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Wildlife as Potential Vectors of African Swine Fever Virus

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Abstract

The African swine fever virus (ASFV) remains contagious for a long time, not only in the carcass, but also in the bone marrow of an infected animal. The scavenging activity of various animals on ASFV-infected carcasses is a likely risk factor for ASFV transmission. Thus, we conducted this study to determine whether scavengers are potential vectors for ASFV. In nonprotected wild boar carcasses on the forest floor, we investigated the seasonal patterns of carcass decomposition and scavenger visits for feeding on them. The duration from fresh to early skeletonization (only bones and leather remaining) of adult carcasses was 37.6±23.1 days (n=3, range=11-51 days) in winter. The duration from fresh to later skeletonization (only bones and some fur remaining) of all carcasses, including subadult carcasses, was 8.3±2.5 days (n=4, range=7-12 days) in summer. At all three study sites, leopard cats (30.3%), large-billed crows (21.6%), and golden eagles (18.1%) were the frequently visiting species, representing more than 10% of the total visits (343 visits) in winter, whereas raccoons (21.9%), grey-backed thrushes (39.4%), and eyebrowed thrushes (14.7%) were the most frequent visitors in summer. In winter, crows or cinereous vultures were the first animals to arrive at a carcass; in summer, raccoons or crows arrived first. Our results showed that wild boars, raccoons, and leopard cats relatively frequently visited wild boar carcasses and stayed there for a long time. Wild rodents chewing on or staying near carcasses were photographed during winter. In addition to wild boars, thus, mammals, such as raccoons, leopard cats and rodents, and birds, such as accipitrids and thrushes, may be spreaders of ASFV in South Korea.

Key Words: wild boar, African swine fever, scavenger, carcass, wildlife

Introduction

In South Korea, African swine fever (ASF) first occurred in pig farms in Paju, Gyeonggi-do on September 16, 2019. Since ASF virus (ASFV) was first detected in the carcass of wild boars in Yeoncheon-gun on October 2, 2019, it has continued to spread from northern Gangwon-do, including the Korean Demilitarized Zone (DMZ) and civilian control zones, to northern Chungcheongbuk-do (APQA 2021).

African swine fever virus can survive at least 11 days in feces, about 15 weeks in decayed serum, and months in the spinal cord (Sánchez-Vizcaíno et al. 2009; EFSA 2014; CFSPH 2015). Therefore, wild boar carcasses are likely an important source of infection for other wild animals until they are completely decomposed (Probst et al. 2019; EFSA

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et al. 2021).

Wild boar carcasses are used as food for other wild animals (Probst et al. 2019) such as canids (Jones 2011; Probst et al. 2019) and vultures (Spradley et al. 2012; Schultz and Mitchell 2018; Probst et al. 2019), and as food for conspecific wild boars (Probst et al. 2017). Scavenging activity on ASFV-infected carcasses is likely a risk factor for ASFV transmission (Carrasco-Garcia et al. 2018; Probst et al. 2019). Therefore, the rapid detection and removal of ASFV-infected carcasses are powerful means of quarantine and can prevent the spread of ASF among wild boars (Probst et al. 2019; EFSA et al. 2021).

Thus, we conducted this study to determine whether scavengers are potential vectors of ASFV. We investigated the seasonal patterns of carcass persistence and scavengers visits for feeding on nonprotected wild boar carcasses on the forest floor.

Materials and Methods

Study area

We selected three study sites in the mountainous area in Dongmak-ri, Geundeok-myeon, Samcheok-si, Gangwon-do (Fig. 1). Site 1 (N37.31942, E129.21488) is a coniferous forest area, with *Pinus dendriflora* as its dominant species, located at an elevation of 115 m. Site 2 (N37.30531, E129.22467) is a mixed forest area located at an elevation of 300 m. Site 3 (N37.30749, E129.22203) is a broad-leaved forest area located at an elevation of 340 m. At all three sites, the diameter at breast height (DBH) of the trees was categorized as the medium tree size class (DBH of 18-28 cm of 50% of all trees) with an age class V.

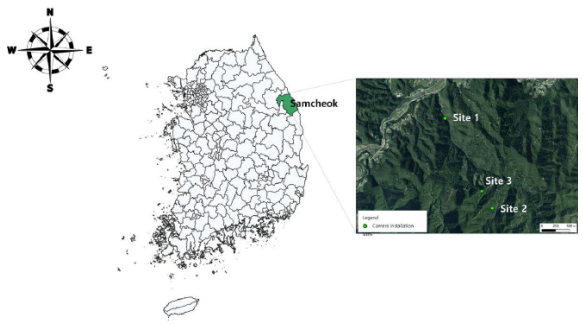

Fig. 1. Location of the study sites where wild boar carcasses were placed in Samcheok-si.

Carcass preparation

Carcasses of wild boars hunted in the forests in Samcheok-si were provided by the Samcheok branch of the Wildlife Management Association. The wild boars were hunted on December 14, 2020, in winter, and June 28, 2021, in summer. We placed the carcasses at the research sites within at least one day of being hunted, and we placed adult carcasses at all sites except for Site 1. It was difficult to obtain adult carcasses of wild boars in summer. Therefore, we placed two subadult carcasses at Site 1. We placed the nonprotected carcasses on the forest floor so that mammals, birds, and invertebrates could access them. In addition, referring to a previous study (Probst et al. 2019), the carcasses were tied and fixed with ropes to the base of the trees equipped with cameras to prevent the carcasses from being dragged out of the camera's field of view by scavengers (Fig. 2).

Camera trapping and decomposition status

We installed a total of nine cameras, three cameras at each site (Fig. 2). We used BTC-6PXD and 8E camera models (Browning Trail Cameras, USA), with motion detection sensors that automatically photograph wildlife when they pass in front of the camera. For the three cameras at each site, we set the camera mode to video in two cameras and to photo mode in the remaining camera. We set the video recording to have a delay time of 1 min after a recording time of 30 s. The photography was set to have a delay time of 1 min after three consecutive photoshoots.

The camera trap period was 212 days from December 15, 2020, to July 14, 2021, encompassing winter, spring, and summer (Table 1). We inspected carcasses and cameras

Fig. 2. Camera traps installed at three positions at each of the three sites, and carcasses tied up with ropes from the tree trunks on which the camera traps were installed.

Table 1. Information on the wild boar carcasses used for this study

Season	Site	Hunting date	Body weight (kg)	Age	Carcass placement/ camera trap start date	Carcass skeletonization date	Duration (day) required for skeletonization from hunting date	Carcass removal date	End of camera trap date
Winter	1	Dec 14, 2020	80 (F)	Adult	Dec 15, 2020	Feb 3, 2021	51	Feb 3, 2021	Jul 14, 2021
	2	Dec 14, 2020	80 (F)	Adult	Dec 15, 2020	Feb 3, 2021	51	Feb 3, 2021	Jul 14, 2021
	3	Dec 14, 2020	80 (F)	Adult	Dec 15, 2020	Dec 25, 2020	11	Feb 3, 2021	Jul 14, 2021
Summer	1	Jun 28, 2021	40 (F)	Subadult	Jun 29, 2021	Jul 5, 2021	7	Jul 14, 2021	Jul 14, 2021
		Jun 28, 2021	40 (F)	Subadult	Jun 29, 2021	Jul 5, 2021	7	Jul 14, 2021	Jul 14, 2021
	2	Jun 28, 2021	120 (M)	Adult	Jun 29, 2021	Jul 10, 2021	12	Jul 14, 2021	Jul 14, 2021
	3	Jun 28, 2021	80 (M)	Adult	Jun 29, 2021	Jul 5, 2021	7	Jul 14, 2021	Jul 14, 2021

every week. We analyzed the decomposition status of the carcasses by comparing the photographs taken using camera traps. We also used photographs of the carcasses captured with a hand camera during the weekly visit to analyze the decomposition state of the carcasses.

To count wildlife visits, we only used data from one of the three cameras installed at each site, to ensure that we avoided that triple counts of animal visits. All images of the same species taken within 30 min were assigned to a single visit. If the time interval between the two images was longer than 30 min, we assigned the image to a new visit. Even if physical contact with the carcass was not confirmed, we considered all species identified around the carcass as visitors.

Results and Discussion

Species richness of visitors at study sites

During the 212 days of camera trap monitoring from December 15, 2020, to July 14, 2021, we detected 11 mammalian species, unidentified rodents, and 21 bird species at the study sites (Table 2). At Site 1, a mammal, the raccoon (49 visits); and two bird species, the grey-backed thrush (74 visits) and the golden eagle (57 visits), visited frequently. At Site 2, leopard cats (84 visits), wild boars (76 visits), and a bird species, the grey-backed thrush (74 visits), appeared relatively frequently. At Site 3, leopard cats (25 visits), raccoons (24 visits), brown-headed thrushes (45 visits), eyebrowed thrushes (37 visits), and large-billed crows (40 visits) visited frequently (Table 2).

Among the mammals, we detected four species (raccoons, leopard cats, Asian badgers, and Siberian chipmunks) at all three sites. Wild boars were noted at Sites 2 and 3 using camera traps, with a higher frequency of visits (76 visits) at Site 2 than at Site 3 (13 visits) (Table 2). Rubbing trees used by wild boars are most commonly found at elevations between 200 and 600 m (Lee and Lee 2014). In our study, Sites 2 and 3 were located at elevations of 311 and 339 m, respectively, falling within the range reported in a previous study to be preferred by wild boars (Lee and Lee 2014). Site 2 is a mixed forest area with conifers and broad-leaved trees. Thus, wild boars likely frequently appeared for activities related to food, such as acorn intake to secure energy in May, when wild boars give birth (Won 1967; Yoon et al. 2002).

Decomposition status of wild boar carcasses

According to previous studies (Parsons 2009; Keough et al. 2017; Probst et al. 2020), the decomposition of a carcass is divided into four stages: fresh, early decomposition, advanced decay, and skeletonization. The early phase of skeletonization occurs when the majority of soft tissue has decomposed or when mummified tissue begins to break down to reveal bones. During the later phases of skeletonization, only grease and bones that are completely dry with little to no soft tissue remain (Parsons 2009; Keough et al. 2017; Probst et al. 2020).

The duration from the fresh to the early skeletonization stage (with only bones and leather left) of adult carcasses was 37.6±23.1 days on average (n=3, range=11-51 days) in winter (Table 1). The duration from the fresh to the later

Table 2. The number of wildlife visits at the study sites from December 15, 2020, to July 14, 2021

Taxonomic group					Number of visits			
Group	Order	Family	Species	English name	Site 1	Site 2	Site 3	Total
Mammals	Carnivora	Canidae	*Canis familiaris*	Domestic dog	0	1	2	3
			Nyctereutes procyonoides	Raccoon dog	49	13	24	86
		Felidae	*Felis catus*	Domestic cat	0	1	3	4
			Prionailurus bengalensis	Leopard cat	4	84	25	113
		Mustelidae	*Martes flavigula*	Marten	6	1	0	7
			Meles leucurus	Asian badger	12	2	3	17
			Mustela sibirica	Siberian weasel	1	0	2	3
	Artiodactyla	Cervidae	*Capreolus pygargus*	Siberian roe deer	0	7	3	10
			Hydropotes inermis	Water deer	1	8	0	9
		Suidae	*Sus scrofa*	Wild boar	0	76	13	89
	Rodentia	Sciuridae	*Eutamias sibiricus*	Siberian chipmunk	13	14	11	38
		Unidentified rodents			20	12	21	53
Birds	Accipitriformes	Accipitridae	*Accipiter gentilis*	Northern goshawk	0	0	2	2
			Aegypius monachus	Cinereous vulture	13	1	8	22
			Aquila chrysaetos	Golden eagle	57	4	2	63
			Buteo buteo	Common buzzard	6	0	1	7
			Haliaeetus albicilla	White-tailed eagle	1	1	0	2
	Passeriformes	Corvidae	*Corvus macrorhynchos*	Large-billed crow	38	29	40	107
		Motacillidae	*Motacilla cinerea*	Grey wagtail	12	0	0	12
		Muscicapidae	*Phoenicurus auroreus*	Daurian redstart	0	0	1	1
		Paridae	*Parus minor*	Japanese tit	0	29	5	34
			Poecile palustris	Marsh tit	0	1	0	1
			Sittiparus varius	Varied tit	0	3	3	6
		Turdidae	*Turdus chrysolaus*	Brown-headed thrush	0	0	45	45
			T. hortulorum	Grey-backed thrush	74	57	0	131
			T. obscurus	Eyebrowed thrush	0	0	37	37
			T. pallidus	Pale thrush	39	5	2	46
			Zoothera dauma	Scaly thrush	0	8	0	8
	Piciformes	Picidae	*Dendrocopos leucotos*	White-backed woodpecker	0	4	2	6
			D. major	Great spotted woodpecker	0	0	1	1
	Galliformes	Phasianidae	*Coturnix japonica*	Japanese quail	0	0	1	1
			Tetrastes bonasia	Hazel grouse	0	11	0	11
	Columbiformes	Columbidae	*Streptopelia orientalis*	Oriental turtle dove	0	18	13	31

skeletonization stage (when only bones and some fur remain) of all carcasses including subadult carcasses was 8.3±2.5 days on average (n=4, range=7-12 days) in summer (Table 1).

Numerous factors, including body size, temperature, and moisture, affect the time for a carcass to skeletonize (Carter et al. 2010; Meyer et al. 2013; Myburgh et al. 2013; Sutherland et al. 2013; Matuszewski et al. 2014; Brooks 2016). The strong influence of scavengers and arthropods on the decay rate of carcasses has been previously noted (Simmons et al. 2010; Probst et al. 2019).

In summer, adult wild boar carcasses are fully skeleton-

ized within a few days, whereas skeletonization takes several months in winter (Probst et al. 2017, 2019, 2020). According to a previous study that was conducted in Greifswald, northeast Germany (54°6 N, 13°23 E) (Probst et al. 2019), in summer, 3.5 and 7 days were required for the skeletonization of a female carcass weighing 40 kg and a male carcass weighing 47 kg, respectively. For two male carcasses each weighing 80 kg, skeletonization took 7 and 14 days, respectively. In winter, a male carcass weighing 80 kg required 42 days for skeletonization (Table 3 in Probst et al. 2019). The median time to skeletonization for adult carcasses was 8 days in summer and autumn and 37 days in winter and spring (Probst et al. 2019). In a previous study (Probst et al. 2019), wild boars weighing 40 kg were classified as adults. In our study, in which we included subadults weighing 40 kg, the average times to skeletonization of the carcasses (8.3 days to the later phase of skeletonization in summer and 37.6 days to the early phase of skeletonization in winter) were similar to the median persistence times (8 days in summer and 37 days in winter to the later phase of skeletonization) of the adult carcasses placed in Greifswald, northeast Germany.

Winter visitors to wild boar carcasses

We used camera traps to monitor the wildlife in the locations where we placed the wild boar carcasses. During the winter period of 51 days from December 15, 2020, to February 3, 2021 (Table 3), only birds visited Site 1 (Table 3). The birds that most commonly visited were golden eagles (56 visits), followed by large-billed crows (33 visits) and cinereous vultures (13 visits). Unidentified rodents (10 visits), four mammal species, and eight bird species visited Site 2. The frequent visitors were leopard cats (79 visits), large-billed crows (29 visits), and Japanese tits (29 visits). Unidentified rodents (13 visits), two mammal species (leopard cats (25 visits) and wild boar (6 visits)), and six bird species visited Site 3. The most frequently visiting birds were large-billed crows (12 visits) and cinereous vul-

Table 3. The number of wildlife visits to carcasses in winter and summer at the three study sites

Taxonomic group			Number of visits in winter					Number of visits in summer				
	Family	Common name	Site 1	Site 2	Site 3	Total visit	Ratio (%)	Site 1	Site 2	Site 3	Total visit	Ratio (%)
Mammals	Canidae	Domestic dog	0	0	0	0	0	0	0	1	1	0.4
		Raccoon	0	3	0	3	0.9	34	5	16	55	21.9
	Felidae	Leopard cat	0	79	25	104	30.3	0	0	0	0	0
	Cervidae	Water deer	0	1	0	1	0.3	0	0	0	0	0
	Suidae	Wild boar	0	3	6	9	2.6	0	0	0	0	0
	Sciuridae	Siberian chipmunk	0	0	0	0	0	2	0	0	2	0.8
	Unidentified rodents		0	10	13	23	6.7	1	0	0	1	0.4
Birds	Accipitridae	Northern goshawk	0	0	2	2	0.6	0	0	0	0	0
		Cinereous vulture	13	1	8	22	6.4	0	0	0	0	0
		Golden eagle	56	4	2	62	18.1	0	0	0	0	0
		Common buzzard	6	0	1	7	2.0	0	0	0	0	0
		White-tailed eagle	1	1	0	2	0.6	0	0	0	0	0
	Corvidae	Large-billed crow	33	29	12	74	21.6	0	0	13	13	5.2
	Motacillidae	Grey wagtail	0	0	0	0	0	12	0	0	12	4.8
	Paridae	Japanese tit	0	29	1	30	8.7	0	0	0	0	0
		Varied tit	0	2	0	2	0.6	0	0	0	0	0
	Turdidae	Grey-backed thrush	0	0	0	0	0	45	54	0	99	39.4
		Eyebrowed thrush	0	0	0	0	0	0	0	37	37	14.7
		Pale thrush	0	0	0	0	0	16	0	0	16	6.4
	Phasianidae	Japanese quail	0	0	0	0	0	0	0	1	1	0.4
		Hazel grouse	0	1	0	1	0.3	0	0	0	0	0
	Columbidae	Oriental turtle dove	0	1	0	1	0.3	0	13	1	14	5.6

tures (8 visits) at Site 2. We observed wild boars and leopard cats at Sites 2 and 3, and raccoons only at Site 2.

Large-billed crows were the first animal species to visit all sites, with the carcass detection time ranging from 1 day at Site 3 to 10 days at Site 1, with an average of 5.7±4.5 days (Fig. 3A-C). In a previous study (Probst et al. 2019), birds more quickly detected the carcass than mammals. In winter, odor does not spread much because of the slow decay rate, whereas birds seem to find carcasses faster than mammals because they can spot carcasses from the air after leaves in mixed forests have fallen to the ground. In all three sites, leopard cats (30.3%), large-billed crows (21.6%), and golden eagles (18.1%) were the most frequently visitors, with more than 10% of total visits (343 visits) (Table 3).

The species with the longest residence time at each site in winter were white-tailed eagles (3,336 s=55.6 min) at Site 1, cinereous vultures (3,627 s=60.45 min) at Site 2, and large-billed crows (5,744 s=95.73 min) at Site 3 (Fig. 4A-C). Birds stayed relatively longer at carcass sites than mammals. In the case of mammals, leopard cats (3,043 s=50.72 min) at Site 2 and wild boars (4,301 s=71.68 min) at Site 3 stayed for a long time. Around the carcass, a leopard cat showed aggressive behavior to prevent raccoons from accessing the carcass (Fig. 5), and a subadult wild boar was photographed eating the bones of the skeletonized carcass at Site 3 on day 49 after carcass release in winter (Fig. 6).

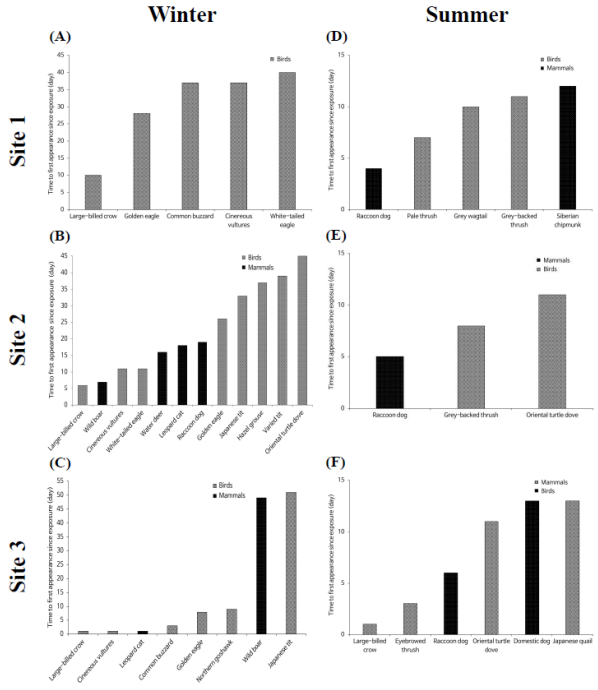

Fig. 3. Time to first appearance of wildlife after carcasses were placed at Sites 1, 2, and 3 in winter (A-C) and summer (D-F).

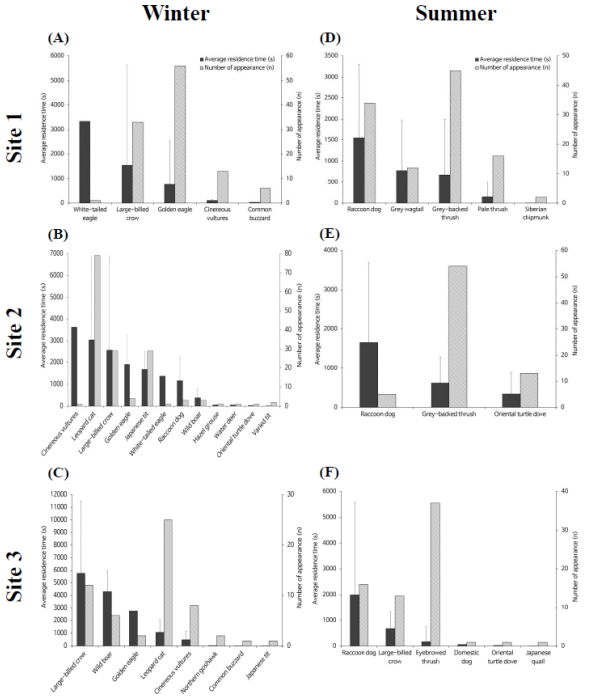

Fig. 4. Average residence time (s) of wildlife appearing at carcasses at Sites 1, 2, and 3 in winter (A-C) and summer (D-F).

Fig. 5. Sequential photos of a leopard cat driving a raccoon away from the carcass at Site 2 in winter.

Fig. 6. Sequential photos of a subadult wild boar feeding on the bones of the skeletonized carcass at Site 3 in winter.

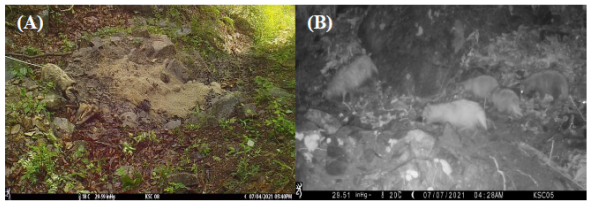

Fig. 7. A raccoon dragging and moving a skull at Site 1 (A) and a raccoon family (six individuals) feeding on a carcass at Site 1 (B) in summer.

Summer visitors on wild boar carcasses

We identified the wild animals visiting the study sites during a 16-day summer period from June 29 to July 14, 2021 (Table 3). An unidentified rodent (one visit), two mammalian species (raccoon and Siberian chipmunk), and three bird species (grey-backed thrush, pale thrush, and grey wagtail) visited Site 1. One mammalian species (raccoon) and two bird species (grey-backed thrush and oriental turtle dove) visited Site 2; grey-backed thrushes (54 visits) were frequently photographed. Six species, including two mammalian and four bird species, visited Site 3, where raccoons (16 visits) and eyebrowed thrushes (37 visits) were frequently visitors. At all three sites, raccoons (21.9%), grey-backed thrushes (39.4%), and eyebrowed thrushes (14.7%) were the most frequently visiting species in summer (Table 3). The wild boars and leopard cats observed in winter were not observed in summer. Raccoons appeared at all sites.

The first species to visit Sites 1 and 2 were raccoons, and the carcass detection time ranged from four days at Site 1 to five days at Site 2 after the placement of the carcass. The first species that visited Site 3 was large-billed crows (Fig. 3D-F).

The species with the longest residence time at the carcass site in summer was raccoons at all sites of Site 1 (1,549 s=25.82 min), Site 2 (1,657 s=27.62 min), and Site 3 (1,994 s=33.23 min) (Fig. 4D-F). A raccoon family was photographed dragging the skull of the carcass and eating it with cubs (Fig. 7).

Implications for management of ASFV

As revealed in this and previous studies (Probst et al. 2019), species visiting carcasses and their residence time at a carcass seem to be affected by the season and age of the carcass. In winter, fresh carcasses slowly become skeletonized and dried skin leather gradually degrades. Therefore, wild animals are more likely to contact ASFV-infected carcasses. In this study, wild boars and leopard cats were carcass visitors during winter. If traces of these species, such as footprints and excrement, are found around ASFV-infected carcasses, the home range of these species should be considered when predicting the range of ASFV infection. In addition, from the photos of wild boar subadults eating the bones of skeletonized carcasses in winter, wild boars seem to be more likely to be directly infected through ASFV-infected carcasses in winter when food is scarce.

Birds that may contribute to the spread of ASFV are winter migratory accipitrid birds and well-known carcass scavengers such as golden eagles and cinereous vultures. These birds have faster carcass discovery times than mammals. In winter, most of the leaves from the tree crown would have fallen in temperate mixed forests, so birds seem to find carcasses more easily from the air than mammals on the ground.

In summer, even if carcass tissue and skin do not persist for long owing to rapid skeletonization, ASFV infection through the skeletonized bones can still occur. In our study, leopard cats and wild boars were not observed around the carcasses in the summer: only raccoons were observed. Raccoons live as a family, and their home area (MCP 100) in the natural ecosystem in summer ranges from 1.43 to 3.58 km^2 (Süld et al. 2017). In this study, raccoon families were photographed visiting and eating carcasses. Therefore, raccoons are likely important spreaders of ASFV in summer. In the case of birds, we did not observe any accipitrid birds, which are winter migratory birds; we observed crows and thrushes. In previous studies, passerine birds were frequently observed on or around carcasses (Probst et

al. 2019). These birds eat the insects and worms that appear around the carcass or carcass decomposition island (CDI).

The results of this study confirmed that wild boars, raccoons, and leopard cats frequently visited wild boar carcasses and remain at the sites for a long time. We also photographed wild rodents chewing or staying on carcasses, mainly during winter. Thus, in winter, when food is scarce, rodents are potential spreaders of the ASFV.

ASFV transmission via mammals, such as raccoons, leopard cats, rodents, or birds, such as accipitrids and thrushes, has little known to date; however, our findings showed that the scavenging activity of wild boars and the aforementioned animals may be a risk factor for ASFV propagation in South Korea.

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