |
| | | Season (autumn) | 0.72 | 0.33 | 0.84 |
| | Zero-inflation | Intercept | 0.71 | 0.53 | |
| | | Bear | 0.04 | 0.05 | 0.29 |
| | | Wild boar (presence) | 0.26 | 0.14 | 0.74 |
| | | Season (autumn) | -1.40 | 0.68 | 0.65 |
| Japanese marten | Count | Intercept | -0.71 | 0.32 | |
| | | Bear | -0.04 | 0.01 | 0.92 |
| | | Wild boar | 0.01 | 0.02 | 0.33 |
| | Zero-inflation | Intercept | 0.08 | 0.51 | |
| | | Season (autumn) | 0.72 | 0.33 | 0.84 |

3.3. Raccoon dog

We recorded 948 visits and 46,105 unique feeding counts of raccoon dogs. We found two top models for the number of visits (Table 2). The variables in the best model included bear ($\beta_{count} = -0.03$), wild boar ($\beta_{count} = -0.03$), and season ($\beta_{count} = 0.35$) in the count model, and no variable in the zero-inflated model (Table 2). The results of model averaging showed that the top variable in the count model and the zero-inflated model was visits of bears ($\Sigma_w = 1.00$, $\Sigma_w = 0.33$, respectively; Table 3). Parameter estimates of model averaging showed that the number of visits decreased by a factor of 0.97 ($\beta_{count} = -0.03$) for each additional visit of bears, and the probability of not visiting increased by a factor of 1.05 ($\beta_{count} = 0.05$) for each additional visit of bears (Table 3, Fig. 2).

We found three top models for the feeding time (Table 4). The variables in the best model included wild boar ($\beta = -0.18$, Table 4). The results of model averaging showed that the top variable was presence of wild boars ($\Sigma_w = 0.68$). Parameter estimates of model averaging showed that the mean feeding times decreased by a factor of 0.84 ($\beta = -0.18$) for each additional visit of wild boars (Table 5, Fig. 2).

3.4. Red fox

We recorded 124 visits and 3236 unique feeding counts of red foxes. We found two top models for the number of visits (Table 2). The variables in the best model included bear ($\beta_{count} = -0.08$) in the count model, and wild boar ($\beta_{zero-inflated} = 0.25$) and season ($\beta_{zero-inflated} = -1.40$) in the zero-inflated model (Table 2). The results of model averaging showed that the top variable in the count model was visits of bears ($\Sigma_w = 1.00$) and the zero-inflated model was visits of wild boar ($\Sigma_w = 0.74$). Parameter estimates of model averaging showed that the number

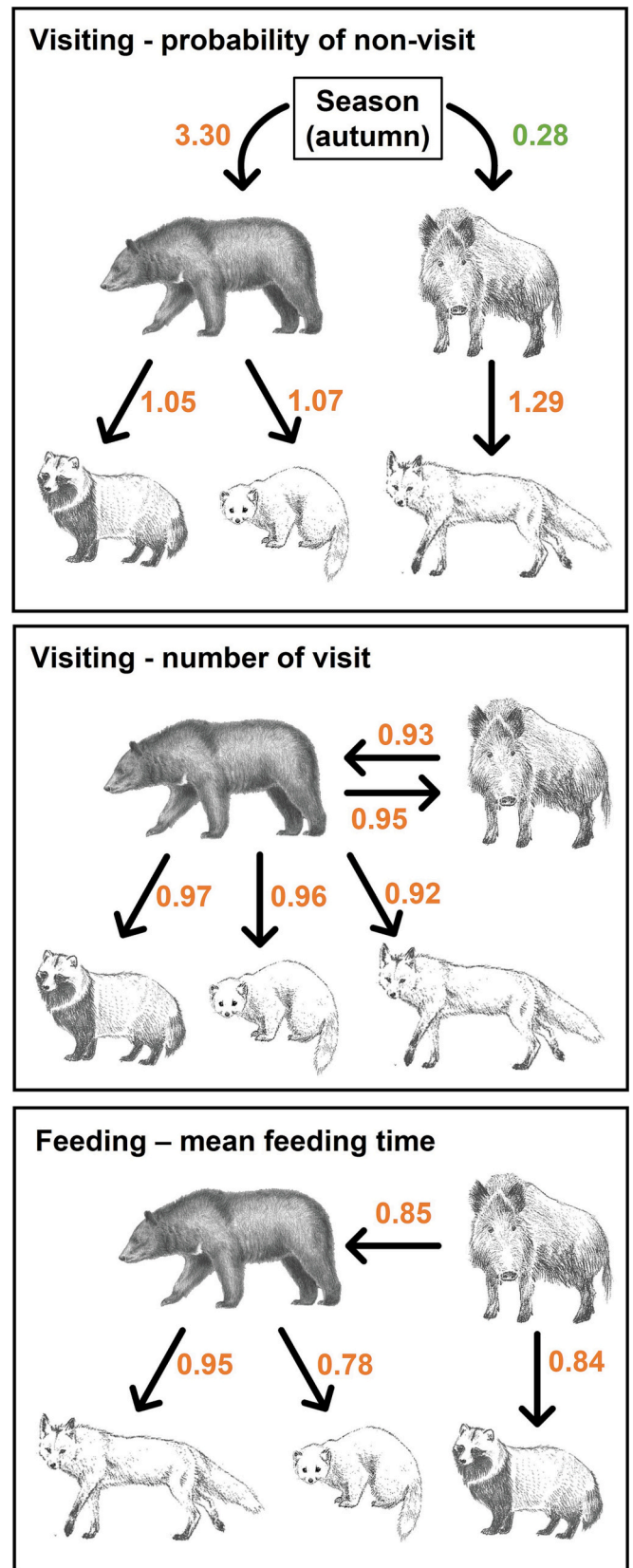


Fig. 2. The effects of the top variables (number of visits of bear, number of visits of wild boar, and season of autumn) for each model. Orange shows the negative effect and green shows the positive effect. The visiting model includes the count models (the number of visits) and the zero-inflated models (the probability of non-visit). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Top models for mean feeding time for each scavenger species using Gamma regression. Variables were ranked on the basis of Akaike information criterion (AICc). We show models with AICc difference of <2 ($\Delta i < 2$) from the best model (see Table S3 for all models). w_i shows the model AICc weights.

| Species | Variable | AICc | Δi | w_i |
|------------------|------------------|--------|------------|-------|
| Asian black bear | wild boar | 356.26 | 0.00 | 0.41 |
| | | 356.68 | 0.42 | 0.34 |
| Wild boar | | 188.05 | 0.00 | 0.61 |
| | wild boar | 399.61 | 0.00 | 0.34 |
| Raccoon dog | bear + wild boar | 400.79 | 1.18 | 0.19 |
| | | 401.33 | 1.72 | 0.14 |
| | | 147.33 | 0.00 | 0.39 |
| Red fox | bear | 148.64 | 1.31 | 0.20 |
| | wild boar | 149.31 | 1.99 | 0.14 |
| Japanese marten | bear + wild boar | 160.22 | 0.00 | 0.44 |
| | bear | 161.53 | 1.31 | 0.23 |

Table 5

Parameter estimates (coefficient and standard error: SE) and model-averaged weights (Σw) of models explaining mean feeding time for each scavenger. The top variables of each model shown in bold. The top model of wild boars was the null model.

| Species | Variable | Coefficient | SE | w |
|------------------|----------------------|--------------|-------------|-------------|
| Asian black bear | Intercept | 0.53 | 0.20 | |
| | Wild boar | -0.16 | 0.08 | 0.56 |
| | Intercept | 0.53 | 0.36 | |
| Raccoon dog | Bear | -0.04 | 0.08 | 0.37 |
| | Wild boar | -0.18 | 0.04 | 0.68 |
| | Intercept | -0.93 | 0.42 | |
| Red fox | Bear | -0.05 | 0.05 | 0.33 |
| | Wild boar (presence) | -0.22 | 0.25 | 0.26 |
| | Intercept | -0.15 | 0.39 | |
| Japanese marten | Bear | -0.25 | 0.07 | 0.91 |
| | Wild boar | -0.16 | 0.06 | 0.60 |

of visits decreased by a factor of 0.92 ($\beta_{\text{count}} = -0.08$) for each additional visit of bears, and the probability of not visiting increased by a factor of 1.29 ($\beta_{\text{count}} = 0.26$) for each additional visit of wild boars (Table 3, Fig. 2).

We found three top models for the feeding time, but the best model was null model (Table 4). The results of model averaging showed that the top variable was visits of bears ($\Sigma w = 0.33$). Parameter estimates of model averaging showed that the mean feeding times decreased by a factor of 0.95 ($\beta = -0.05$) for each additional visit of bears (Table 5, Fig. 2).

3.5. Japanese marten

We recorded 193 visits and 4199 unique feeding counts of Japanese martens. We found eight top models for the number of visits (Table 2). The variables in the best model included bear and season ($\beta_{\text{count}} = -0.04$ and $\beta_{\text{count}} = 0.74$, respectively) in the count model and bear ($\beta_{\text{zero-inflated}} = 0.07$) in the zero-inflated model (Table 2). The results of model averaging showed that the top variable in both the count model and the zero-inflated model was bears ($\Sigma w = 0.92$ and $\Sigma w = 0.50$, respectively). Parameter estimates of model averaging showed that the number of visits decreased by a factor of 0.96 ($\beta_{\text{count}} = -0.04$) for each additional visit of bears, and the probability of not visiting increased by a factor of 1.07 ($\beta_{\text{zero-inflated}} = 0.06$) for each additional visit of bears (Table 3, Fig. 2).

We observed one outlier in the mean feeding time (F1610; 119.38 mean feeding time). The carcass was visited 34 times by bears and not by wild boars, but a marten feeding extremely long time (666 unique feeding counts) before the bears visited. We excluded this outlier from the analysis. We found two top models for the feeding time (Table 4). The variables in the best model included bear and wild boar ($\beta_{\text{count}} =$

-0.25 and $\beta_{\text{count}} = -0.16$, respectively; Table 4). The results of model averaging showed that the top variable in the model was bears ($\Sigma w = 0.91$). Parameter estimates of model averaging showed that the mean feeding times decreased by a factor of 0.96 ($\beta_{\text{count}} = -0.25$) for each additional visit of bears (Table 5, Fig. 2).

4. Discussion

It is important to understand the factors that influence carrion consumption for scavengers because of their importance in ecological processes. These energy pathways can help stabilize food webs, and also provide links from the individual to population levels in communities. There were some drawbacks of our experiments that limited our ability to draw conclusions. We lost some of the consumption information by programming the camera to pause for 30 s, and this could have led to create a zero inflated bias in the number of visits and feeding times. We also used carcasses with only partial data where the entire consumption process could not be recorded, but this may have resulted in bias in the feeding model due to the censored data. Nevertheless, we found that Asian black bears and wild boars affect the carrion consumption (i.e., visiting and feeding on carcasses) of other scavengers, similar to other large carnivores (Allen et al., 2015; Panda et al., 2022), supporting prediction 2 and 3. We also found that there appeared to be seasonal effects on carcass visitation, especially for large scavengers which can have effects on other scavenger species, partially supporting prediction 1.

The phenology of the potential importance of nutrition from carrion can change the foraging ecology for scavenger species (Allen et al., 2021). We found an association with season in the visitation to the carcasses, but season was not an important variable in feeding time for all species. This indicates that carrion consumption strategies changing by season may be related to the visitation, the first step in carcass consumption, rather than actual feeding behavior. Our results showed that bears had an increased probability of not visiting (i.e., zero) in autumn compared to summer; in contrast, wild boars had an increased probability of visiting in autumn compared to summer. We also conducted a supplemental potential abundance survey in our study area using camera traps in 2017 (Fig. S1). This survey showed that there was no significant difference in mean relative abundance (RA) of bears and wild boars between summer and autumn, although wild boars tended to have increased mean RA in autumn (t-test_{bear}: $p = 0.84$, t-test_{wild boar}: $p = 0.06$, Fig. S1). These results suggest that seasonal changes in the importance of carcasses are associated with the availability of other food resources not the potential abundances and this can affect probability of visitation. Bears are strongly dependent on seasonal pulsed resources (such as hard masts) particularly during hyperphagia in autumn (Koike, 2010). Wild boars also utilize hard masts, but animal matter also increases in their diets from summer to autumn (Koba et al., 2009; Kodera and Kanzaki, 2001). However, further study of the seasonal importance of carrion for large scavengers in this system is needed, especially compared to the relative amount of various other food resources. We also suggest that the increased visitation in autumn by wild boars and other mesocarnivores was caused by the carcasses remaining available longer in the autumn due to low temperatures and less microbial activity. This likely increases the availability of carrion for vertebrate scavengers, especially wild boars are slower to detect carcasses than other species (Inagaki et al., 2022).

Bears and wild boars also affected each other; with the top models for number of visits (count model) and mean feeding time by bears included the variables of wild boar, and the top models for number of visits (count model) by wild boars included variables of bear. Among these models, the mutual limiting effects of bear and wild boar were more important variables than season. This suggests that bears and wild boars have a competitive relationship that limits the number of visits they each make to carcasses. Asian black bears are the dominant scavengers in this system (Inagaki et al., 2020), but wild boars could interfere with bear

carcass consumption by limiting both visitation and feeding time in this system. It may be necessary to consider body size differences between individuals to understand the true relationship between bears and wild boars because their body sizes vary based on sexual dimorphism but also vary largely among individuals (Ohdachi et al., 2009). However, we could not include the body size in our analysis due to the difficulty in estimating mass accurately from camera traps and the resulting lack of appropriate sample sizes.

Carion consumption by mesocarnivores (i.e., raccoon dogs, red foxes and martens) was more related to the effects of large scavengers than to season despite they changing their food seasonally (Ohdachi et al., 2009; Sasaki and Kawabara, 1994; Tsuji et al., 2019). Furthermore, these effects of large scavengers on mesocarnivores were all negative for the top variables for both bears and wild boars. Large and/or apex scavengers can not only reduce the available carion largely but also create a landscape of fear around carcasses for subordinate scavenger species (Moleón and Sánchez-Zapata, 2021; Panda et al., 2022). Our results supported the hypothesis of landscape of fear in this system, despite neither bears nor wild boars being direct predators of mesocarnivores. Instead, these dominant scavengers might influence ecological processes in mesocarnivores through changing individual responses such as habitat preferences and chronic stress (Clinchy et al., 2013; Gaynor et al., 2019). But it is important to note that bears had a stronger effect on the carion consumption by mesocarnivores than wild boars. Bears have a higher visit frequency and mean number of visits per carcass than wild boars, which may make mesocarnivores more susceptible to fear from bears. Besides, bears as the dominant consumers of carion among all species (Inagaki et al., 2020) exerted a significant influence on the biomass of carion remains. We would need to develop additional models to evaluate the relationship between the consumption effects and the landscape of fear by large scavengers. In addition, all of the bear variables in the top models for mesocarnivores had negative effects, however, an increase in the number of visits by wild boars had a positive or no effect to the visitation process by martens. Wild boars had a lower mean number of visits per carcass and feeding time per visit than other species, and may also play a role by opening the thick skins of deer carcasses and facilitate the carion consumption of martens, which is the smallest scavengers in this system (Selva et al., 2003). Among mesocarnivores, marten tended to longer feeding time per visit and less frequent number of visits. Therefore, it is inefficient for martens to stay for longer periods to feed at a carcass in a landscape of fear as their gut capacity limits how much they can eat at one time, as well as increase competitive risks due to contact with other scavenger species. Martens may efficiently acquire carion by increasing their visiting rate but decreasing the feeding time per visit. These flexible strategies of mesocarnivores to acquire limited resources is also in common with flexible changes in foraging behavior in response to human activity (Osugi et al., 2022).

We found that season was a key factor in the potential probability of visitation for large scavengers, and that large scavengers would affect carion consumption for mesocarnivores. This finding suggests that top-down regulation from large scavengers to mesocarnivores may change with season, especially in temperate regions with distinct seasons. It may therefore be necessary to consider these temporal changes in evaluating scavenging dynamics including generalist species that depend on pulsed resources. Further study of evaluating the quantitative interaction between carion consumption and other food resources is needed. Additionally, bears and wild boars had a competitive relationship, but had different effects on carion consumption by mesocarnivores, with one possible result being that mesocarnivores may have a net energy gain as a result of wild boars limiting bears. Thus, the sympatric presence of bears and wild boars likely contributes to maintaining the food web in this system, and our results highlight the complex interactions among scavengers and the potential seasonal factors that affect them.

CRediT authorship contribution statement

Akino Inagaki: Conceptualization, Writing – original draft, Investigation, Methodology, Data curation, Funding acquisition. **Maximilian L. Allen:** Methodology, Writing – review & editing. **Kahoko Tochigi:** Methodology. **Tetsuya Maruyama:** Investigation. **Shinsuke Koike:** Conceptualization, Supervision, Writing – review & editing, Funding acquisition.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors didn't use any AI and AI-assisted tool.

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

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fooweb.2023.e00324>.

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