Chapter 21
Vertebrate Scavenging on Sika Deer Carcasses and Its Effects on Ecological Processes

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Abstract The impacts of sika deer on ecological communities often focus on the effects of "alive" deer, but how "dead" deer affect organisms and the environment currently receives little attention. Dead animals (i.e., carcasses) are a high-quality food resource for scavengers that provide ecosystem services, and scavenging plays an important role in ecosystem stability. Forest ecosystems in Japan have an overabundance of deer and need constant population control via culling. Consequently, the deer carcasses from natural mortality and hunting and/or culling by human are a large food resource for many vertebrate scavengers. In the forest ecosystem of Honshu Island, we documented a vertebrate scavenger guild that feeds on deer carcass, which is composed of six mammals and three birds. Vertebrate scavenging is widespread, and the scavenging links from carcass to vertebrate scavengers are one of the essential energy transfers in food webs. Furthermore, sika deer carcasses were consumed entirely in about 1 week; thus, vertebrate scavengers contribute ecosystem services to remove potentially infectious carcasses from ecosystems. Future carcass availability related to overabundant deer populations and their management could alter the function of the scavenging community. Considering carrion management is a critical aspect in evaluating the widespread impact of deer and their ecological processes and could lead to proper ecosystem management.

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21.1 Introduction

The direct impacts of sika deer (*Cervus nippon*) on ecosystems often focus on the negative processes of deer foraging and trampling behavior. For example, the increased browsing and debarking pressure associated with overabundant deer populations cause serious damage to plant survival biodiversity and structure (Akashi and Nakashizuka 1999; Takahashi and Kaji 2001; Suda et al. 2001; Yokoyama et al. 2001; Nomiya et al. 2003; Suzuki et al. 2008; Takatsuki 2009; Nagaike 2012). In addition, the trampling by high densities of sika deer leads to physical disturbance and loss of the soil surface (Tsujino and Yumoto 2004; Niwa 2020). These impacts caused by "alive" deer have been well-studied (see Chaps. 16 and 23), but how "dead" deer affect organisms and their environment has received very little attention.

Dead animals (i.e., carcasses) are a high-quality and ephemeral food resource for scavengers that consume it and provide ecosystem stability and services. Scavenging is a widespread feeding behavior (Wilson and Wolkovich 2011; Beasley et al. 2019), and various biological groups from decomposers (e.g., invertebrates and microbes) to vertebrates shape the characteristic scavenging communities (DeVault et al. 2003). Vertebrate scavenging from carcasses shapes energy transfer links in food webs, and these additional links promote food web complexity and stability (Selva and Fortuna 2007; Wilson and Wolkovich 2011). Vertebrate scavengers also remove carcasses that are a source of harmful pathogens from ecosystems quickly by consuming carrion (DeVault et al. 2003; Moleón et al. 2014; Inger et al. 2016). In cases of carrion with large biomass, like ungulate carcass, a greater number and more diverse scavenger species are attracted to compete for the nutrition from the carcass, contributing to biodiversity maintenance (Barton et al. 2013; Moleón et al. 2015).

Japanese forests have high-density sika deer populations, and ongoing population management is being implemented by government. For example, approximately 465,700 deer were culled throughout the year by population management and approximately 137,200 were hunted in the recreational hunting season (generally 15 November to 15 February) in 2019 (Ministry of Environment, Japan 2020). These deer carcasses from hunting, culling, and natural mortalities may be an important food resource for vertebrate scavengers. However, deer carcass as a food resource has been overlooked, thereby lacking common, widespread obligate scavenger (i.e., that feed solely on carrion) species, like vultures, or large predators that regularly kill ungulates (see study area for a description of scavenger community) in Japan. Furthermore, it is difficult to find and observe natural mortalities because mountain forests often consist of steep terrain. For these reasons, little is known about the fate of these deer carcasses and the vertebrate scavenging process of deer carcass in Japan.

In this chapter, we report the utilization and consumption time of deer carcasses by vertebrate scavengers. We also discuss the ecological role of vertebrate scavengers and how changes in the deer population (i.e., the availability of deer carcass) may alter scavenging and its ecological function.

21.2 Material and Methods

21.2.1 Study Area

Nikko National Park is located in central Honshu Island (mainland Japan) at latitude 36°36′N–37°05′N, longitude 139°19′E–139°51′E. The area occupies 1159 km^2 and at elevations between 300 and 1300 m. The climate is temperate, with the mean annual temperature of 7.7°C and the mean annual rainfall of 2131 mm. The forest is characterized by deciduous broadleaved forests (composed mainly of *Quercus serrata*, *Q. crispula Blume*, and *Cerasus jamasakura*), conifer plantation forests (comprising mainly *Cryptomeria japonica*, *Chamaecyparis obtusa*, and *Larix kaempferi*), and also patchy mixed forests. The bamboo grasses (*Sasa* spp.) primarily covered each type of forest floor.

Sika deer are the largest herbivorous mammal in the forest, and the estimated population of sika deer in the study area is 13,429 deer (11.59 deer/km^2) in 2019 (Oze-Nikko National Park Wide-Area Council for the Control of Sika Deer 2020). Wolves (*Canis lupus*) were extirpated by 1905 (Hiraiwa 1981), and none of the other predators kill adult deer, although Asian black bears (*Ursus thibetanus*) are known to kill neonatal deer (Hashimoto and Takatsuki 1997). The mammalian scavengers on deer carcasses include Asian black bear, wild boar (*Sus scrofa*), red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), masked palm civet (*Paguma larvata*), and Japanese marten (*Martes melampus*) (Inagaki et al. 2020; Fig. 21.1a). The bird scavengers include jungle crow (*Corvus macrorhynchos*), black kite (*Milvus migrans*), and mountain hawk-eagle (*Nisaetus nipalensis*) (Inagaki et al. 2020, Fig. 21.1b).

21.2.2 Monitoring of Deer Carcass

We used video camera traps to observe the vertebrate scavenging of deer carcasses. From June to November in 2016 and 2017, we placed 42 fresh deer carcasses (18 male and 24 female; mean weight = 43 kg [range 10–70 kg]) that had not been scavenged in the mature deciduous broadleaved forests and patchy mixed forests (Inagaki et al. 2020). We secured the deer carcasses to the nearest tree using wire rope to prevent them from being removed by scavengers. We programmed the camera (Ltl-Acorn 6210 MC; Green Bay, Wisconsin, USA) to record 30-s videos at each trigger with a 30-s refractory period. We monitored a carcass until there was little available carrion (e.g., bones and skin) for vertebrate scavengers remaining.

Fig. 21.1 Vertebrate scavenger species (**a**, mammal; **b**, bird) on deer carcass on Honshu Island, Japan. (**a**) The species starting from the upper left, Asian black bear, wild boar, and raccoon dog, and from the lower left, red fox, Japanese marten, and masked palm civet. (**b**) The species starting from the left, mountain hawk-eagle, black kite, and jungle crow

21.2.3 Utilization of Deer Carcass

To evaluate the utilization of deer carcass by vertebrate scavengers, we determined (1) scavenging frequency, (2) feeding duration, and (3) seasonal differences of scavenging frequency among species and groups (i.e., mammal vs. bird).

Scavenging Frequency We calculated the number of deer carcasses that each species scavenged (fed on carrion). We used Fisher's exact tests to determine differences in the proportions of scavenged carcasses between mammals and birds. We then tested pairwise comparisons with Fisher's exact tests using Holm's multiple comparison adjustment in RVAideMemoire package (Hervē 2019) to determining differences in the proportions of scavenged carcasses among scavenger species.

Feeding Duration We calculated total feeding times (minutes) at each deer carcass for each species. In cases where there were more than five jungle crows in one video, we estimated total feeding time by summing the feeding time of five randomly selected individuals and multiplying this value by the maximum number of individuals during the visit divided by five. We used Wilcoxon rank sum test to examine differences in the mean feeding times between the groups (mammals vs. birds).

Seasonal Differences of Scavenging Frequency We classified the seasons as summer (June to August) and autumn (September to November). We tested for differences in the proportions of scavenged carcasses seasonally between groups (mammals vs. birds) and among species using Fisher's exact test. We then used Wilcoxon rank sum test to examine differences in feeding duration seasonally between groups (mammals vs. birds).

21.2.4 The Elapsed Time of Deer Carcass Consumption

To determine the elapsed time of deer carcass consumption, we calculated the period from when we set out each carcass until all edible portions except bones and skins were consumed (Sebastián-González et al. 2020).

21.3 Results

21.3.1 Utilization of Deer Carcass

We monitored 42 deer carcasses (summer = 20 deer, autumn = 22 deer), and all the carcasses were scavenged by at least one scavenger. We documented scavenging by mammals (97.6%; $n = 41$) at a significantly higher number of carcasses than birds (42.9%; $n = 18$) ($p < 0.001$, Fig. 21.2). The most frequent scavenger species were raccoon dogs (85.7%; $n = 36$) and secondly, Asian black bears (73.8%; $n = 31$, Fig. 21.3). They scavenged at a significantly higher number of carcasses than other scavengers ($p < 0.001$). In contrast, the least frequent scavengers were masked palm civets (2.4%; $n = 1$), black kites (9.5%; $n = 4$), and mountain hawk-eagles (11.9%; $n = 5$, Fig. 21.3). Scavenging by these species was at a significantly lower number of carcasses than other scavengers ($p < 0.001$).

For feeding duration, the mean feeding time (min) at carcasses was longer for mammals (80.2 ± 90.0 SD min) than for birds (29.3 ± 80.0 min, $p < 0.001$). Among

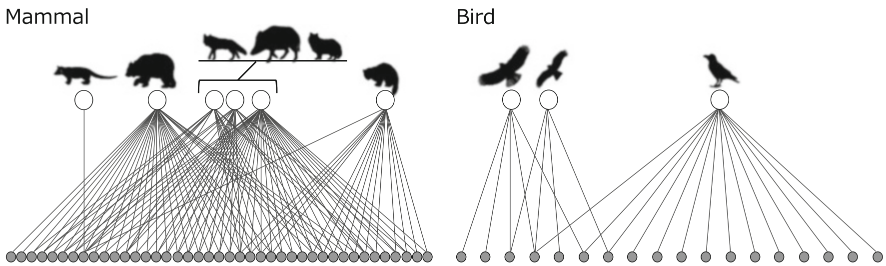

Fig. 21.2 Bipartite graphs depicting scavenging interactions between the vertebrate scavengers (open circles) and deer carcasses (filled circles)

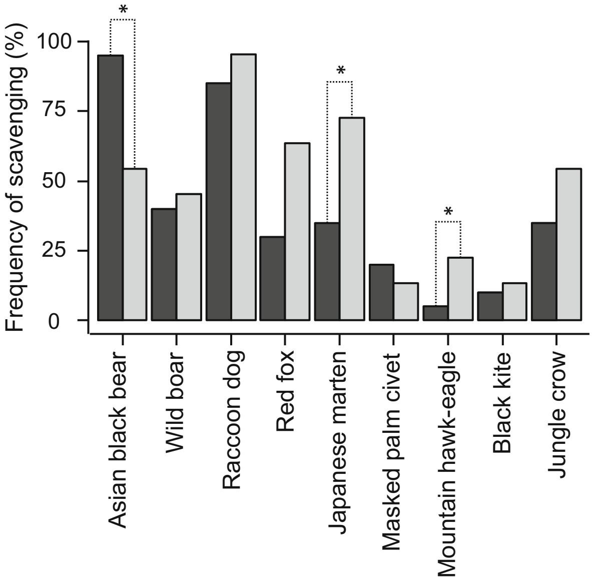

Fig. 21.3 The frequency (%) of scavenging for each species. Dark colors indicate summer; light colors indicate autumn. The asterisks indicate significant differences between summer and autumn ($p < 0.05$)

scavenger species, Asian black bears (36.9 ± 34.9 min) and raccoon dogs (52.6 ± 78.1 min) fed for longer durations (Fig. 21.4).

For seasonal differences of scavenging frequency, mammals had significantly higher scavenging frequency ($\text{frequency}_{\text{summer}} = 100\%$, $p_{\text{summer}} < 0.001$; $\text{frequency}_{\text{autumn}} = 95.5\%$, $p_{\text{autumn}} < 0.001$) and mean feeding time ($\text{mean}_{\text{summer}} = 53.1 \pm 53.4$ min, $p_{\text{summer}} = 0.023$; $\text{mean}_{\text{autumn}} = 106.0 \pm 108.3$ min, $p_{\text{autumn}} < 0.001$) than birds ($\text{frequency}_{\text{summer}} = 40.0\%$, $\text{frequency}_{\text{autumn}} = 45.5\%$; $\text{mean}_{\text{summer}} = 13.1 \pm 20.4$ min, $\text{mean}_{\text{autumn}} = 37.5 \pm 95.8$ min) in both seasons. The scavenging by Asian black bears decreased significantly from summer to autumn ($p = 0.0042$), while scavenging by Japanese martens and mountain hawk-eagles significantly increased ($p_{\text{Japanese martens}} = 0.0289$, $p_{\text{mountain hawk-eagles}} = 0.0492$, Fig. 21.3). Red foxes also slightly increased the scavenging frequency from summer to autumn ($p = 0.0577$, Fig. 21.3).

21.3.2 *The Elapsed Time of Carcass Consumption*

The mean carcasses consumption time was 6.8 days (median = 6.5 days) with ranges from 2.3 to 16.5 days. We illustrate the process of carcass decomposition for one carcass that was consumed at 6.5 days in Fig. 21.5. This carcass was detected first by raccoon dog at about 3.6 days after carcass placing and then scavenged by Asian black bear, raccoon dog, and red fox. We also observed invertebrate colonization mainly composed of flies and maggots.

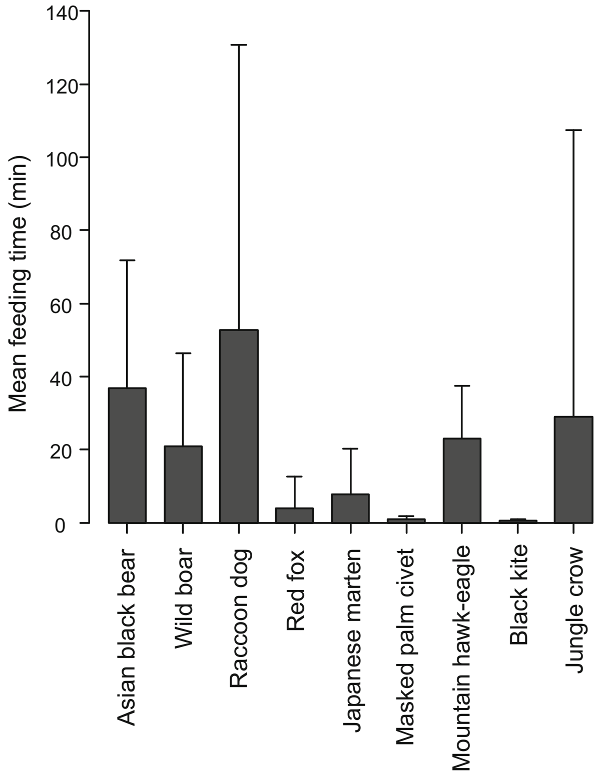

Fig. 21.4 The mean feeding time (min) for each species. The vertical solid bars indicate standard deviations (SD)

Fig. 21.5 An example of the consumption process of a deer carcass across 6.5 days. This deer carcass was placed on October 6, 2016 (the picture to the left), and totally consumed by October 13

21.4 Discussion

21.4.1 Vertebrate Scavenging and Its Ecological Role

Forest ecosystem in Honshu includes a vertebrate scavenger guild at deer carcass that is composed mainly of omnivorous carnivores, as well as a few forest bird species (Inagaki et al. 2020). All deer carcasses that we placed were scavenged by at least one vertebrate species, but scavenging by birds was likely restricted by the dense tree canopy and grass understory (Ogada et al. 2012). Raccoon dogs and Asian black bears are key scavengers in this system, because they fed on more deer carcasses and for longer durations than other scavengers. Despite little previous study, we found that scavenging is widespread as in other regions (e.g., Mateo-Tomás et al. 2015; Sebastián-González et al. 2020), and "dead" deer carcasses are a high-quality food and pulsed resource for vertebrate scavengers. Thus, scavenging links from carcasses to vertebrate scavengers provide one of the important energy transfers in food webs (Selva and Fortuna 2007; Wilson and Wolkovich 2011; Moleón et al. 2014).

Considering the direct interactions between deer carcass and vertebrate scavengers, how dependent each scavenger is for carrion should not be overlooked for their individual health and population maintenance. For example, the high utilization of carcasses by raccoon dogs overall suggest that they may be heavily dependent on nutrition from carrion. In other words, variation in the carcass availability may have an effect on the diet of raccoon dogs. Some scavenger species like Asian black bear and mountain hawk-eagle changed their frequency of carcass utilization by season. Omnivores are known to switch their feeding strategies by season in accordance with the availability of their primary food sources (Inagaki et al. 2020). In addition, carrion is an important supplemental food resource in severe winters (Tannerfeldt et al. 1994). Therefore, not only carcass availability but also other food sources and their phenology may affect scavenging. Quantifying how each scavenger depends on carcasses and the relevance with other food resources under various food conditions could lead to understanding the dynamics of facultative scavenging on food webs in the future.

Another important aspect of scavenger ecology is their ecosystem services, as shown by sika deer carcasses being consumed in about 1 week on average. Mean consumption time in temperate habitats has been reported to be 11.3 days in black-tailed deer (*Odocoileus hemionus columbianus*; Allen et al. 2014), 10.0 days in wild boar (Turner et al. 2017), and 3.1–4.2 days in ungulates (Mateo-Tomás et al. 2015; Morales-Reyes et al. 2019), where obligate scavengers are present. Also, it is 8.8 days in roe deer (*Capreolus capreolus*), where obligate scavenger is absent (Krofel 2011). As these results show, sika deer carcasses in Japan were consumed at a relatively faster rate, despite there being no predators of adult deer or obligate scavengers in the ecosystem. Considering the widespread scavenging by vertebrates, vertebrate scavengers do contribute to the removal of carcass from ecosystems. In general, large predators or vultures are key species that promote carcass consumption through interspecific interactions (Selva and Fortuna 2007; Mateo-Tomás et al. 2015). On the other hand, invertebrates that are common in certain environments also can compete with vertebrates and accelerate the decomposition process (Beasley et al. 2012; Pereira et al. 2014). To understand the ecological role of vertebrate scavengers, it is necessary to examine what contributes to the consumption of deer carcasses from both biological factors (e.g., carcass size, interaction between vertebrates and invertebrates) and non-biological factors (e.g., environmental characteristics) and how ecological significance vertebrate scavengers has to faster removal of carcasses from ecosystem.

21.4.2 Deer Impact on Scavenging Community

The availability of deer carcasses related to deer overabundance and its population management (i.e., anthropogenic carrion) could alter scavenging function, consequently triggering changes to ecological processes at various scales. Oro et al. (2013) suggested that aspects of biological fitness at an individual level (including body mass, fecundity, survival, and dispersal) are directly affected by the biomass of anthropogenic carrion. These effects on individuals also lead to effects at the population level such as population size and fluctuations, foraging behavior, and diet. In addition, the ecosystem and populations could be changed not only relation to interspecific competition and food webs but also species composition, habitat characteristics, and human-wildlife conflict. Indeed, the diet of Asian black bear has changed to high deer dependence with habitat conditions caused by overabundant sika deer (Koike et al. 2013). Thus, carrion availability is the foundation of scavenging dynamics and its interspecific interactions.

If natural and anthropogenic carcasses increase with their increasingly overabundant population and switch from competitive to excessive food resource, the impact of scavenging on ecological processes will require special attention. In Japan, there has not been a management method based on scientific knowledge established for the treatment of deer carcasses resulting from intense population control for overpopulated deer. According to "Wildlife Protection and Hunting Management Law," captured animals should be taken out in principle, only in unavoidable cases should they be buried in an appropriate manner that does not affect the ecosystem. However, in reality, the waste in forest is often buried or remains on site (Yamada 2018). In this gap between the current system and the situation, it is not clear how impact the carcass has on the ecosystem. It needs for further research to accumulate scientific knowledges in carcass management, such as whether carcasses should be left behind or removed. Simultaneously, fundamental knowledge that reveals relationships between deer carcasses and its scavengers and their ecological function should be further investigated, not only for vertebrates but also for invertebrates. In summary, considering carrion management is important to evaluate widespread impacts of deer and their ecological process and is needed for proper ecosystem management.

References

Akashi N, Nakashizuka T (1999) Effects of bark-stripping by Sika deer (*Cervus nippon*) on population dynamics of a mixed forest in Japan. For Ecol Manage 113:75–82

Allen ML, Elbroch LM, Wilmers CC, Wittmer HU (2014) Trophic facilitation or limitation? Comparative effects of pumas and black bears on the scavenger community. PLoS One 9(7): e102257

Barton PS, Cunningham SA, Lindenmayer DB, Manning AD (2013) The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171: 761–772

Beasley JC, Olson ZH, Devault TL (2012) Carrion cycling in food webs: comparisons among terrestrial and marine ecosystems. Oikos 121:1021–1026

Beasley JC, Olson ZH, Selva N, DeVault TL (2019) Ecological functions of vertebrate scavenging. In: Olea PP, Mateo-Tomás P, Sánchez Zapata JA (eds) Carrion ecology and management. Springer, Cham, pp 125–157

DeVault TL, Rhodes OE Jr, Shivik JA (2003) Scavenging by vertebrates: and evolutionary on an important perspectives in terrestrial transfer energy pathway ecosystems. Oikos 102:225–234

Hashimoto Y, Takatsuki S (1997) Food habits of Japanese black bears: a review. Mamm Sci 37:1–19. (in Japanese with English abstract)

Hervē M (2019) RVAideMemoire: testing and plotting procedures for biostatistics. Retrieved from. https://cran.r-project.org/web/packages/RVAideMemoire/index.html. Accessed 28 Sep 2021

Hiraiwa Y (1981) Wolves: their ecology and history. Ikeda-Shoten, Tokyo. (In Japanese)

Inagaki A, Allen ML, Maruyama T, Yamazaki K, Tochigi K, Naganuma T, Koike S (2020) Vertebrate scavenger guild composition and utilization of carrion in an East Asian temperate forest. Ecol Evol 10:1223–1232

Inger R, Cox DT, Per E, Norton BA, Gaston KJ (2016) Ecological role of vertebrate scavengers in urban ecosystems in the UK. Ecol Evol 6:7015–7023

Koike S, Nakashita R, Naganawa K, Koyama M, Tamura A (2013) Changes in diet of a small, isolated bear population over time. J Mammal 94:361–368

Krofel M (2011) Monitoring of facultative avian scavengers on large mammal carcasses in Dinaric forest of Slovenia. Acrocephalus 32:45–51

Mateo-Tomás P, Olea PP, Moleón M, Vicente J, Botella F, Selva N, Vinuela J, Sánchez-Zapata JA (2015) From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Divers Distrib 21:913–924

Ministry of Environment, Japan (2020) The number of captured animals by hunting and culling. https://www.env.go.jp/nature/choju/docs/docs4/hokakusuu.pdf. Accessed 28 Sep 2021

Moleón M, Sánchez-Zapata JA, Margalida A, Carrete M, Owen-Smith N, Donázar JA (2014) Humans and scavengers: the evolution of interactions and ecosystem services. Bioscience 64: 394–403

Moleón M, Sánchez-Zapata JA, Sebastián-González E, Owen-Smith N (2015) Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos 124:1391–1403

Morales-Reyes Z, Martín-López B, Moleón M, Mateo-Tomás P, Olea PP, Arrondo E, Donázar JA, Sánchez-Zapata JA (2019) Shepherds' local knowledge and scientific data on the scavenging ecosystem service: insights for conservation. Ambio 48:48–60

Nagaike T (2012) Effects of browsing by sika deer (*Cervus nippon*) on subalpine vegetation at Mt. Kita, central Japan. Ecol Res 27:467–473

Niwa S (2020) Characteristics and temporal trends of a ground beetle (*Coleoptera: Carabidae*) community in Ooyamazawa Riparian Forest. In: Sakio H (ed) Long-term ecosystem changes in riparian forests, Ecological research monographs. Springer, Singapore, pp 179–200

Nomiya H, Suzuki W, Kanazashi T, Shibata M, Tanaka H, Nakashizuka T (2003) The response of forest floor vegetation and tree regeneration to deer exclusion and disturbance in a riparian deciduous forest, central Japan. Plant Ecol 164:263–276

Ogada DL, Torchin ME, Kinnaird MF, Ezenwa VO (2012) Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. Conserv Biol 26: 453–460

Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A (2013) Ecological and evolutionary implications of food subsidies from humans. Ecol Lett 16:1501–1514

Oze-Nikko National Park Wide-Area Council for the Control of Sika Deer (2020) Oze-Nikko National Park policy for deer management. http://kanto.env.go.jp/1_onshika19_houshin_b.pdf. Accessed 28 Sep 2021

Pereira LM, Owen-Smith N, Moleón M (2014) Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mammal Rev 44:44–55

Sebastián-González E, Morales-Reyes Z, Botella F, Naves-Alegre L, Pérez-García JM, Mateo-Tomás P, Olea PP, Moleón M, Barbosa JM, Hiraldo F, Arrondo E, Donázar JA, Cortés-Avizanda A, Selva N, Lambertucci SA, Bhattacharjee A, Brewer A, Anadón JD, Abernethy E, Turner K, Beasley JC, DeVault TL, Gerke HC, Rhodes OE Jr, Ordiz A, Wikenros C, Zimmermann B, Wabakken P, Wilmers CC, Smith JA, Kendall CJ, Ogada D, Frehner E, Allen ML, Wittmer HU, Butler JRA, Du Toit JT, Margalida A, Oliva-Vidal P, Wilson D, Jerina K, Krofel M, Kostecke R, Inger R, Per E, Ayhan Y, Ulosoy H, Vural D, Inagaki A, Koike S, Samson A, Perrig PL, Spencer E, Newsome TM, Heurich M, Anadon JD, Buechley ER, Sánchez-Zapata JA (2020) Network structure of vertebrate scavenger assemblages is driven by ecosystem productivity and human impact at a global scale. Ecography 43: 1143–1155

Selva N, Fortuna MA (2007) The nested structure of a scavenger community. Proc Royal Soc Biol Sci 274:1101–1108

Suda K, Araki R, Maruyama N (2001) The effects of sika deer on the structure and composition of the forests on the Tsushima islands. Biosphere Conserv 4:13–22

Suzuki M, Miyashita T, Kabaya H, Ochiai K, Asada M, Tange T (2008) Deer density affects ground-layer vegetation differently in conifer plantations and hardwood forests on the Boso Peninsula, Japan. Ecol Res 23:151–158

Takahashi H, Kaji K (2001) Fallen leaves and unpalatable plants as alternative foods for sika deer under food limitation. Ecol Res 16:257–262

Takatsuki S (2009) Effects of sika deer on vegetation in Japan: a review. Biol Conserv 142:1922–1929

Tannerfeldt M, Angerbjorn A, ArvidSon B (1994) The effect of summer feeding on juvenile arctic fox survival-a field experiment. Ecography 17:88–96

Tsujino R, Yumoto T (2004) Effects of sika deer on tree seedlings in a warm temperate forest on Yakushima Island, Japan. Ecol Res 19:291–300

Turner KL, Abernethy EF, Conner LM, Rhodes OE Jr, Beasley JC (2017) Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. Ecology 98:2413–2424

Wilson EE, Wolkovich EM (2011) Scavenging: how carnivores and carrion structure communities. Trends Ecol Evol 26:129–135

Yamada M (2018) Establishment of appropriate and efficient disposal system for captured wildlife. In: Environment research and technology development fund. https://www.erca.go.jp/suishinhi/seika/pdf/seika_1_h30/3K162012_2.pdf. Accessed 28 Sep 2021

Yokoyama S, Maeji I, Ueda T, Ando M, Shibata EI (2001) Impact of bark stripping by sika deer, *Cervus nippon*, on subalpine coniferous forests in central Japan. For Ecol Manage 140:93–99