Bear marking sites and scats create diverse species interactions: roles in chemical communication and resource use

（ヒグマのマーキングサイトと糞が生み出す多様な種間相互作用：化学コミュニケーションと資源利用における役割）

Hinako Katsushima

Department of Biosphere Sciences

Graduate School of Environmental Science

Hokkaido University

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I. General Introduction

1.1. Mammals as key players in ecosystems

Mammals play a crucial roles in most of the ecosystems in the world (Lacher et al., 2019). Some mammalian species exert significant nutritional or engineering impacts, and they are considered keystone species as their influence is not only disproportionately large relative to their population size but also functionally irreplaceable (e. g., Long & Racey, 2007). We are currently in the midst of the sixth mass extinction event, and large mammals, with their ability to modify the environment, are disappearing due to conflicts with human activities (Estes et al., 2011). The decline, regional extinction, or global extinction of mammal populations leads to the loss of their ecological roles, affecting a wide range of other species (Bogoni et al., 2020; Cox et al., 2022; Matsubayashi et al., 2015; Pimiento et al., 2020). Therefore, elucidating their ecological functions is of critical importance.

1.2. The role of marking sites in mammalian communication

Mammals establish specific marking sites, such as the rubbing trees used by cheetahs and bears (Clapham et al., 2014; Edwards et al., 2022) or the communal latrines utilized by otters, raccoons, and rhinoceroses (Dinerstein, 1991; Laurentino et al., 2023; Weinstein et al., 2018). These sites function as key mechanisms for intraspecific communication, enabling individuals to maintain social structures by exchanging information across temporal and spatial separations. This is achieved through the deposition of chemical signals, such as scents, and visual markers, including body rubs and claw marks. Consequently, marking sites play a crucial role in facilitating information

transmission between individuals or groups (Allen et al., 2016; Edwards et al., 2022). This chemical or olfactory communication is especially beneficial for solitary species with limited opportunities for direct encounters (Delbarco-trillo et al., 2011; Laurentino et al., 2023). Chemical communication via olfactory semiochemicals are central to mammalian social behavior and reproduction (Apps, 2013). The chemical signals deposited at marking sites primarily originate from secretions of odor glands, including two types of sweat glands and sebaceous glands, as well as from excretions such as scats and urine (Wyatt, 2003, 2010) . These chemical compounds, including fatty acids and steroids, convey essential information regarding territorial boundaries, sex, age class, mating status, and individual identify (Gorman & Mills, 1984; Gosling, 1982).

Marking site typically take the form of a conspicuous marking trees or a communal latrines, where the accumulation of scat enhances their visibility (Alberts, 1992; Buesching et al., 2016; Corona & Lévy, 2015; Edwards et al., 2022; L. E. King et al., 2017). Strategically placing marking sites along pathways frequently used by multiple individuals allows animals to maximize communication efficiency while minimizing energy expenditure (Gorman & Mills, 1984).

1.3. Expanding perspectives: beyond intraspecific communication

Since the early 2000s, the widespread adaptation of automated camera traps has transformed wildlife research by enabling continuous, low-level monitoring of animal behavior. These cameras have largely replaced direct observation methods, allowing for the systematic documentation of interactions at marking sites (Makuya & Schradin, 2024). Their increased accessibility and affordability have accelerated studies on interspecific

communication, revealing behavioral interactions that were previously overlooked (Burton et al., 2015).

With increasing observations, reports of different species utilizing multiple marking sites have become more common (Allen et al., 2017; Apfelbach et al., 2005; Apps et al., 2019; Cornhill & Kerley, 2020). Historically, researchers noted the presence of other species at marking sites, but these occurrences were often considered incidental to studies focused on intraspecific communication. These sites, often referred to as communication trees or billboards, were hypothesized to serve as platforms for both intraspecific and interspecific communication. Their strategic placement at trail junctions, where multiple species are likely to intersect, further supported this idea (Green & Mattson, 2003; McTavish & Gibeau, 2010; Tattoni, Rovero, et al., 2021) . However, past studies remained largely descriptive and fragmentary, and the underlying reasons for interspecies visitation were poorly understood (Apps et al., 2019)

One major reason for this oversight is the conceptual limitation in defining communication, as terms like "communication" and "pheromones" have traditionally been applied to intraspecific interactions, failing to account for interspecific exchanges (Karlson & Lüscher, 1959). Additionally, historical research has primarily focused on single-species communication, with early anthropological studies concentrating on behaviorally social species and rodent models rarely being examined in an interspecies context. The challenges associated with observing solitary mammals have further contributed to this gap, as research has largely centered on tracking individuals movements, overlooking the possibility that other species might visit and interact with intraspecific marking sites. Moreover, skepticism toward interspecies communication has historically led to the dismissal of the idea that such interactions could be ecologically

meaningful. Finally, the absence of appropriate monitoring tools previously restricted the ability to document interspecific behaviors. However, the widespread adoption of automatic camera traps has significantly advanced research on these interactions, providing continuous, non-invasive monitoring of animal behavior at specific locations rather than relying on individual tracking. Many of the species utilizing these sites are solitary, traditional tracking methods ineffective in capturing their social interactions. Camera traps have thus provided crucial insights into how animas use these sites to receive and transmit information (Apps et al., 2019). Their increased affordability and improved technological capabilities have further facilitated their integration into ecological studies (Burton et al., 2015; Nakashima et al., 2018). These technological advancements have revealed that interspecific interactions at marking sites are not incidental but may represent an important, yet previously overlooked, aspect of mammalian communication.

These factors highlight the need for a broader perspective when evaluating marking sites, considering them not only as intraspecific communication hubs but also as potential focal points for interspecies interactions.

1.4. The overlooked role of scats as temporal signals

While previous studies have primarily focused on fixed marking sites, such as communal latrines or repeatedly used rubbing trees, the ecological significance of more transient chemical signals has been largely overlooked. Scats, which are randomly deposited across the landscape, may function as temporary communication tools, yet their role in chemical signaling remains understudied. Unlike fixed sites, scats are not consistently revisited, making their chemical messages more ephemeral. Despite this, it is reasonable to assume

that they may contain similar olfactory information to that found at marking sites and can serve as indicators of an individual's presence, reproductive status, or dietary habits.

The lack of attention to scats as a communication medium is surprising given that many mammalian species, even those that do not form communal latrines, not only possess specialized anal glands but also release chemical signals through their secretions and symbiotic bacteria, which mediate the synthesis of volatile chemical compounds (Berüter et al., 1974; Janssenswillen et al., 2021; Leclaire et al., 2017; Manaf et al., 2003; McColl, 1967; Zhou et al., 2021). These signals, embedded in feces, have the potential to convey complex information about the individual that deposited them. Moreover, undigested seeds and plant material within scats provide additional ecological functions, acting as foraging resources for other species and contributing to seed dispersal (Maciunas et al., 2022; Rubalcava-Castillo et al., 2021; Shakeri et al., 2018). The transient nature of scats suggests that they may facilitate different types of interactions compared to fixed marking sites, potentially playing a more dynamic role in structuring mammalian communication networks.

Recognizing scats as an important but underappreciated form of chemical signaling could lead to a more comprehensive understanding of how mammalian communication extends beyond traditional marking behaviors. By considering both fixed and ephemeral marking strategies, we can better assess the broader ecological implications of chemical communication in wildlife communities.

1.5. Beyond the guild and communication purpose

Carnivores exhibit overlapping behavioral ranges, and their interspecific communication is sufficiently frequent to contribute significantly to ecosystem processes

and structure. This dynamic likely plays an essential role in conservation and management strategies. While conventional studies have primarily focused on mesocarnivores, carnivores are integral to the broader faunal network in natural environments. Beyond even-toed ungulates, rodents, and other mammals, birds also inhabit these ecosystems, forming a complex web of interspecific interactions. However, it remains unclear whether rodents and birds are merely incidental visitors or they approach large carnivores' marking sites with a specific purpose.

Visits to marking sites by different species are not solely for communication but are often influenced by additional ecological factors, including resources acquisition (L. E. King et al., 2017; Wikenros et al., 2017). Expanding the focus to taxa that utilize these sites primarily for foraging is essential. Scavengers such as foxes frequently visit large carnivores' marking sites or scats to exploit food remnants derived from predation or scavenging activity. Additionally, undigested seeds and plant matter within carnivore scats attract birds and mammals, facilitating seed dispersal and secondary foraging (Koike et al., 2012; Logiudice, 2001; K. Page et al., 2001; L. K. Page et al., 1999). Furthermore, trees used as marking sites may serve as foraging grounds for insectivorous birds, as damage caused by large mammals creates microhabitats that harbor insect populations (Zyśk-Gorczyńska et al., 2015).

1.6. The ecological significance of brown bear

Brown bears (*Ursus arctos*) are large, omnivorous carnivores widely distributed across the Northern Hemisphere. As non-territorial animals that primarily lead solitary spend lives (Zedrosser et al., 2023), they rely on marking sites for communication (Clapham et al., 2012; Noyce & Garshelis, 2014). These sites typically consist of trees,

surrounding ground and footprints leading them (Revilla et al., 2021; Sergiel et al., 2017). The selection of marking trees is species-specific and varies by region (Sato et al., 2014) . Many sites are positioned along forest roads, increasing their accessible to multiple individuals. Dominant males deposit glandular secretions and excretions through dorsal rubbing, foot rubbing, and urination (Clapham et al., 2014; Sato et al., 2014; Seryodkin, 2014). Notably, odor glands are present on the dorsum, footpads, and anal glands, with sex-based differences in glandular secretions. The dorsum glands in adult males enlarge during the breeding season, while subadult males and females rarely engage in scent marking behaviors (Clapham et al., 2014, 2023; Rosell et al., 2011; Sergiel et al., 2017; Tomiyasu et al., 2018).

Marking sites not only facilitate intraspecific communication but also attract a variety of other species. Studies in North America and Europe have documented carnivores, mesocarnivores, and ungulates interacting with brown bear sites, exhibiting behaviors such as urination, scratching, rubbing, and defection (McTavish & Gibeau, 2010; Tattoni, Rovero, et al., 2021). However, these studies lacked control comparisons, leaving it unclears whether these interactions are interactions are specific to brown bear marking sites. Additionally, interactions between rodents and birds and brown bears at these sites remain undocumented. Beyond communication, these locations may serve as ecological hubs that influence other species' behavior. Trees modified by bears may support insect populations, which in turn attract insectivorous bird (Zyśk-Gorczyńska et al., 2015). However, no studies have quantitatively examined the foraging behavior of birds. The ecological consequences of such cascading interactions, particularly in relation to avian foraging, remain largely unexplored.

Brown bears also scatter scats that are visually and chemically prominent, functioning as both information sources and ecological resources (García-Rodríguez et al., 2021). As widely recognized seed dispersers across continents, their scats content significant amounts of undigested plant material, including seeds and fruit remnants, reflecting their omnivorous diet (Coogan et al., 2018; Nawaz et al., 2019). These scats provide critical foraging resource, attracting granivorous and frugivorous species, while also facilitating plant regeneration through endozoochorous seed dispersal (Koike et al., 2012).

Brown bear scats not only contribute to nutrient cycling but may also function as transient chemical signals, conveying individual identify, dietary history, reproductive status, and overall health condition. These scattered scat serve as important foraging resources, attracting a range of scavengers, including mesocarnivores and birds, due to the presence of undigested plant material and seeds (Coogan et al., 2018; Koike et al., 2012; Nawaz et al., 2019). Unlike fixed marking sites, which are revisited and reinforced over time, scats represent ephemeral signals dispersed throughout the landscape. This randomness, coupled with the presence of anal gland secretions, suggests that scats could play a role in dynamic, short-term information exchange among conspecifics and other sympatric species. Investigating the ecological and communicative functions of bear scats could provide deeper insights into their contribution to interspecies interactions and forest ecosystem processes.

1.7. Research objectives

In this thesis, I investigated the potential interaction networks around brown bears, one of the largest terrestrial mammals in the Northern Hemisphere, by examining their

marking sites and scats as communication hubs and dietary resources. While marking sites are conventionally regarded as fixed structures facilitating intraspecific communication, I explored their roles in mediating interactions among multiple species, including carnivores, ungulates, rodents, and birds. Additionally, I examined the potential of scats as more ephemeral, randomly distributed hubs that may contribute to both information exchange and foraging dynamics.

This dissertation is structures as fellows: chapter 2 focuses on brown bear marking sites, investigating their dual function as sites for mammalian intraspecific and interspecific communication and as foraging sites for birds. Chapter 3 shifts the focus to brown bear scats, examining their roles as temporary information hubs and their ecological significance as food resources.

To achieve these objectives, I utilized automatic camera traps to systematically monitor species interactions at marking sites in Hokkaido forests. Given that traditional camera placements may overlook small mammals and birds, I implemented an alternative setup with vertically positioned cameras to improve detection of species engaging with these sites. By incorporating a wider range of taxa and employing improved observation techniques, this study aimed to provide a comprehensive understanding how brown bear marking sites function as key components of interspecific communication and ecosystem structure.

II. Local biodiversity hotspot created by brown bear: rubbing tree as a scent communication hub and feeding site

Abstract

Many mammals have marking sites, such as rubbing trees or communal latrines, for intraspecific communications. However, these sites may also be used by other animals, for example, to detect predators or to feed. To investigate the potential roles of bear marking sites in intra- and inter-specific communications and resource use, I evaluated the behaviors of other animals by camera trapping survey in Hokkaido Island, northern Japan. Over a 2-years study period, 25 infra-red cameras set at 17 bear rubbing trees and 8 control trees recorded over 4909 events from 15 mammal and 39 bird species. A network analysis demonstrated that many mammals visited and sniffed bear marking sites more frequently than control sites. In addition, meso-carnivores, such as red fox, raccoon dogs, and sables, overmarked (e.g. body rubbing, urination) at the marking sites, to which the same and different animal species responded. To the contrary, species association was much weaker at the control sites, mainly consisted of sika deer. These results suggested that bear marking sites were intensively utilized by many mammals as inter- and intra-specific odor communication. Birds also visited bear marking sites more frequently than control sites. They often fed on the ground and the trunk of the marking trees. Because bears remove the barks of marking trees and release urines on the grounds, they might modify local environments and attract some insects that may be preyed by birds. Collectively, I suggest that bear marking sites create local biodiversity hotspot not only for intra- and inter-specific communication hubs but also for foraging sites.

2.1. Introduction

Many mammalian species establish marking sites, such as the rubbing trees of cheetahs and bears (Clapham et al., 2014; Edwards et al., 2022) or the communal latrines of otters, raccoons, and rhinoceroses (Dinerstein, 1991; Laurentino et al., 2023; Weinstein et al., 2018). These sites are considered to facilitate intraspecific communication, conveying information about territory boundaries, dominance hierarchies, reproductive status, group affiliations, and individual identity (Marneweck et al., 2018). The chemical signals utilized in these interactions derive from glandular secretions and fecal deposits. Volatile and non-volatile chemical compounds emitted from these substrates can persist in the environment, enabling spatiotemporally distant conspecifics to receive and interpret these signals. This chemical or olfactory communication is particularly advantageous for solitary species with limited opportunities for direct encounters (Delbarco-trillo et al., 2011; Laurentino et al., 2023).

It is well-documented that marking sites are often visited by other animals (Apps et al., 2019). For instance, mesocarnivores investigate the marking sites of apex predators and may even engage in counter-marking behaviors. Such interactions have been proposed as a form of interspecific or intraspecific communication (Apps et al., 2019; Edwards et al., 2022; McTavish & Gibeau, 2010). However, given that marking sites are typically located in areas of high animal activity, it remains uncertain whether these visits are intentional responses to the chemical information by other species or simply coincidental, overlapping with their own marking sites. Additionally, much of the evidence to date has been fragmented, with relatively few studies explicitly focusing on the functional use of marking sites created by other species.

Recent advancements in infrared camera technology have facilitated quantitative and long-term investigations into the utilization of marking sites by various species (Apps et al., 2019). Edwards et al. (2022), for example, employed camera traps on cheetah marking trees and control trees to specifically examine interspecific and intraspecific interactions mediated through these sites. Their study provided significant insights into species interactions, including the detection of apex predators by prey and mesocarnivores, intra-guild communication among non-interacting species, and the acquisition of resource information by scavengers. However, statistically significant patterns were identified in only a few of the 29 mammalian species recorded, indicating that the prevalence and ecological significance of such interactions require further exploration.

Importantly, the use of marking sites by other species has primarily been reported within the same ecological guilds or among medium- to large-bodied mammals (Paquet, 1991). This bias is partially attributable to the detection limitations of infrared camera systems, which targets relatively large animals. The localized environmental changes in around marking sites caused by urine, scats, or physical damage to marking trees may attract some smaller organisms, such as invertebrates. For example, Zysk-Gorczynska et al. (2014) have hypothesized that bark removal by bears weakens trees, thereby attracting insects that oviposit in the damaged trunks, which in turn serve as prey for insectivorous birds like woodpeckers. Similarly, communal latrines may serve as feeding sites for mammals and birds that consume undigested foods, although the associated risk of pathogen exposure may deter some species (Weinstein et al., 2018). Overall, the marking sites of large mammals may serve diverse ecological functions, benefiting a variety of species across trophic levels.

Brown bears (*Ursus arctos*) represent an ideal model species for exploring the ecological roles of marking sites in inter- and intraspecific chemical communication and resource utilization by other animal species. These large carnivores inhabit boreal forests widely across the Northern Hemisphere and establish conspicuous marking sites comprising focal trees and around the base of the trees (Clapham et al., 2014; Green & Mattson, 2003; Sato et al., 2014). These sites are typically located in highly visible and accessible areas, such as along forest roads, likely to optimize intraspecific communication (Green & Mattson, 2003; Sato et al., 2014). Brown bears engage in tree-rubbing behavior, depositing chemical signals from glandular secretions located on their back and Rumps (Tomiyasu et al., 2018), often coupled with bark removal that serves as a visual marker (Penteriani et al., 2021). Additional behaviors, such as foot-stamping and urination around the base of the trees, further contribute to chemical signaling (Sergiel et al., 2017).

These marking activities typically involve a preference for coniferous trees, irrespective of their condition (live or dead) (Clapham et al., 2014; Green & Mattson, 2003; Sato et al., 2014). Dominant males predominantly create these marks during the breeding season, suggesting their primary function is to assert dominance over subdominant males and to signal their presence to potential mates (Clapham et al., 2014; Penteriani et al., 2021). However, observations of marking behavior by females and subadult males outside the breeding season indicate additional roles beyond reproductive communication (Clapham et al., 2014; Revilla et al., 2021; Sato et al., 2014). Multiple individuals leave (i.e., marking) and/or receiving (i.e., sniffing) information from the same trees, often lasting more than 10 years (Sato et al., 2014).

The visitation of other mammalian species to brown bear marking sites has also been documented (McTavish & Gibeau, 2010; Tattoni, Rovero, et al., 2021). Although primarily qualitative, McTavish and Gibeau (2010) described diverse species utilizing these sites in Canada's Mountain National Parks. For example, mountain goats and wolverines engaged in back-rubbing behaviors, while carnivores such as cougars and lynxes scratched the ground or defecated at these sites. Tattoni et al. (2021) quantified the frequency of visits and suggested that mesocarnivores used brown bear marking sites for interspecific communication, though their study lacked a comparison with control sites. In addition, Zyśk-Gorczyńska et al. (2015) hypothesized that bear marking sites could serve as foraging grounds for woodpeckers, as bark removal might attract insects that oviposit eggs in tree trunks. These observations suggest that brown bear marking sites may fulfill diverse ecological functions, catering to various species for distinct purposes.

In this study, I investigated the use of brown bear marking trees by other animal species in Hokkaido, Japan. To overcome the limitations of traditional infrared camera systems, I developed a localized camera trap system designed to detect small mammals and birds. Over a two-year period, I deployed these traps at both marking and control trees and analyzing behavioral responses for the visiting species. Based on prior research (Edwards et al., 2022; Tattoni, Rovero, et al., 2021), I formulated the following hypotheses: (1) prey species and subordinate carnivores avoid marking sites or engage in sniffing behavior to assess predation risk; (2) some mesocarnivores counter-mark at brown bear sites, potentially as a form of intraspecific communication; and (3) certain bird species, such as woodpeckers, visit these sites for foraging opportunities.

2.2. Materials and methods

Study areas

The study took place on Teshio Experimental Forest of Hokkaido University (TEF), northernmost experimental forest in Japan, with an area of 225 km2 (44–45°N, 141–142°E). The vegetation observed in TEF can be classified as a Conifer-broadleaf mixed forest dominated by *Picea jezoensis*, *Abies sachaliensis*, *Quercus cripula*, *Tila japonica*, and *Betula plathphylla* (Ito et al., 2022). The south-eastern TEF is connected to the largest preserve in Japan, Daisetsuzan Nationl Park, through mountain forests (Takinami et al., 2021). The main industry in the surrounding area is dairy farming.

Brown bears are largest terrestrial mammal in Japan and top predator. However, their main diets are plants, seeds, fruits, and small insects (García-Rodríguez et al., 2021). They eat salmon whenever available, although dams and fisheries prevent salmon from migrate upstream of rivers (Fukushima et al., 2007). Brown bears in Hokkaido opportunistically prey sika deer *Cervus nippon* but mainly calves. No other mammal meats have been reported from the scats of brown bears. However, this diet may be highly affected by human activities, because the stable isotope analysis indicate that they had consumed much higher proportions of deer and salmon meats in hundreds or thousands of years ago (Matsubayashi et al., 2015). In the populations of Alaska, the same species of brown bear (also known as Grizzly bear) rely much more on salmon and other mammals, including ground squirrels (Barker et al., 2015; Levi et al., 2012). Because brown bears are largest terrestrial mammal and top predator in Japan, all sympatric mammals are potential prey of brown bears. Major sympatric mammals in TEF include the sika deer, the red fox *Vulpes vulpes*, the racoon dog *Nyctereutes viverrinus*, the sable *Martes zibellina*, the Eurasian red squirrel *Sciurus vulgaris*, the Siberian chipmunk

Tamias sibiricus, the Siberian flying squirrel *Pteromys Volans*. Nonnative racoon *Procyon lotor* and domestic cat *Felis silvestris* also observed. The gray wolf *Canis lupus* also inhabit Hokkaido but went extinct in the late 19th century. Various bird species are also recorded in TEF (Ohtsubo et al., 2023).

Marking and control site selection

I selected marking sites with active use by brown bears. Eighteen sites were selected that met the following characteristics: 1) bark peeling was present on the marking trees, 2) fur was attached, 3) bark had a reddish-brown discoloration with a distinct brown bear scent, 4) footprint depressions were clearly marked along the trail leading to the marking trees, and 5) the understory vegetation of the marking trees was reduced by brown bear trampling and urination. One site had one or two marking trees. Trees with abundant and various fresh and old marks were determined as intensively used marked trees. I combined marked trees in groups if the distance between the next tree was less than 5 maters (c.f. Seryodkin, 2014).

In order to create artificial marking sites, I first scanned forest roads throughout the study area at 10-20 km/h to characterize the marking sites in the study area. From May 2 to 7, 2023 (6 days) marking sites with living, vigorous trees marking trees along the trail were recorded. A total of 178 marking sites were recorded and that 60% of the tree species were *Abies sachalinensis*, 33% were red spruce, and the remaining few % were black spruce and other conifers. Marking trees showed footprints, bark stripping, and coat attachment. At the study site, bark stripping was observed at an average height of 176 cm and approximately 80 cm in length (Unpublished data).

An artificial control site similar to the marking site was created. *Abies sachalinensis*, the most common tree species in the study area, was selected as the control tree, with a breast height diameter (approximately 1.2 m from the ground) of 30-60 cm, and the condition was the lower side of the slope on the forest road, at a close distance from the forest road edge. Along the same trails as the marking trees, the distance between trees was kept to within approximately 1000 m to avoid differences in the frequency of use by animals in different sites. Candidate sites were carefully screened to avoid sites already in constant use by other mammals, and sites with any mammalian cover on the trees or scats observed on the ground were excluded.

Two groups of control sites were prepared: 1) no treatment on the trunks and 2) bark stripping on the trunks. Artificial bark strips were made using a cutter to create an oval shaped bark strip, 80 cm vertically in total, centered at a height of 176 cm from the ground, in order to apply bark strips under conditions similar to those left by bark strips on marked trees in the study area. All field study sites were cleared of rust in the understory vegetation to prevent camera malfunction, and the lower branches of some trees were removed. Note that brown bear marking trees are almost always straight and have few branches, and the marking sites found at this study site met similar conditions. No bait was used to avoid any attractive or repulsive effect. in this study, but one of the marking sites has experienced creosote application in the past year (2017) for a hair trap survey by another research team.

Camera trap monitoring

A total of 18 marking sites were selected from the entire study area. I also selected 8 control sites for each of the 4 sites (2 years of observation at the natural marking

sites and 1 year at the control sites). I monitored the brown bear marking sites for 4781 camera trap days from 25 May 2022 to 19 October 2022, 23 May 2023 to 21 November 2023, and two control sites for 1355 camera trap days from 23 May 2023 to 21 November 2023. Each marking sites was monitored with two cameras. The cameras were programmed to take 60 seconds of video length and 1 second interval of (although some camera models had a minimum interval unit of 5 seconds). These cameras were checked for sensor angle and trigger speed in advance to ensure that the differences between the models would not be a problem when introducing them to the current system: the animals stay for a long time, so slight differences in trigger speed are not a problem. Sensor angles, sensitivity, and distances are similar. With the exception of a few models, the base was waterproofed to the extent possible, and the outer frame, screw holes, and DC port holes were sealed with silicone.

To observe the behavior of animals, it is essential to observe from their perspective. The conventional method of installing a camera in front of the marking site, which has often been used to observe brown bear behavior, has the limitation that it is difficult to photograph birds and small mammals that visit the site. Therefore, to capture these visitors the camera was mounted vertically downward from the top of the tree, 3.5 m above the ground (**Fig. 1**). The front-facing camera cannot capture birds and small mammals, and often misses medium-sized mammals as well. At the marking site, in addition to a vertical camera, we took pictures from the front of the tree, and at the control site, we installed a camera only on the top of the tree. Cameras were equipped with rainproof covers made of miso cups for waterproofing.

Video analysis of mammals and birds behaviors

I used vertical camera video to analyze visitor species and behavior. The survey effort was quantified by the total number of camera-days, where each 24h continuous operation of an infrared camera in the field counts as one camera day. Data for sites with video capture rates lower than 25% due to camera malfunctions or changes in angle of view caused by brown bears were excluded; data for one marking site in 2022 were excluded. I included camera trap data for analysis when an animal was recorded approaching a tree and walking around tree rather than walking in the background. ground rodents were excluded from the analyses. An independent capture events was defined as any sequence for a given species taken more than 30 min after the previous sequence of that species for the same location (O'Brien et al., 2003). The duration between independent events was calculated by the number of minutes between the end of one video and the beginning of the next video. I recorded the behaviors of species during independent events and classified them into two categories (1) "receiving information", which included sniffing on the marking trees and their basis, and (2) "leaving information", which included scent marking in the form of urination, defection, pawing, tree scratching, debarking, facial rubbing and body rubbing, according to the methods suggested by Edwards et al. (2022). In this study, body rubbing was performed by brown bear, deer, fox, squirrel. Other behaviors such as interesting with the camera, grazing/feeding, observing the environment (vigilance), playing, jumping on the tree, grooming, resting or pass were used to count visiting events but not allocated to one of the two defined communication categories.

The relative independent capture (RIC) was also calculated according to the methods suggested by (Zahoor et al., 2021), as a species quantitative index to assess the

abundance of species within the study area. The RIC were calculated using these formulae:

$$\mathrm{RIC} = \frac{\mathrm{Ai}}{\mathrm{N}} \times 1000$$

where Ai represents the number of independent events of the i-th species and N is the total number of camera-days (Tang et al., 2019).

Bird behavior was divided into three categories: (1) foraging behavior, (2) resting (sunbathing, sand bathing, grooming, and sitting still (if the bird did not move from the site for more than 20 seconds, it was identified as a behavior different from temporal migration), and (3) others (temporal use, migration, searching, carrying nest materials, etc.). The three types of behavior were classified as follows. Foraging behavior included both cases where actual foraging scenes were filmed and cases where pecking behavior was observed. I also recorded whether the foraging location was on a tree or on the ground. I divided the tree tops into two cases, one is the case where the animals used the trunk of the tree, and the other is the case where they used the branches of the tree. However, vines wrapped around the tree were treated the same as branches, and trees close to the ground (rotting trees and stumps lying on their sides) were counted as ground. Trees other than marking trees that were in close proximity to a marking tree that fell within the camera's angle of view were also counted as arboreal. If both tree and ground were used, both were counted as 1. All events captured in the camera's angle of view were included in the analysis.

To identify significant behaviors, we referred to pre-existing ethograms defining the each behaviors in mammals (Clapham et al., 2014; Revilla et al., 2021; van Beeck Calkoen et al., 2021) and birds (Hashizume et al., 2024).

Statistical analysis

All analyses were conducted, and figures were generated in R (version 4.4.1; R Development Core Team 2024). GLMMs (generalized linear mixed models) were run by glmmTMB package (version 1.1.8). Networks analysis was performed using "igraph" (version 2.1.2; Csardi and Nepusz 2006). Statistical test results were considered significant if the p-value was ≤ 0.05.

Due to limited sample size and similar observed trends, data from the two control site categories (i.e., bark removal and non-mark removal) were pooled and compared with marking site data. Similarly, due to the lack of sample size for individual bird species, I also pooled data on taxonomy basis, such as woodpeckers, tits, thrushes, raptors, whenever applicable.

Frequencies of visits, receiving and leaving information at marking and control sites

To determine whether individual species exhibited a preference for or avoidance of brown bear marking sites, I constructed generalized linear mixed models (GLMMs) with a log link and negative binomial error distribution. The response variable was the number of visits, while the explanatory variable was the site category (marking site or control site). Site ID was included as a random effect, and camera trap days were incorporated as an offset term to account for effort.

To assess whether mammals more frequently receive information from marking sites compared to control sites, I constructed GLMMs with a logit link and binomial error distribution. The response variable was whether animals exhibited sniffing behavior (sniffed = 1, no response = 0), with site category (marking site or control site) as the explanatory variable. Site ID was again included as a random effect. Additionally, a

similar GLMM framework was employed to investigate whether mammals leave information at the sites (e.g., counter-marking or rubbing behavior, marked = 1, no response = 0).

For the behavioral response of birds, I investigated if birds use bear marking sites for foraging. A GLMM with a logit link and binomial error distribution was constructed. The response variable was whether birds exhibited foraging behavior (foraging = 1, no foraging = 0), with site category (marking site or control site) as the explanatory variable. Site ID was again included as a random effect.

To visualize differences in animal responses between marking and control sites, relative frequencies of RIC, numbers of receiving and leaving information were calculated. These relative frequencies were determined by dividing the observed frequencies at marking sites by those at control sites. A value of 1 indicates equal frequencies, a value between 0 and 1 indicates higher frequencies at control sites, and a value greater than 1 indicates higher frequencies at marking sites.

Time dependency of mammal responses to marking

Because the chemical signals degrade over time, time dependency of animal responses to the last marking events was evaluated. In addition, not only bears but also other mammals engaged in marking behaviors (e.g. rubbing and urination) at marking and control sites. Consequently, the responses of each species to the marking activity of conspecifics and heterospecifics were evaluated. By assessing time dependency, intra-specific and inter-specific chemical communication patterns can be inferred (Tattoni, Bragalanti, et al., 2021).

To investigate which scent cues visitors respond to, the relationship between scent persistence time and visitor behavior was analyzed using GLMM. Prior to the analysis, data related to birds and rodents were excluded, as the focus was on "receiving information" and "leaving information" behaviors. The response variables were defined as "receiving information" and "leaving information." The explanatory variables included the elapsed time since brown bear marking (*deltat_bear*), the elapsed time since the last visit by the same species (*deltat_same sp.*), and the elapsed time since the last visit by other mesocarnivores (*deltat_other carnivora*). All explanatory variables were standardized prior to inclusion in the analysis. Marking site (tree) and study year were included as random effects. This approach was applied to each of the mammal species with enough sample sizes (i.e., $n > 25$) to evaluate the effects of the three explanatory variables—*deltat_bear*, *deltat_same sp.*, and *deltat_other carnivora*—on visitor behaviors. The same analyses were also conducted for control sites. Results for models with non-convergence or unstable estimates were excluded from the analysis.

Network analysis for species interactions

To evaluate potential species interactions, I constructed directed and weighted social networks based on the behaviors, i.e., receive information and leave information, separately, using R package "igraph" (version 2.1.2; Csardi and Nepusz 2006). Separate networks were also created for marking sites and control sites to analyze differences between the two conditions. All data were used for calculating general network metrics, such as node and edge counts. However, for identifying the top 5 heaviest weighted edges of marking sites, data with a sample size of 10 or less were excluded. This exclusion

applied only to the selection of the top 5 edges and did not affect the calculation of other network features.

I estimated the potential species interactions based on how often each mammal responded to the marking of conspecifics and heterospecifics. Since the chemical signals degraded over time, I initially calculated the time thresholds for the signals considered to be effective. The elapsed time from the previous marking to the next visitor exhibiting either receiving information or leaving information was calculated, and its distribution was visualized using a histogram. A mixture of normal distributions was fitted to the histogram using a maximum likelihood estimation approach to identify key peaks. Two peaks were identified, one with a width of approximately 10,000 minutes (~7 days; weight = 0.30) and another with a width of approximately 50,000 minutes (~35 days; weight = 0.34). Based on the results, the duration of scent persistence was conservatively defined as 10,000 minutes.

Social networks were constructed from 1844 independent events at marking sites and 816 independent events at control sites. The weights were calculated by summing the number of receive information events performed by each species across all sites within the presumed duration during which the chemical signals remained detectable (i.e. 10,000 minutes or 7 days) prior to the observation of sniffing or marking behavior by visitors. Subsequently, the weights for each species were normalized by dividing by the number of observed receiving and leaving information events. To further analyze the structural properties of these networks, global clustering coefficients were calculated for each network using the transitivity function in the R package "igraph". Degree-preserving randomized networks were generated for comparison to determine whether the observed clustering coefficients were significantly higher than expected by chance. For each

network, a degree-preserving random network was created using the sample_degseq function with the "configuration" method. This method ensures that the degree of each node in the randomized network matches that of the observed network. The observed and randomized clustering coefficients were then compared to evaluate the structural significance of the original network. Reproducibility was ensured by setting a random seed (set. seed (123)) prior to the randomization process.

2.3. Results

Using 17 brown bear marking sites and 8 control sites, I detected 4,790 independent events of 15 mammal species and 119 independent events of at least 39 bird species across all cameras (**Table 1, Table 2**).

I initially established two control sites; however, as there was no apparent difference in the observed trends between them, I treated them as a single control for analysis. Although one of the treatment plots involved bark stripping on tree trunks, I found no significant effect of bark stripping and thus did not consider it in the analysis. Therefore, I discuss the results based on a comparison between marking sites and the combined control sites.

Intraspecific communication of the brown bear

Throughout the study period, natural marking sites (n=17) were visited a total of 340 times by brown bears of various sex and age classes, including adult brown bears, subadults, and mothers and cubs, of which 54% left visual and olfactory signals such as bark stripping, back rubbing, foot rubbing, and urination (**Table 1**). There were also a

few brown bear visits to control sites (n=26), and one site had additional bark stripping and rubbing on artificial bark stripping (n=5).

Frequencies of visits, receiving and leaving information by other mammals

At least eight mammal species besides brown bears visited the marking and control sites: sika deer; four mesocarnivores: red foxes, raccoon dogs, raccoons, and sables; three arboreal rodents: squirrels, chipmunks, and flying squirrels. Bats, ground rodents, rabbits *Lepus timidus*, domestic cats *Felis catus*, American minks *Neogale vision*, and least weasels *Mustela nivalis* were also recorded but excluded from the counts because they were photographed infrequently. The number of relative independent events recorded at each sites varied greatly (**Fig. 2**).

Sika deer, potential prey of brown bear, exhibited the clearest response to bear marking sites. They visited marking site much less frequently compared to control sites (GLMM, $p < 0.05$). On the other hand, when visited, they sniffed bear marking trees more frequently (64%) than control trees (42%) (GLMM, $p < 0.001$). Sika deer often rubbed their faces and bodies on control trees (15%), but this behavior was extremely rare (1%) in bear marking trees (GLMM, $p < 0.001$). Interestingly, mostly adult males counter-marked on bear marking sites during deer's mating season.

The frequencies of visits were not significantly different between marking and control sites in most of other mammals analyzed (**Fig. 3**): only Eurasian squirrels visited bear marking sites more frequently than control sites (GLMM, $p < 0.001$). On the other hand, all mammals received information more frequently from marking sites compared to control sites, although statistical significance was detected only in fox (GLMM, $p < 0.001$) and raccoon (GLMM, $p < 0.01$), which is partly due to the lack of statistical power

because raccoon dog and chipmunk sniffing only in marking sites (i.e. no data in control sites, **Fig. 4**). Red fox, raccoon dog, and sable often exhibited counter marking, mostly urination and defection. Sable left the information in bear marking sites more frequently than control sites (GLMM, $p < 0.05$), whereas no significant difference was detected in red fox, raccoon dog and raccoon (**Fig. 5**). Some foxes (n = 13) rubbed their faces and chests on the marking trees of brown bear. Flying squirrel and chipmunk never showed counter marking or other behaviors considered as leaving information. Although the frequency was rare, some squirrels looked rubbing their bodies against the base of the marking trees (n = 6).

Frequencies of visits and foraging activity by birds

All the bird species or groups visited bear marking sites 2-8 times more frequently than control sites (**Fig. 6**). GLMM analysis showed that the visitation frequency was significantly higher at bear marking sites compared to control sites in the Eurasian jay *Garrulus glandarius* (**Table2**, $p < 0.01$) and the Thrushes (6 species) ($p = 0.0118$), whereas the p-value was 0.07 for the Ural owl *Strix uralensis*, probably due to the lack of sample size (27 events). Other birds showed no statistical difference, although the visitation frequency was always higher at marking sites.

Most bird species or groups foraged exclusively at bear marking sites, i.e. no foraging events at control sites (**Fig. 7**). For the species/groups that foraged both at marking and control sites, no significant difference was observed between the foraging probability between these sites.

The Eurasian jay *Garrulus glandarius* was the most frequently photographed bird (196 events) and visited bear marking sites significantly more than control sites

(**Table2**, GLMM, $p < 0.01$). They foraged nearly 50% at the marking sites, primarily on the grounds, whereas it was 25% at the control sites, although the difference was not statistically significant (**Fig. 7**). The Ural owl *Strix uralensis* (27 events) also visited bear marking sites more frequently than control sites (**Fig. 6**, GLMM, $p = 0.07$). In addition, foraging was observed only at bear marking sites, although the difference was not statistically significant, probably due to the lack of sample size (**Fig. 7**, GLMM, $p = 1$). For woodpeckers (5 species, 74 events), there were no significant differences in visiting and foraging frequencies between marking and control sites. They foraged both on the grounds and tree trunks. Thrushes (6 species, 141 events) visited bear marking sites more frequently than control sites, whereas foraging frequency was not different between the sites (**Fig. 7**, GLMM, $p = 0.0118$). They foraged on the grounds. For other bird groups, such as tits, doves, and grouses, no significant differences in visiting and foraging frequencies were observed between marking and control sites (**Fig. 7**, GLMM, $p = 0.899$).

Time dependency of mammal responses to marking

At marking sites, GLMM analysis showed that bears exhibited a significant time-dependent receiving and leaving information to the marking of mesocarnivores, including red foxes, raccoon dogs, sables, and raccoons (**Table 4**, **Table 5**, **Fig. 8**, **9**, GLMM, $p < 0.001$). No other significant time-dependency were observed; however, several GLMMs exhibited p-values between 0.05 and 0.1, indicating potential trends. The logistic regression curves of these models showed smaller vertical ranges on the Y-axis compared to the significant regression curve for bears yet still demonstrated notable slopes. This suggests that the lack of statistical significance may have been due to insufficient sample size, resulting in reduced statistical power. Two mesocarnivores showed trends in

response to bear marking. Raccoon dogs exhibited a tendency to sniff more frequently when bear marking was new (GLMM, $p = 0.06$), and raccoons showed a similar trend (GLMM, $p = 0.09$). Sika deer were found to avoid leaving information at marking sites when bear was recently marked (GLMM, $p = 0.05$). Furthermore, foxes were observed to sniff the marking of other mesocarnivores, such as raccoon dogs and sables (GLMM, $p = 0.05$), indicating a diverse response to heterospecific scents.

At control sites, sika deer were the only species that showed significant communication through scent-marking and sniffing behaviors. Sika deer exhibited significant sniffing and marking behaviors shortly after the marking of conspecifics (**Table 5**, **Fig. 10**, **11**, GLMM, both $p < 0.05$).

Network analysis for potential species interactions

Four interaction networks, receiving and leaving information networks for both marking and control sites, were constructed (**Table 6**, **Fig. 12**). Networks for marking sites exhibited much larger network sizes and higher edge counts compared to networks for control sites. They also showed greater interspecific interaction weights. In the receiving information network at marking site, the highest degree centrality was observed in bears (Degree = 16), while red foxes exhibited the highest betweenness centrality (Betweenness = 26). For the leaving information network at marking site, both degree and betweenness centralities were highest in bears (Degree = 13, Betweenness = 14). At the control sites, sika deer dominated both degree and betweenness centralities in the receiving information network (Degree = 5, Betweenness = 1). In the leaving information network, sika deer also exhibited the highest degree centrality (Degree = 3), while no significant differences were observed for betweenness centrality across nodes. Interestingly, in the marking site

networks, interactions among mesocarnivores formed a dense structure, whereas in the control site networks, deer mainly engaged in intraspecific interactions, leading to sparser networks overall. To evaluate the significance of these network structures, degree-preserving randomized networks were generated, and the observed clustering coefficients were compared to those of the randomized networks. The global clustering coefficients for the receiving information network at marking sites (Observed = 0.723, Randomized = 0.667) and the leaving information network at marking sites (Observed = 0.698, Randomized = 0.444) were significantly higher than those of their corresponding randomized networks. This indicates that the marking site networks exhibit non-random, densely clustered structures. In contrast, at control sites, the global clustering coefficients for both the receiving information (Observed = 0.000, Randomized = 0.000) and leaving information networks (Observed = NaN, Randomized = 0.000) showed no significant deviation from randomized expectations, reflecting their sparse and fragmented structure.

These findings suggest that the dense clustering observed in marking site networks may facilitate interspecific interactions and efficient information exchange, while the sparse clustering in control site networks limits such interactions, leading to primarily intraspecific communication.

2.4. Discussion

Our newly developed camera trap system revealed that at least 15 mammalian and 39 avian species visited bear marking sites. Most mammal species displayed specific behavioral responses, particularly sniffing and counter-making, to bear marking sites. Additionally, many bird species were observed visiting marking sites more frequently than control sites, generally engaging in foraging behaviors. In addition, network analysis

showed complex species interactions both within and among mammals only in bear marking sites. These results suggest that a wide range of species, beyond those within similar ecological guilds or direct trophic interactions, utilize brown bear marking sites for diverse purposes. Thus, marking trees of brown bears serves local biodiversity hotspots in northern boreal forests. Here, I examine the responses of various species or groups in detail and propose potential hypotheses to explain why different species visit marking sites established by other taxa.

Prey species avoid the potential predators via chemical signals

Sika deer, only reported prey mammal of brown bear in Hokkaido, showed the strongest responses to marking sites. Consistent to the predictions, sika deer avoided the bear marking site with the visiting frequency being less than 50% compared to control sites. Because the encounter risk is higher at the potential predator's marking sites, avoiding marking sites is reasonable. When sika deer visited bear marking sites, they actively acquired information from the marking trees. This is also reasonable to assess the risks of encountering with potential predators. If prey species avoid risky areas, food resources remain intact in these areas. Therefore, when predators are temporarily absent from such areas, benefits entering the areas outperform the encounter risk. This explains why prey species visit the marking sites of predators. Sika deer frequently visited control sites and often leave their information. Since Sika deer have suborbital glands on their face, this group-living mammal may also communicate via chemical signals put on trees. Males, females, and calves all exhibited this behavior throughout the study periods. This form of intraspecific chemical communication is suggested in sika deer and often reported in other Cervus species (Rehorek et al., 2005). Interestingly, only male deer rubbed their faces

and bodies on bear marking trees during breeding seasons. Like the mud bathing with their urines, male deer put bears order on the body to exhibit their dominancy to potential mates and/or rivals.

Complex interactions of meso-carnivores around the bear marking sites

Red foxes, raccoon dogs, raccoons, and sables often visited bear marking sites at a similar or slightly higher frequency compared to control sites. This indicates that these meso-carnivores do not strongly interact with brown bears, consistent to the no evidence of bear predation on these animals. Most of them sniffed marking trees, as well as grounds of the trees, receiving some information from the chemical signals left at marking sites. Apart from detecting potential predators, they might get some information for available resources (Edwards et al., 2022). However, brown bears in Hokkaido do not frequently attack sika deer (K. Kobayashi et al., 2012) and there was no report on scavenging their leftovers by these meso-carnivores. Further research is needed about what information they utilized. Rather, these meso-carnivores may react to the information left by the same guide because red foxes, raccoon dogs and sable defecated or urinated around the grounds of the marking trees. Because they also create their own marking sites at the conspicuous site to facilitate intra-specific chemical communications (Kent & Tang-Martínez, 2014; McLean et al., 2021; Ruchkina et al., 2022), bear marking trees serves as such conspicuous sites both visually and chemically. In fact, sable counter-marked at the bear marking sites more frequently than the control sites, and the meso-carnivores, including sable themselves, often sniffed the points where they defecated or urinated. While there are few studies that investigated the interactions among these meso-carnivores (Gómez-Ortiz et al., 2015), it is reasonable for them to receive information from the chemical

signals left by the same guilds rather than brown bears. It remains unknown who's signals these meso-carnivores reacted and why, but it is clear that bear marking sites offers inter- and intra-specific communication hubs.

Potential interactions between bears and small mammals

Eurasian red squirrels visited bear marking sites more frequently than control sites and occasionally sniffed marking sites even though sniffing was rarely observed in control sites. Similarly, Siberian chipmunks and Eurasian flying squirrels exhibited exploratory behaviors exclusively at marking sites. This indicates that some unreported interactions exist between the bears and these arboreal rodents. Because they are mostly arboreal, predation risk should be low. Also, the sniffing frequency was not high. Therefore, high frequency of marking tree usage may be association or indirect effects. Brown bears in Hokkaido highly select *Abies sachalinensis* as a rubbing tree. Eurasian red squirrels eat corns of this conifers and also make nests on the trees. Brown bears should affect *Abies sachalinensis* by removing barks and change the soil chemistry by urines. This might increase the corn productions or modify the leaf densities, which may benefit to red squirrels. Eurasian flying squirrels also frequently use *Abies sachalinensis* for nesting and foraging the leaves (Suzuki et al., 2011). Some individuals showed receiving information on the area where barks were removed. Although the video resolutions did not allow the specific behavior, this seemed to lick the conifer sap or eat insects. However, unlike the cases in red squirrels, no significant differences were observed between marking and control sites. Therefore, the functions of bear marking sites is likely differ between the small rodents. Siberian chipmunk showed no specific responses to bear marking trees, except for the 3 events of escaping behaviors right after sniffing the bear marking points.

Intraspecific vs. interspecific interactions

The observed differences in network structures between marking sites and control sites highlight the impact of marking behavior on interspecific and intraspecific interactions. The higher node and edge counts in marking networks suggest that marking sites facilitate more frequent interactions among species. This is consistent with the hypothesis that marking sites act as hubs for communication and information exchange among mammals. Contrary to our initial prediction, interactions among mesocarnivores were more prominent in the marking site networks, suggesting that these species utilize marking sites not only for information gathering but also for interspecific interactions. This finding aligns with prior studies showing that carnivores often investigate markings left by other species. In control sites, the dominance of deer in both sniffing and marking networks indicates that these locations primarily function as arenas for intraspecific communication among deer, leading to overall sparser networks. The absence of significant betweenness centrality differences in the control site marking network suggests a lack of intermediaries facilitating interactions among species. These results emphasize the ecological significance of marking sites in promoting interspecific interactions, particularly among carnivores, while control sites primarily serve as intraspecific hubs. Future studies should investigate how environmental variables or seasonality influence these network patterns.

Birds visits to bear marking sites

Various groups of bird species visited bear marking sites more frequently than control sites. Frequency of foraging did not differ between marking and control sites, but the birds generally engaged in foraging in both sites. Therefore, foraging events were significantly higher at bear marking sites, suggesting that bear marking sites offer good

opportunity for bird foraging. Contrary to initial predictions, visitation and foraging frequency of woodpecker were not different between marking and control sites. Rather, significant differences were observed for the species that foraged on the grounds. Soil conditions should be altered by foot-stamping and urine of bears, as well as urine and scats of meso-carnivores. This may increase or change soil invertebrates and birds gather around the bear marking trees. Interestingly, Ural owl often preyed small rodents that might have also been attracted for soil invertebrates. On the other hand, no specific behaviors other than foraging, such as body rubbing, was not observed in bird species.

Implication of chemical camouflage by non-bear species

Although sample sizes are limited, there are some behaviors that should be noted in ecological perspectives. Red foxes rubbed their cheeks and chests, while opening mouth half, on the tree trunks where bear rubbed glandular secretions on their backs or hips (13 events). Eurasian squirrels also rubbed their berries on the place where bear rubbed glandular secretions on their or hips (6 events). The grey fox *Urocyon cinereoargenteus* has been also reported to exhibit cheek-rubbing in scent marking areas of puma (Allen et al., 2017). The authors hypothesized that putting the odors of apex predators may function as predator avoidance or dominance appeal to conspecifics. Such “chemical camouflage” has been also documented in chipmunks putting the odors of snakes to reduce predation risks (T. Kobayashi, 2000). It is particularly interesting why Eurasian red squirrels exhibited this behavior because this group of rodents do not usually form dominance hierarchy and perform intra-specific chemical communications.

Table 1. Number of independent events and the behaviors "leaving information" and "receiving information" recorded at 17 brown bear marking sites and 8 control sites in northern Hokkaido.

Species	2022 Marking sites 1932 camera trap days (N=17)			2023 Marking sites 2489 camera trap days (N=16)			Control sites 1 680 camera trap days (N=4)			Control sites 2 675 camera trap days (N=4)		
	Independent events	Behavior		Independent events	Behavior		Independent events	Behavior		Independent events	Behavior	
		Receive info.	Leave info.		Receive info.	Leave info.		Receive info.	Leave info.		Receive info.	Leave info.
Brown bear (*Ursus arctos*)	157	147	91	183	180	94	12	12	0	13	12	5
Shika deer (*Cervus nippon*)	223	151	8	371	236	5	183	89	43	161	47	10
Red fox (*Vulpes vulpes*)	92	46	10	445	159	90	85	1	1	47	2	3
Raccoon dog (*Nyctereutes viverrinus*)	23	4	3	75	14	24	3	0	0	11	0	0
Raccoon (*Procyon lotor*)	34	18	1	34	8	0	6	1	0	12	0	0
Sable (*Martes zibellina*)	45	4	1	162	20	31	19	0	0	17	1	0
Eurasian red squirrel (*Sciurus vulgaris*)	848	37	5	839	20	1	62	0	0	121	2	0
Siberian Chipmunk (*Tamias sibiricus*)	166	4	0	159	2	0	7	0	0	32	0	0
Siberian flying squirrel (*Pteromys volans*)	73	17	0	29	4	0	16	0	0	9	3	0

Table 2. Number of independent events and foraging behavior of birds at 17 bear marking sites and 8 control sites in northern Hokkaido.

Family	Species	Marking sites Camera (N=35)		Control sites 1 Camera (N=4)		Control sites 2 Camera (N=4)	
		Independent events	feeding	Independent events	feeding	Independent events	feeding
Phasianidae	*Tetrastes bonasia*	81	21	6	0	2	0
Cuculidae	*Cuculus optatus*			1	1		
	Cuculus spp.	2	1				
Columbidae	*Streptopelia orientalis*	59	43	3	2	1	1
Scolopacidae	*Scolopax rusticola*	32	6	2	0	2	0
Accipitridae	*Accipiter gentilis*			1	1		
Accipitridae	*Buteo japonicus*	4	1				
Strigidae	*Strix uralensis*	27	3	1	0		
Picidae	*Yungipicus kizuki*	1		1	0		
	Dendrocopos major	26	21	3	3	4	2
	Dendrocopos leucotos	1				1	1
	Dryocopus martius	30	15				
	Picus canus	16	15	1	1	5	4
Corvidae	*Garrulus glandarius*	196	90	13	3	5	2
	Corvus corone	6	0				
	Corvus macrorhynchos						
Paridae	*Periparus ater*	16	13				
	Poecile montanus	1					
	Parus minor	10	6				
	Poecile spp.	10	5	6	0		
Cettiidae	*Urosphena squameiceps*						
Phylloscopidae	*Phylloscopus coronatus*			1	0		
Cettiidae	*Horornis diphone*	1	0	1	0		
Regulidae	*Regulus regulus*	1	0				
Troglodytidae	*Troglodytes troglodytes*	1	0				
Sittidae	*Sitta europaea*	40	22	3	0		
Certhiidae	*Certhia familiaris*	3	1	4	1	1	0
Turdidae	*Zoothera aurea*	9	3	3	1		
	Geokichla sibirica	22	9				
	Turdus cardis	2	1				
	Turdus pallidus	1	1				
	Turdus chrysolaus	10	5				
	Turdus eunomus	26	8	2	1	1	0
	Turdidae spp.	71	24			2	1
Muscicapidae	*Muscicapidae* spp.	1					
	Muscicapa dauurica	1	0				
	Calliope calliope	2	0				
	Calliope sp.	1	1				
	Larvivora cyane	8	4	1	0		
	Ficedula narcissina	2	0	1	0		
	Tarsiger cyanurus	10	0	2	0	1	0
Fringillidae	*Coccothraustes coccothraustes*	1	0				
Emberizidae	*Emberiza personata*	2	1	3	0		
	Emberiza variabilis	1	0				
	Emberizidae spp.	2	0				
Unknown	Unknown	3	0	4	0	3	1

Table 3. Time-dependency of receiving information for each species to the last marking of other species (deltat_b; bear, deltat_oc; other carnivores, deltat_s; sika deer) at 17 bear marking sites. Results are from a generalized linear mixed model (GLMM); significant terms indicated in bold. In the behavior column, 'Invest' represents receiving information.

species	predictor	behabior	term	randam effect	estimate	std.error	statistic	p-value
bear	deltat_b	*Invest*	(Intercept)		4.048	0.983	4.118	0.000
bear	deltat_b	*Invest*	deltat_b		-0.161	0.279	-0.578	0.564
bear	deltat_b	*Invest*	sd__(Intercept)	site	0.920			
bear	deltat_b	*Invest*	sd__(Intercept)	year	0.982			
bear	deltat_oc	*Invest*	(Intercept)		4.183	1.150	3.637	0.000
bear	deltat_oc	*Invest*	deltat_oc		1.347	1.155	1.167	0.243
bear	deltat_oc	*Invest*	sd__(Intercept)	site	1.443			
bear	deltat_oc	*Invest*	sd__(Intercept)	year	0.403			
deer	deltat_b	*Invest*	(Intercept)		0.737	0.184	4.006	0.000
deer	deltat_b	*Invest*	deltat_b		0.003	0.107	0.033	0.974
deer	deltat_b	*Invest*	sd__(Intercept)	site	0.534			
deer	deltat_b	*Invest*	sd__(Intercept)	year	0.000			
deer	deltat_s	*Invest*	(Intercept)		1.065	0.295	3.616	0.000
deer	deltat_s	*Invest*	deltat_s		-0.232	0.214	-1.082	0.279
deer	deltat_s	*Invest*	sd__(Intercept)	site	0.118			
deer	deltat_s	*Invest*	sd__(Intercept)	year	0.000			
deer	deltat_oc	*Invest*	(Intercept)		0.530	0.145	3.661	0.000
deer	deltat_oc	*Invest*	deltat_oc		-0.216	0.136	-1.592	0.111
deer	deltat_oc	*Invest*	sd__(Intercept)	site	0.218			
deer	deltat_oc	*Invest*	sd__(Intercept)	year	0.000			
fox	deltat_b	*Invest*	(Intercept)		-0.698	0.328	-2.130	0.033
fox	deltat_b	*Invest*	deltat_b		-0.098	0.148	-0.665	0.506
fox	deltat_b	*Invest*	sd__(Intercept)	site	0.901			
fox	deltat_b	*Invest*	sd__(Intercept)	year	0.063			
fox	deltat_s	*Invest*	(Intercept)		0.290	0.342	0.847	0.397
fox	deltat_s	*Invest*	deltat_s		-0.376	0.316	-1.189	0.234
fox	deltat_s	*Invest*	sd__(Intercept)	site	0.715			
fox	deltat_s	*Invest*	sd__(Intercept)	year	0.000			
fox	deltat_oc	*Invest*	(Intercept)		-0.625	0.412	-1.515	0.130
fox	deltat_oc	*Invest*	deltat_oc		-0.383	0.198	-1.937	0.053
fox	deltat_oc	*Invest*	sd__(Intercept)	site	1.020			
fox	deltat_oc	*Invest*	sd__(Intercept)	year	0.000			
raccoondog	deltat_b	*Invest*	(Intercept)		-1.498	0.293	-5.111	0.000
raccoondog	deltat_b	*Invest*	deltat_b		-0.863	0.467	-1.850	0.064
raccoondog	deltat_b	*Invest*	sd__(Intercept)	site	0.000			
raccoondog	deltat_b	*Invest*	sd__(Intercept)	year	0.000			
raccoondog	deltat_s	*Invest*	(Intercept)		-1.611	1.086	-1.483	0.138
raccoondog	deltat_s	*Invest*	deltat_s		-2.631	2.167	-1.214	0.225
raccoondog	deltat_s	*Invest*	sd__(Intercept)	site	0.000			
raccoondog	deltat_s	*Invest*	sd__(Intercept)	year	1.020			
raccoondog	deltat_oc	*Invest*	(Intercept)		-1.345	0.383	-3.510	0.000
raccoondog	deltat_oc	*Invest*	deltat_oc		-0.572	0.529	-1.082	0.279
raccoondog	deltat_oc	*Invest*	sd__(Intercept)	site	0.000			
raccoondog	deltat_oc	*Invest*	sd__(Intercept)	year	0.000			
raccoon	deltat_b	*Invest*	(Intercept)		-0.359	0.781	-0.460	0.645
raccoon	deltat_b	*Invest*	deltat_b		-0.516	0.313	-1.646	0.100
raccoon	deltat_b	*Invest*	sd__(Intercept)	site	0.442			
raccoon	deltat_b	*Invest*	sd__(Intercept)	year	0.986			
raccoon	deltat_oc	*Invest*	(Intercept)		-0.788	0.821	-0.959	0.337
raccoon	deltat_oc	*Invest*	deltat_oc		-0.328	0.652	-0.503	0.615
raccoon	deltat_oc	*Invest*	sd__(Intercept)	site	0.000			
raccoon	deltat_oc	*Invest*	sd__(Intercept)	year	0.944			
sable	deltat_b	*Invest*	(Intercept)		-1.955	0.225	-8.702	0.000
sable	deltat_b	*Invest*	deltat_b		-0.275	0.244	-1.127	0.260
sable	deltat_b	*Invest*	sd__(Intercept)	site	0.000			
sable	deltat_b	*Invest*	sd__(Intercept)	year	0.000			
sable	deltat_s	*Invest*	(Intercept)		-2.025	0.296	-6.833	0.000
sable	deltat_s	*Invest*	deltat_s		-0.246	0.368	-0.669	0.503
sable	deltat_s	*Invest*	sd__(Intercept)	site	0.000			
sable	deltat_s	*Invest*	sd__(Intercept)	year	0.000			
sable	deltat_oc	*Invest*	(Intercept)		-2.060	0.292	-7.055	0.000
sable	deltat_oc	*Invest*	deltat_oc		-0.004	0.249	-0.015	0.988
sable	deltat_oc	*Invest*	sd__(Intercept)	site	0.000			
sable	deltat_oc	*Invest*	sd__(Intercept)	year	0.000			

Table 4. Time-dependency of leaving information for each species to the last marking of other species (deltat_b; bear, deltat_oc; other carnivores, deltat_s; sika deer) at 17 bear marking sites. Results are from a generalized linear mixed model (GLMM); significant terms indicated in bold. In the behavior column, 'Mark' represents leaving information.

species	predictor	behabior	term	randam effect	estimate	std.error	statistic	p-value
bear	deltat_b	*Mark*	(Intercept)		0.233	0.223	1.044	0.296
bear	deltat_b	*Mark*	deltat_b		-0.119	0.115	-1.031	0.303
bear	deltat_b	*Mark*	sd__(Intercept)	site	0.672			
bear	deltat_b	*Mark*	sd__(Intercept)	year	0.000			
bear	deltat_oc	*Mark*	(Intercept)		-0.019	0.510	-0.037	0.971
bear	deltat_oc	*Mark*	deltat_oc		-0.753	0.222	-3.399	**0.001***
bear	deltat_oc	*Mark*	sd__(Intercept)	site	1.505			
bear	deltat_oc	*Mark*	sd__(Intercept)	year	0.000			
deer	deltat_b	*Mark*	(Intercept)		-4.113	0.550	-7.478	0.000
deer	deltat_b	*Mark*	deltat_b		0.521	0.267	1.951	0.051
deer	deltat_b	*Mark*	sd__(Intercept)	site	1.140			
deer	deltat_b	*Mark*	sd__(Intercept)	year	0.000			
deer	deltat_s	*Mark*	(Intercept)		-2.801	0.971	-2.885	0.004
deer	deltat_s	*Mark*	deltat_s		-0.544	0.768	-0.708	0.479
deer	deltat_s	*Mark*	sd__(Intercept)	site	0.787			
deer	deltat_s	*Mark*	sd__(Intercept)	year	0.842			
deer	deltat_oc	*Mark*	(Intercept)		-4.581	0.761	-6.018	0.000
deer	deltat_oc	*Mark*	deltat_oc		-0.110	0.783	-0.141	0.888
deer	deltat_oc	*Mark*	sd__(Intercept)	site	0.000			
deer	deltat_oc	*Mark*	sd__(Intercept)	year	0.618			
fox	deltat_b	*Mark*	(Intercept)		-1.985	1.077	-1.843	0.065
fox	deltat_b	*Mark*	deltat_b		0.098	0.196	0.503	0.615
fox	deltat_b	*Mark*	sd__(Intercept)	site	2.257			
fox	deltat_b	*Mark*	sd__(Intercept)	year	1.086			
fox	deltat_s	*Mark*	(Intercept)		-0.344	0.450	-0.764	0.445
fox	deltat_s	*Mark*	deltat_s		-0.382	0.363	-1.054	0.292
fox	deltat_s	*Mark*	sd__(Intercept)	site	0.621			
fox	deltat_s	*Mark*	sd__(Intercept)	year	0.432			
fox	deltat_oc	*Mark*	(Intercept)		-1.902	1.150	-1.654	0.098
fox	deltat_oc	*Mark*	deltat_oc		-0.321	0.279	-1.147	0.251
fox	deltat_oc	*Mark*	sd__(Intercept)	site	2.189			
fox	deltat_oc	*Mark*	sd__(Intercept)	year	0.830			
raccoondog	deltat_b	*Mark*	(Intercept)		-1.593	0.675	-2.359	0.018
raccoondog	deltat_b	*Mark*	deltat_b		-0.677	0.455	-1.489	0.137
raccoondog	deltat_b	*Mark*	sd__(Intercept)	site	1.172			
raccoondog	deltat_b	*Mark*	sd__(Intercept)	year	0.000			
raccoondog	deltat_s	*Mark*	(Intercept)		-0.638	0.505	-1.265	0.206
raccoondog	deltat_s	*Mark*	deltat_s		-0.118	0.456	-0.258	0.796
raccoondog	deltat_s	*Mark*	sd__(Intercept)	site	0.816			
raccoondog	deltat_s	*Mark*	sd__(Intercept)	year	0.000			
raccoondog	deltat_oc	*Mark*	(Intercept)		-0.365	0.366	-0.997	0.319
raccoondog	deltat_oc	*Mark*	deltat_oc		0.041	0.376	0.110	0.912
raccoondog	deltat_oc	*Mark*	sd__(Intercept)	site	0.508			
raccoondog	deltat_oc	*Mark*	sd__(Intercept)	year	0.000			
raccoon	deltat_b	*Mark*	(Intercept)		-18.023			
raccoon	deltat_b	*Mark*	deltat_b		-5.375			
raccoon	deltat_b	*Mark*	sd__(Intercept)	site	55.057			
raccoon	deltat_b	*Mark*	sd__(Intercept)	year	0.000			
raccoon	deltat_oc	*Mark*	(Intercept)		-15.218	16.563	-0.919	0.358
raccoon	deltat_oc	*Mark*	deltat_oc		-1.565	22.400	-0.070	0.944
raccoon	deltat_oc	*Mark*	sd__(Intercept)	site	58.794			
raccoon	deltat_oc	*Mark*	sd__(Intercept)	year	0.002			
sable	deltat_b	*Mark*	(Intercept)		-2.295	0.804	-2.856	0.004
sable	deltat_b	*Mark*	deltat_b		-0.344	0.231	-1.486	0.137
sable	deltat_b	*Mark*	sd__(Intercept)	site	0.000			
sable	deltat_b	*Mark*	sd__(Intercept)	year	0.901			
sable	deltat_s	*Mark*	(Intercept)		-1.399	0.238	-5.872	0.000
sable	deltat_s	*Mark*	deltat_s		-0.164	0.266	-0.618	0.536
sable	deltat_s	*Mark*	sd__(Intercept)	site	0.000			
sable	deltat_s	*Mark*	sd__(Intercept)	year	0.000			
sable	deltat_oc	*Mark*	(Intercept)		-1.327	0.226	-5.876	0.000
sable	deltat_oc	*Mark*	deltat_oc		-0.282	0.226	-1.247	0.212
sable	deltat_oc	*Mark*	sd__(Intercept)	site	0.000			
sable	deltat_oc	*Mark*	sd__(Intercept)	year	0.000			

* Indicates a significant result of < 0.05

Table 5. Time-dependency of receiving information for each species to the last marking of other species (*deltat_b*; bear, *deltat_oc*; other carnivores, *deltat_s*; sika deer) at 8 control sites. Results are from a generalized linear mixed model (GLMM); significant terms indicated in bold. In the behavior column, 'Invest' represents receiving information, and 'Mark' represents leaving information.

species	predictor	behabior	term	randam effect	estimate	std.error	statistic	p.value
deer	deltat_b	*Invest*	(Intercept)		-0.531	0.229	-2.316	0.021
deer	deltat_b	*Invest*	deltat_b		-0.140	0.259	-0.543	0.587
deer	deltat_b	*Invest*	sd__(Intercept)	site	0.000			
deer	deltat_s	*Invest*	(Intercept)		-0.374	0.328	-1.142	0.254
deer	deltat_s	*Invest*	deltat_s		-0.427	0.166	-2.571	**0.010***
deer	deltat_s	*Invest*	sd__(Intercept)	site	0.758			
deer	deltat_oc	*Invest*	(Intercept)		-0.220	0.276	-0.800	0.424
deer	deltat_oc	*Invest*	deltat_oc		-0.222	0.272	-0.815	0.415
deer	deltat_oc	*Invest*	sd__(Intercept)	site	0.000			
fox	deltat_s	*Invest*	(Intercept)		-3.319	1.278	-2.597	0.009
fox	deltat_s	*Invest*	deltat_s		0.499	0.542	0.919	0.358
fox	deltat_s	*Invest*	sd__(Intercept)	site	0.000			
fox	deltat_d	*Invest*	(Intercept)		-5.098	2.708	-1.883	0.060
fox	deltat_d	*Invest*	deltat_d		0.406	1.016	0.400	0.689
fox	deltat_d	*Invest*	sd__(Intercept)	site	1.301			
sable	deltat_d	*Invest*	(Intercept)		-3.759	2.436	-1.543	0.123
sable	deltat_d	*Invest*	deltat_d		-0.552	1.585	-0.348	0.728
sable	deltat_d	*Invest*	sd__(Intercept)	site	1.108			
bear	deltat_oc	*Mark*	(Intercept)		-6.070	38.619	-0.157	0.875
bear	deltat_oc	*Mark*	deltat_oc		5.213	43.145	0.121	0.904
bear	deltat_oc	*Mark*	sd__(Intercept)	site	43.580			
deer	deltat_b	*Mark*	(Intercept)		-3.206	0.762	-4.206	0.000
deer	deltat_b	*Mark*	deltat_b		-1.086	0.815	-1.332	0.183
deer	deltat_b	*Mark*	sd__(Intercept)	site	0.439			
deer	deltat_s	*Mark*	(Intercept)		-1.707	0.301	-5.671	0.000
deer	deltat_s	*Mark*	deltat_s		-0.608	0.257	-2.370	**0.018***
deer	deltat_s	*Mark*	sd__(Intercept)	site	0.508			
deer	deltat_oc	*Mark*	(Intercept)		-1.795	0.431	-4.164	0.000
deer	deltat_oc	*Mark*	deltat_oc		-0.802	0.451	-1.778	0.075
deer	deltat_oc	*Mark*	sd__(Intercept)	site	0.000			
fox	deltat_s	*Mark*	(Intercept)		-3.319	1.278	-2.597	0.009
fox	deltat_s	*Mark*	deltat_s		0.499	0.542	0.919	0.358
fox	deltat_s	*Mark*	sd__(Intercept)	site	0.000			
fox	deltat_d	*Mark*	(Intercept)		-3.701	0.717	-5.159	0.000
fox	deltat_d	*Mark*	deltat_d		0.002	0.791	0.003	0.998
fox	deltat_d	*Mark*	sd__(Intercept)	site	0.000			

* Indicates a significant result of < 0.05

Table 6. Key metrics of four interaction networks, including network size, total edge count, intraspecific and interspecific weights, the node with the highest degree centrality (node name, centrality value, and edge percentage), the node with the highest betweenness centrality (node name and value), and the five strongest weighted edges (from, to, and weight).

Metric	Marking sites		Control sites	
	Receiving information	Leaving information	Receiving information	Leaving information
Network Size	9	7	3	3
Number of Edges	39	29	5	3
Intraspecific_Weight	2.89	4.34	0.64	1.01
Interspecific_Weight	5.96	4.90	0.49	0.02
Highest Degree Centrality				
Node	Bear	Bear	Sika deer	Sika deer
Centrality Value	16	13	5	3
Edge percentage (%)	41	44.8	100	100
Highest Betweeness Centrality				
Node	Red fox	Bear	Sika deer	NA
Centrality Value	26	14	1	NA
Top 5 heviest weighted Edges (From -> To, weight)				
1st	Red fox -> Red fox, 1.18	Red fox -> Red fox, 1.76	Sika deer -> Shika deer, 0.60	Sika deer -> Sika deer, 0.81
2nd	Raccoon dog -> Red fox, 1.16	Raccoon -> Bear, 1	Bear -> Shika deer, 0.46	Bear -> Bear, 0.2
3rd	Raccoon dog -> Raccoon dog, 0.72	Raccoon dog -> Red fox, 0.93	Bear -> Bear, 0.04	Sika deer -> Red fox, 0.02
4th	Sable -> Sable, 0.50	Raccoon dog -> Raccoon dog , 0.64	Shika deer -> Bear, 0.01	
5th	Bear -> Bear, 0.43	Bear -> Bear, 0.42	Shika deer -> Red fox, 0.01	

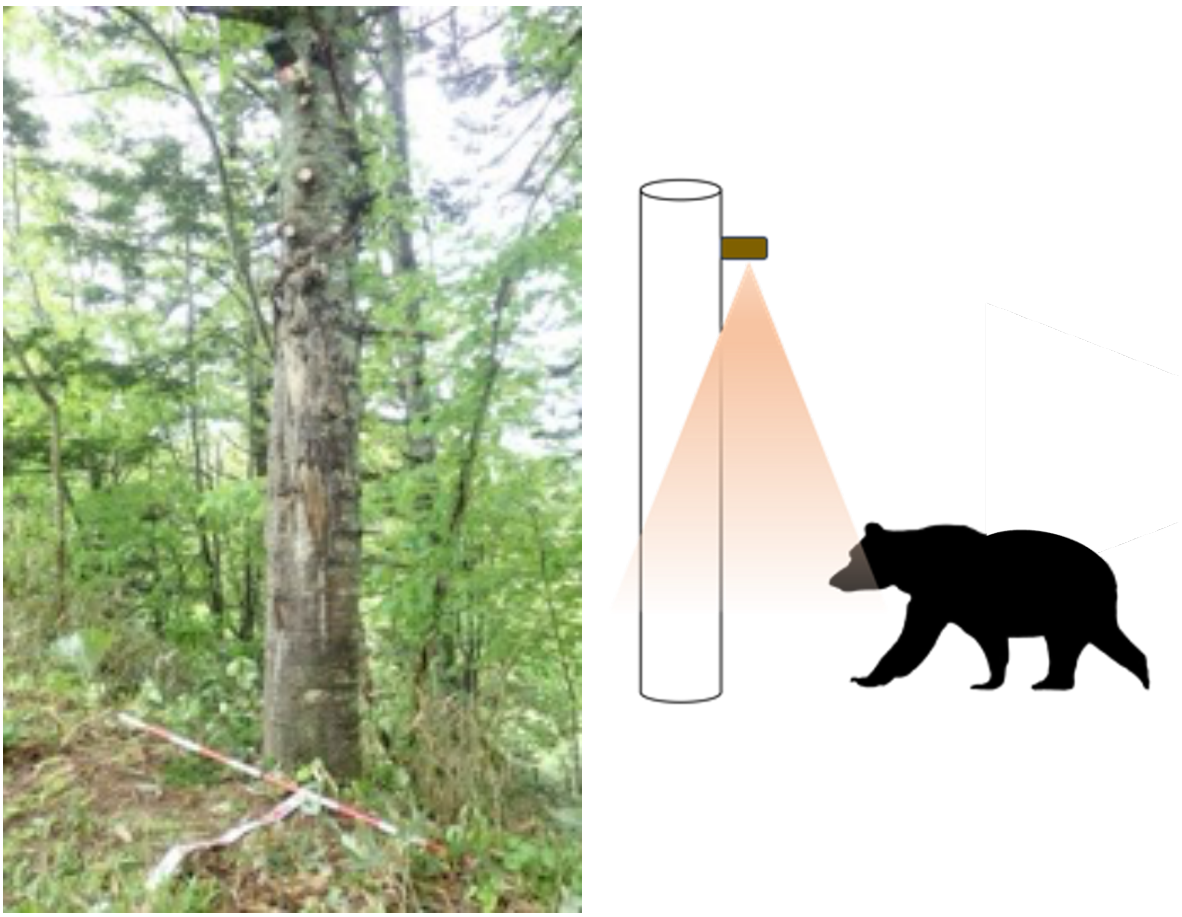


Figure 1. Camera trap system utilized in this study (left) and examples of animal images captured by the system (right). The camera was installed vertically downward at the top of a tree to monitor animal behavior effectively.

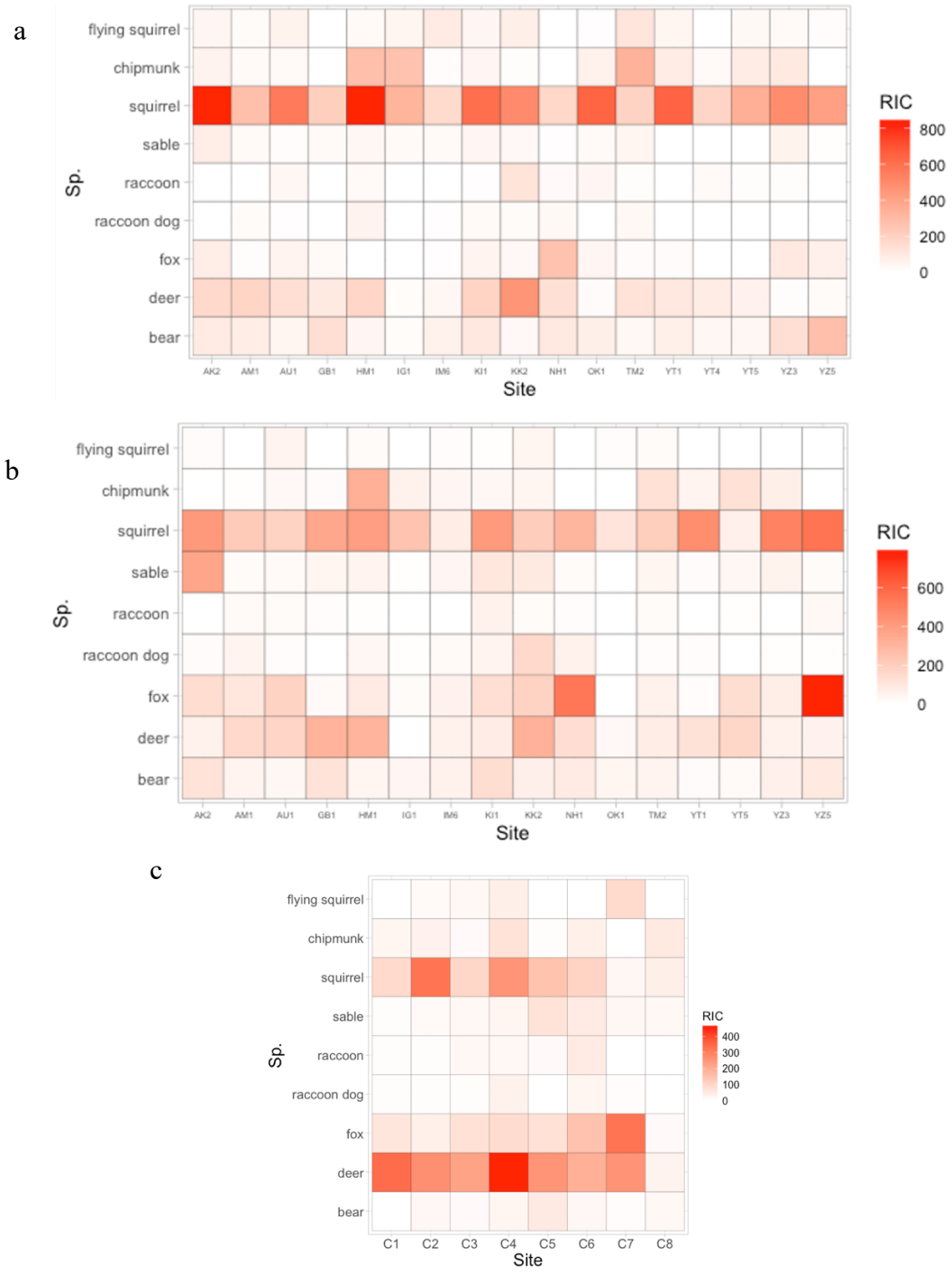


Figure 2. Mammal richness and number of relative independent events at 17 bear marking sites in 2022 **(a)** and 2023 **(b)** and 8 control sites **(c)** in northern Hokkaido. Each cell of the plot represents the total number of relative independent events per sites of a given species cumulated for all samplings.

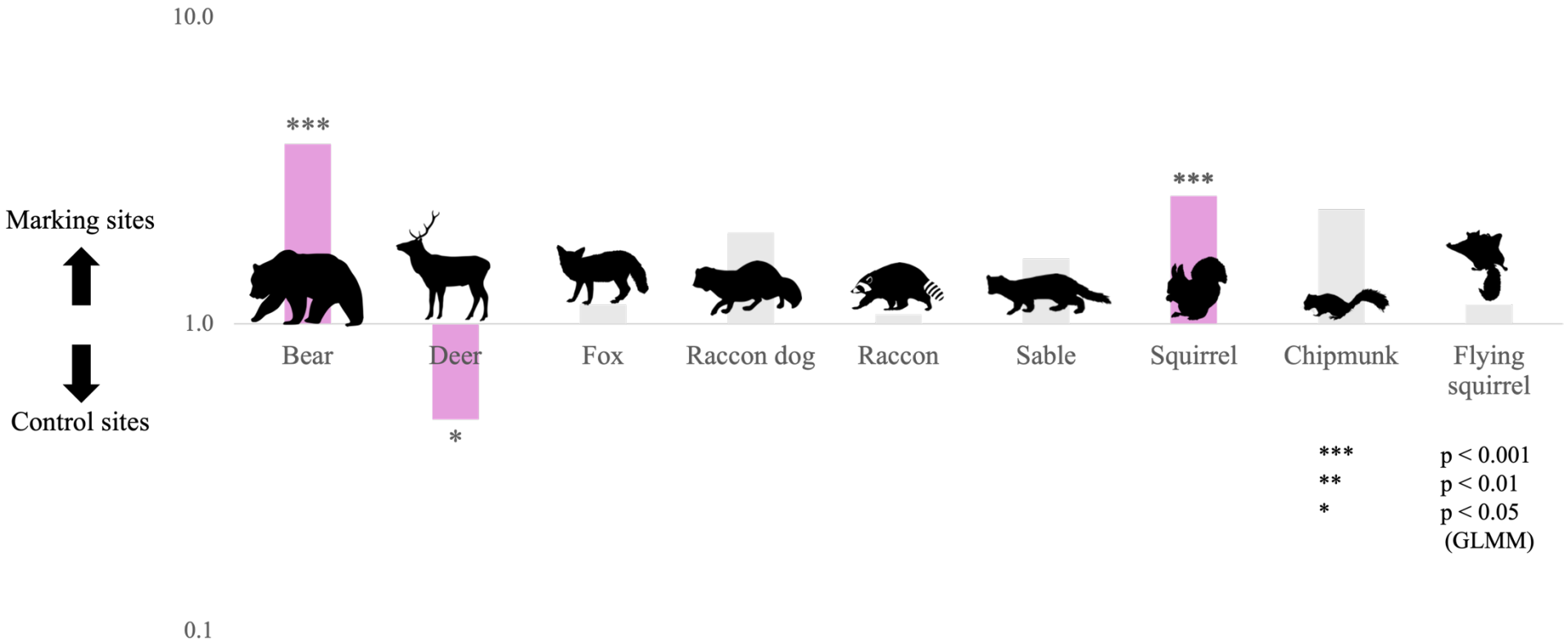


Figure 3. The relative visitation frequencies, calculated by RIC, of different species to 17 bear marking sites compared to 8 control sites. The y-axis is presented on a logarithmic scale, with a value of 1 serving as the baseline, indicating equal visitation frequencies between marking and control sites. Asterisks represent significant differences in visitation frequency between marking and control sites based on GLMMs (see details in the text).

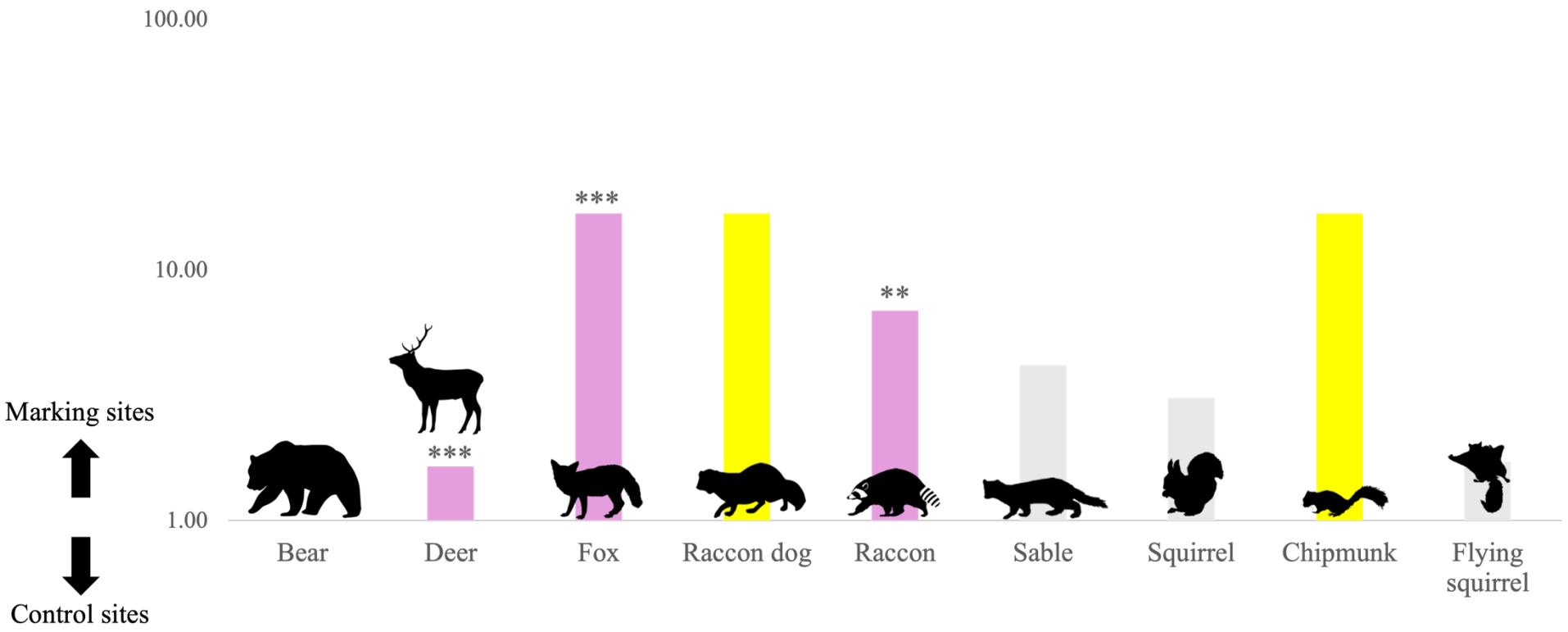


Figure 4. Relative receiving information behavior of species at 17 marking sites compared to 8 control sites. The y-axis is presented on a logarithmic scale. All mammal species received information from the bear marking sites. Asterisks represent significant differences in the probability of receiving information between marking and control sites based on GLMMs (see details in the text). Raccoon dogs, sables, and chipmunks did not exhibit scent sniffing at the control sites (shown at the same size as the foxes for visualization).

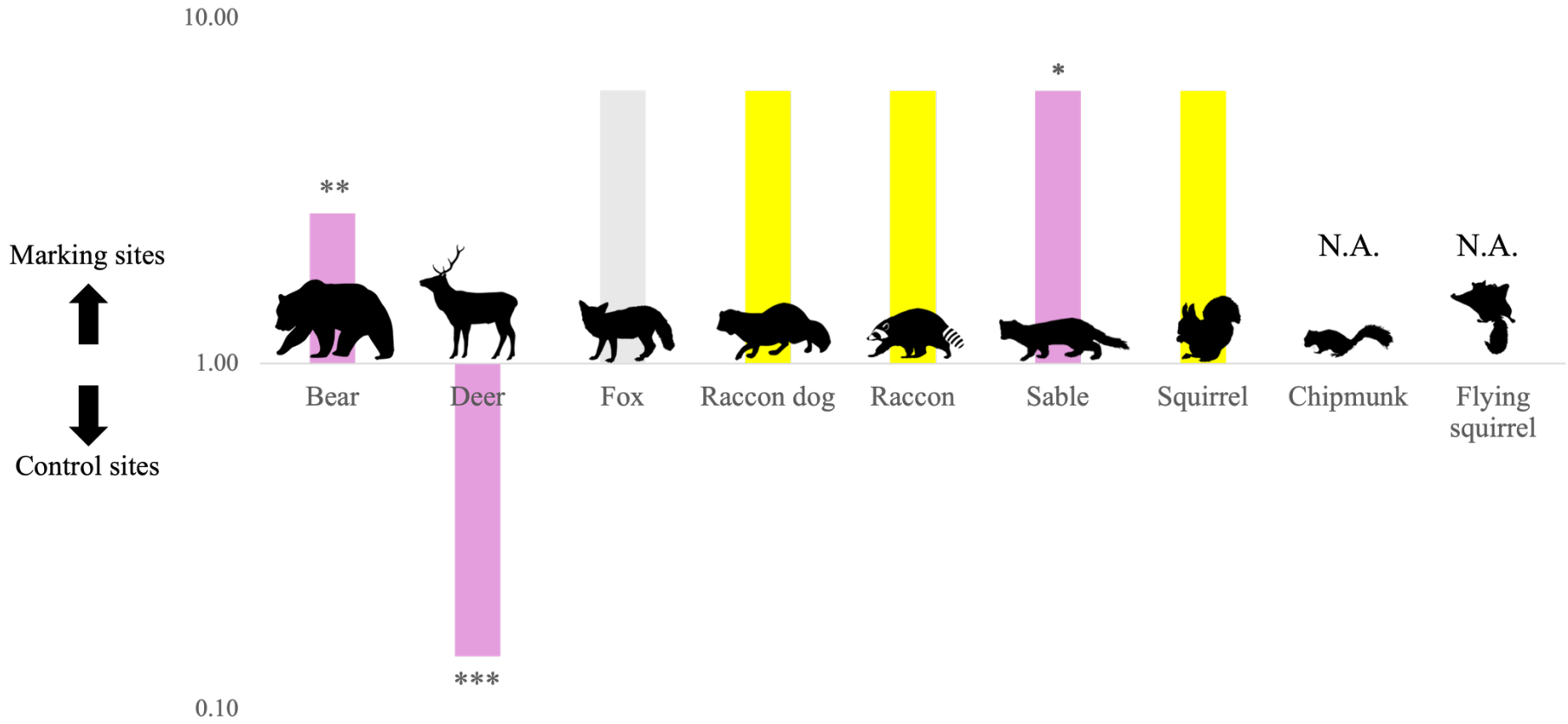


Figure 5. Relative leaving information behavior of species at 17 marking sites compared to 8 control sites. The y-axis is presented on a logarithmic scale. Bears and sables significantly left scent at marking sites, while sika deer actively avoided scent-marking at these sites. Raccoon dogs, raccoons, and red squirrels deposited scent exclusively at marking sites (displayed at the same scale as foxes). In contrast, chipmunks and flying squirrels did not exhibit scent-marking behavior at either marking or control sites. Asterisks represent significant differences in the probability of leaving information between marking and control sites based on GLMMs (see details in the text).

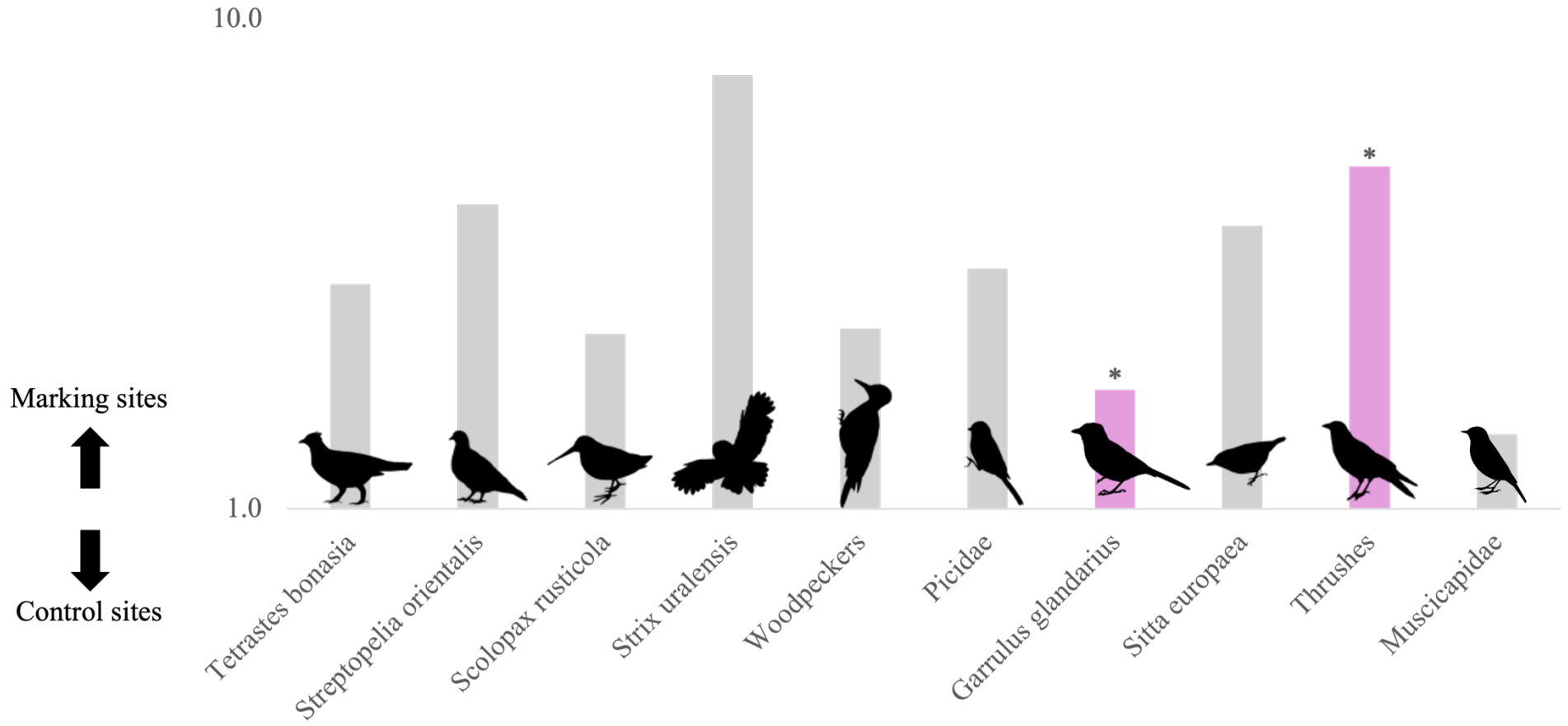


Figure 6. The relative visitation frequencies, calculated by RIC, of different bird species or groups to 17 bear marking sites compared to 8 control sites. The y-axis is presented on a logarithmic scale. Asterisks represent significant differences in visitation frequency between marking and control sites based on GLMMs (see details in the text).

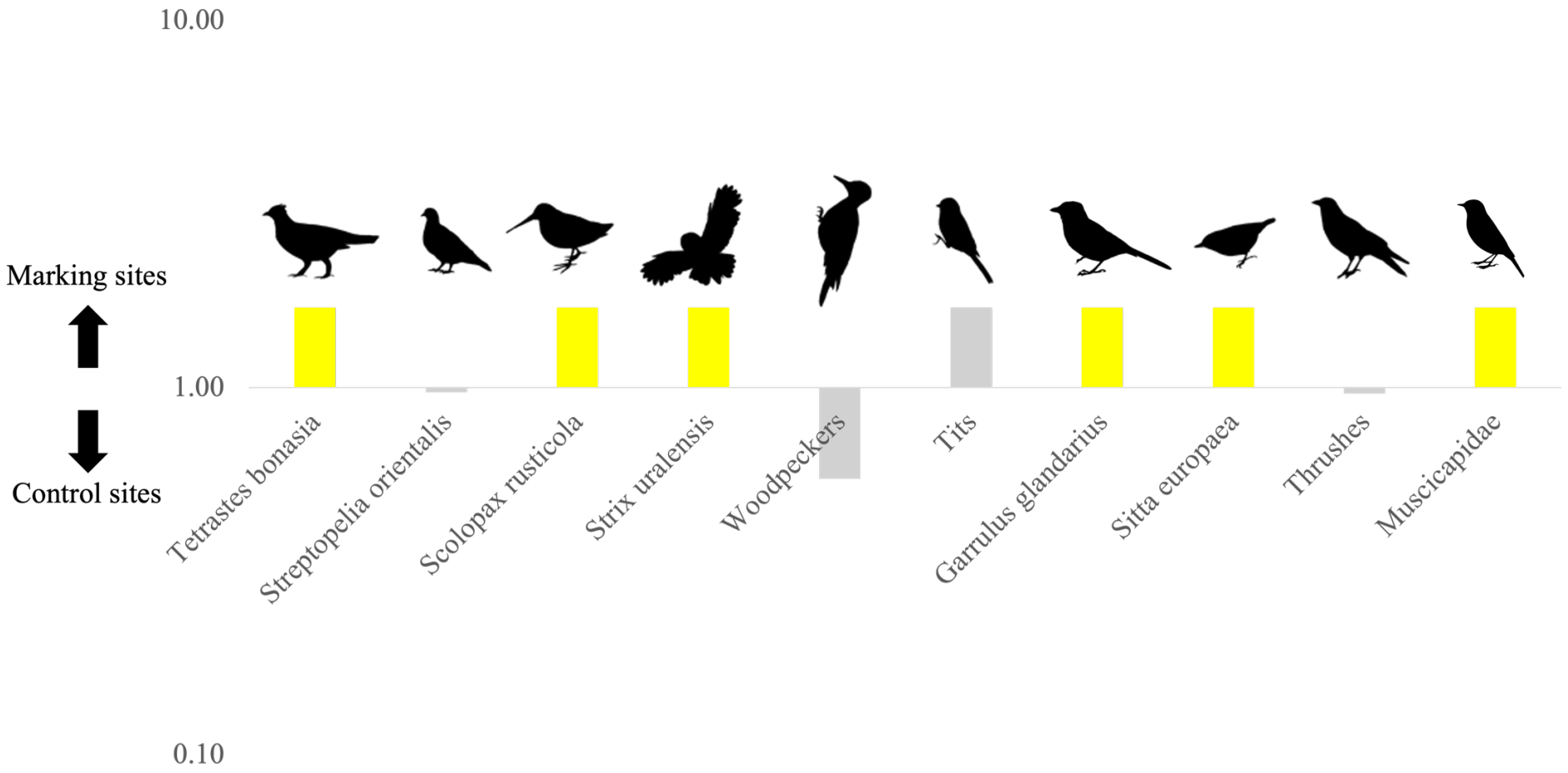
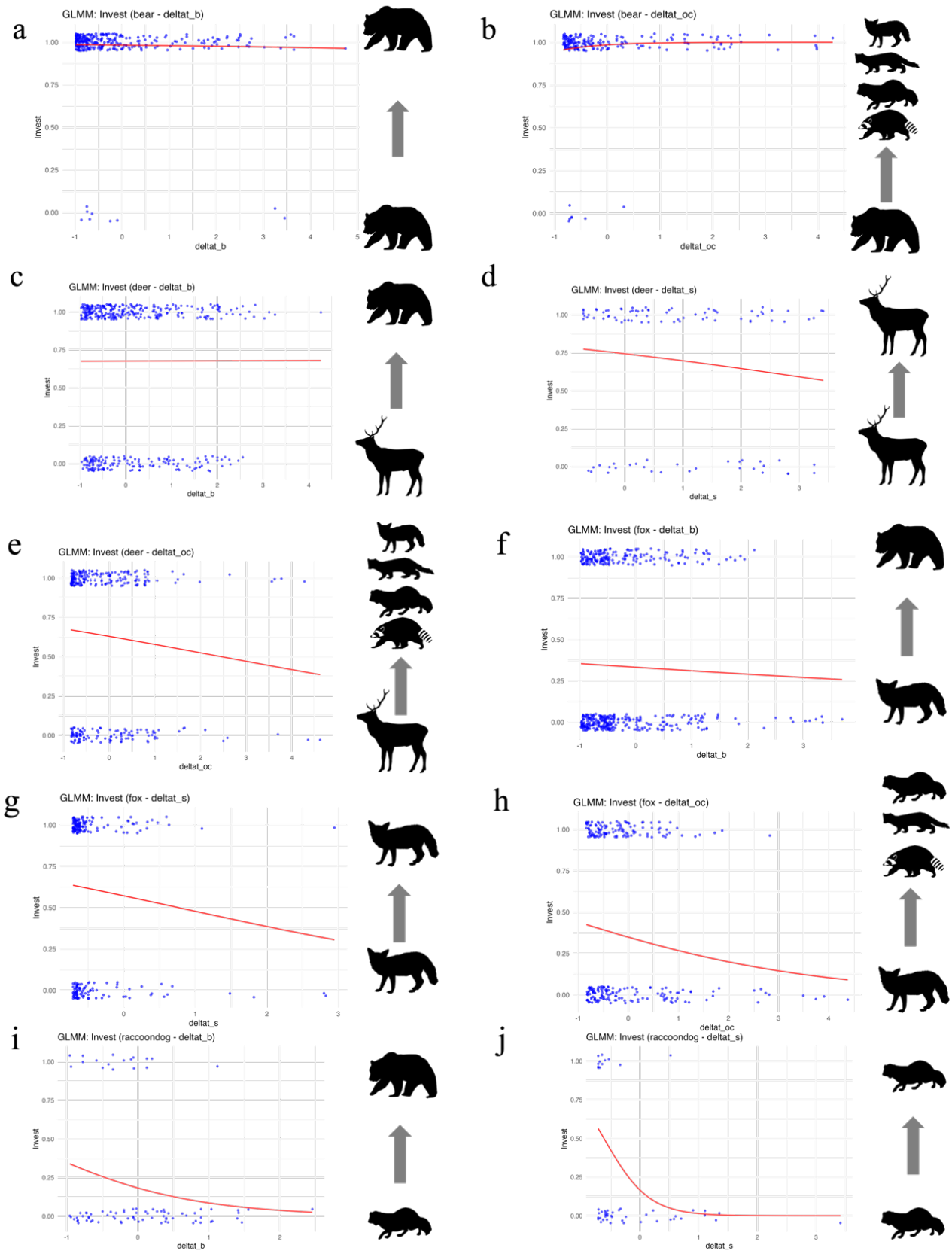


Figure 7. The relative foraging frequencies of different bird species or groups to 17 bear marking sites compared to 8 control sites. The y-axis is presented on a logarithmic scale. Most bird species/groups exhibited feeding behavior exclusively at marking sites (indicated by yellow bars). The yellow bars were adjusted to match the maximum value observed for Picidae to prevent them from diverging to infinity. In contrast, Oriental Turtle Dove (*Streptopelia orientalis*), woodpeckers, Picidae, and Thrushes were observed feeding at both marking and control.


a
GLMM: Invest (bear - deltat_b)
Invest
deltat_b
b
GLMM: Invest (bear - deltat_oc)
Invest
deltat_oc
c
GLMM: Invest (deer - deltat_b)
Invest
deltat_b
d
GLMM: Invest (deer - deltat_s)
Invest
deltat_s
e
GLMM: Invest (deer - deltat_oc)
Invest
deltat_oc
f
GLMM: Invest (fox - deltat_b)
Invest
deltat_b
g
GLMM: Invest (fox - deltat_s)
Invest
deltat_s
h
GLMM: Invest (fox - deltat_oc)
Invest
deltat_oc
i
GLMM: Invest (raccoondog - deltat_b)
Invest
deltat_b
j
GLMM: Invest (raccoondog - deltat_s)
Invest
deltat_s

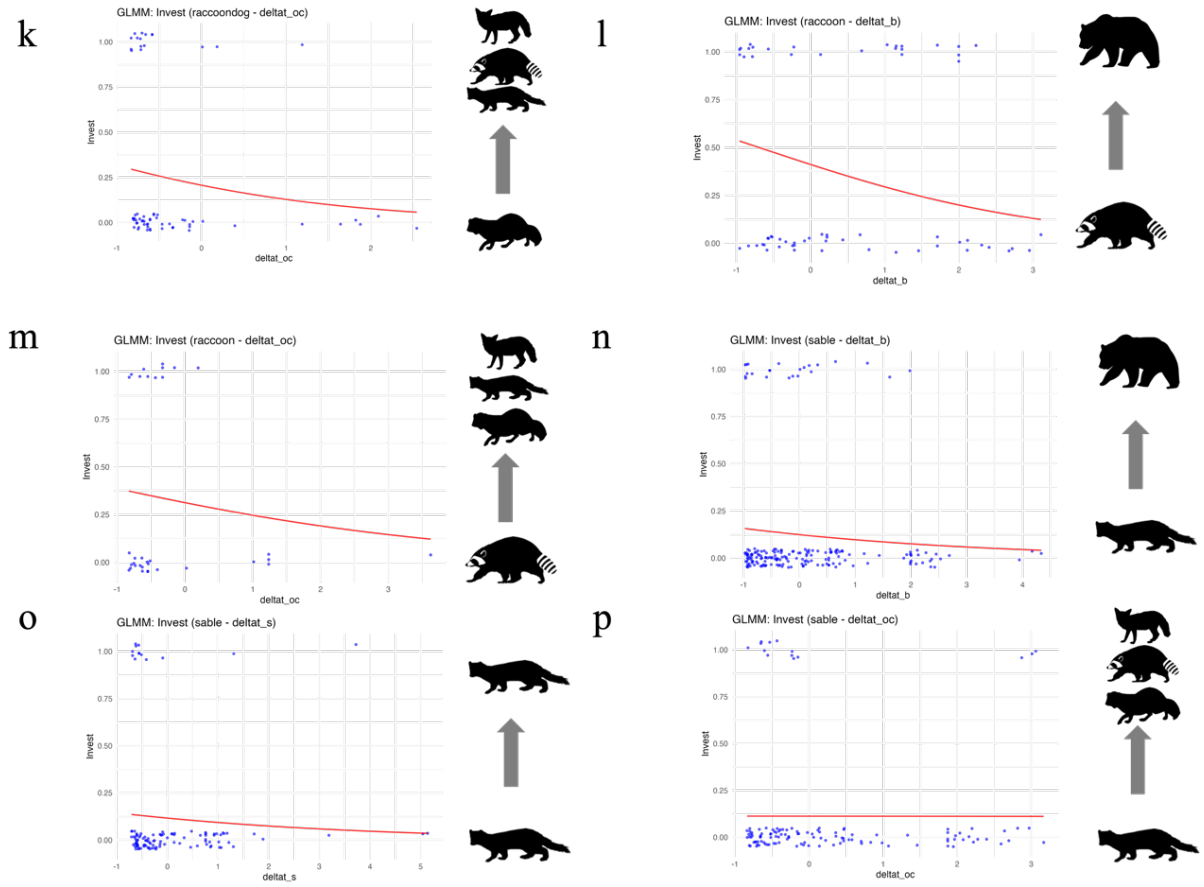
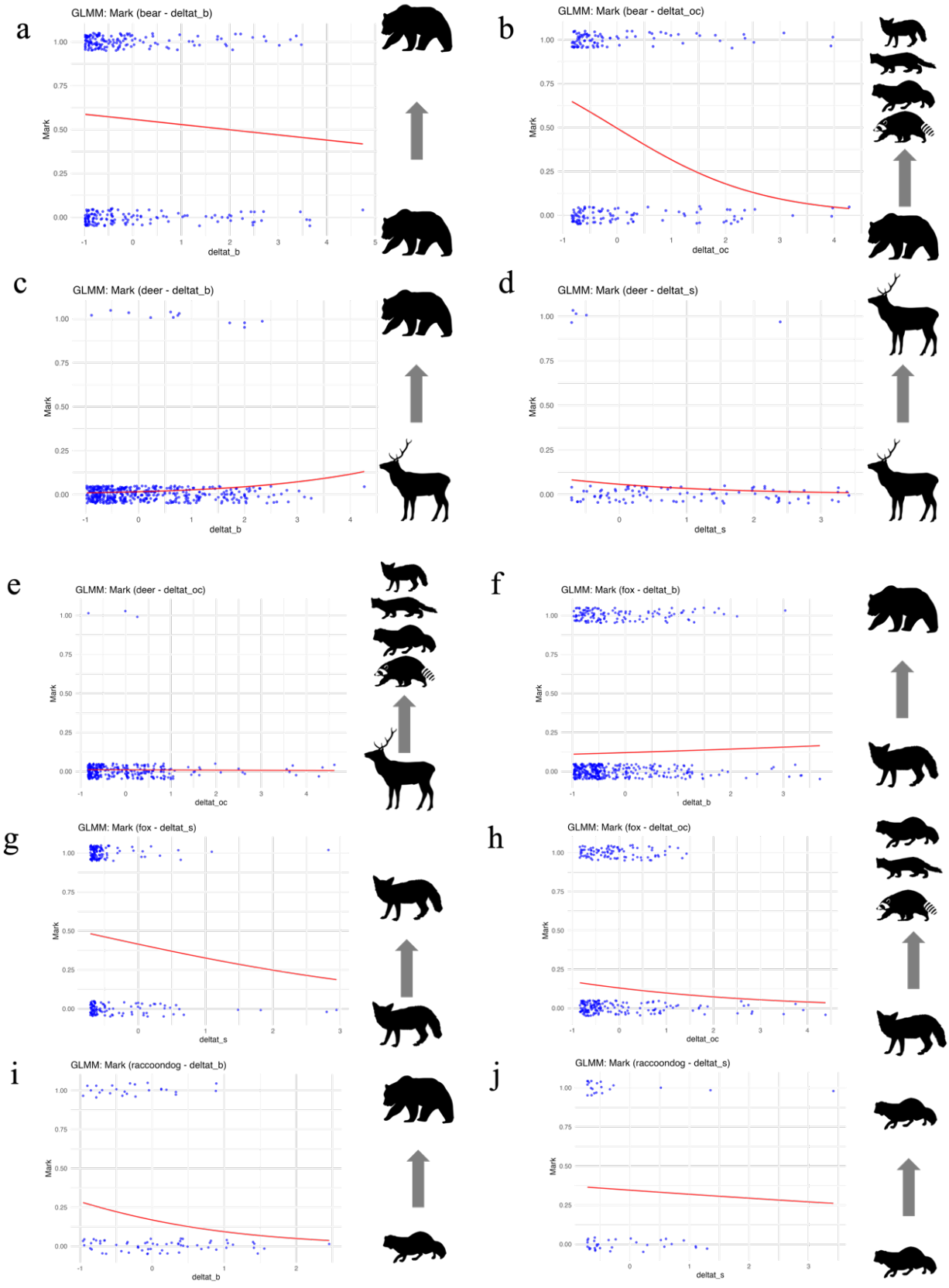


Figure 8. Time-dependency of mammal responses (receiving information behavior) to marking. This figure illustrates the behavioral responses of visitors to scents at 17 bear marking sites across species. The x-axis represents the elapsed time since the scent was deposited, while the y-axis indicated the behavioral response of visiting individuals, where 1 represents the occurrence of sniffing behavior, and 0 indicates the absence of this behavior. Panel **a** shows interactions where bears responded to scents left by other bears, while panel **b** highlights responses of bears to scents from mesocarnivores. Panels **c**, **d**, and **e** focus on sika deer, showing their responses to scents from bears, conspecifics, and mesocarnivores, respectively. Similarly, panels **f**, **g**, and **h** explore the responses of red foxes to scents from bears, conspecifics, and mesocarnivores. For raccoon dogs, panels **i**, **j**, and **k** present their behavioral responses to scents from bears, conspecifics, and mesocarnivores. The behaviors of raccoons are illustrated in panels **l** and **m**, highlighting their interactions with scents from bears and mesocarnivores. Lastly, the responses of sable are shown in panels **n**, **o**, and **p**, where their interactions with scents from bears, conspecifics, and mesocarnivores are analyzed. Each panel emphasizes how elapsed time since scent deposition influences sniffing behaviors across species.


a
GLMM: Mark (bear - deltat_b)
Mark
deltat_b
b
GLMM: Mark (bear - deltat_oc)
Mark
deltat_oc
c
GLMM: Mark (deer - deltat_b)
Mark
deltat_b
d
GLMM: Mark (deer - deltat_s)
Mark
deltat_s
e
GLMM: Mark (deer - deltat_oc)
Mark
deltat_oc
f
GLMM: Mark (fox - deltat_b)
Mark
deltat_b
g
GLMM: Mark (fox - deltat_s)
Mark
deltat_s
h
GLMM: Mark (fox - deltat_oc)
Mark
deltat_oc
i
GLMM: Mark (raccoondog - deltat_b)
Mark
deltat_b
j
GLMM: Mark (raccoondog - deltat_s)
Mark
deltat_s

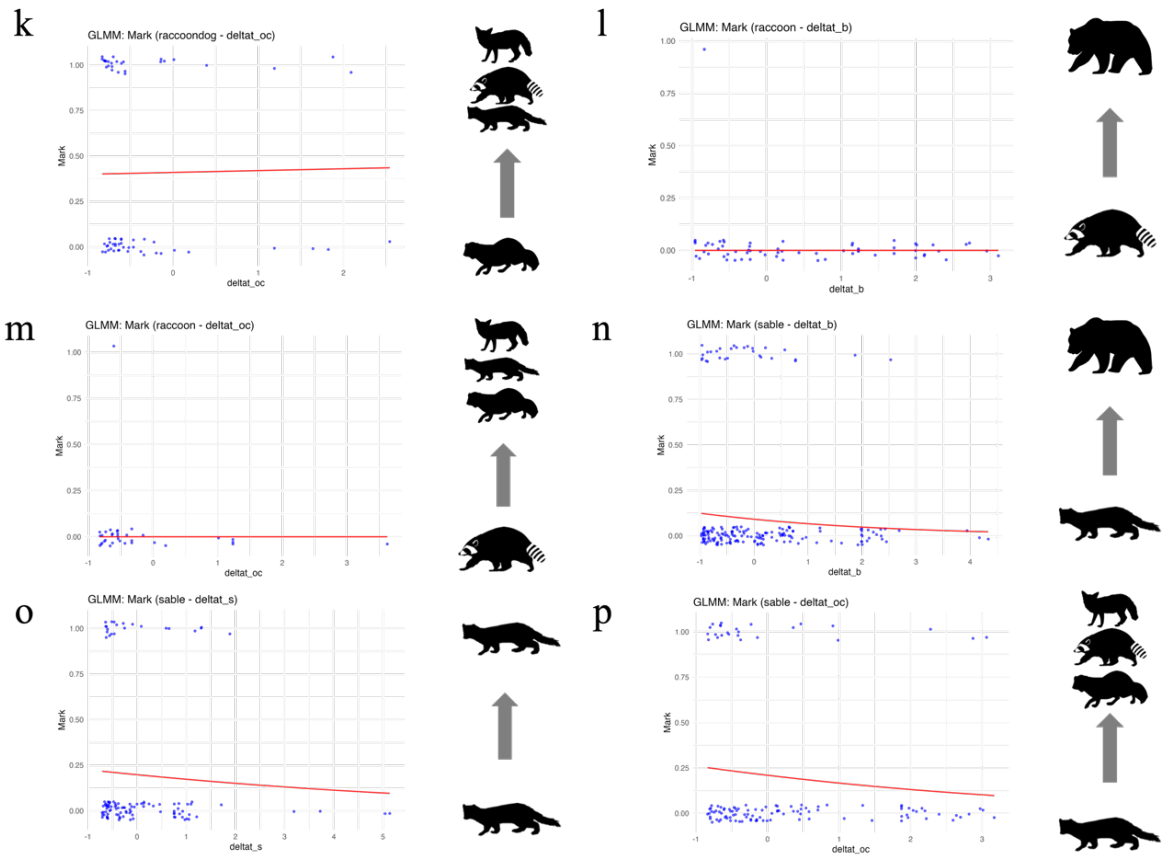
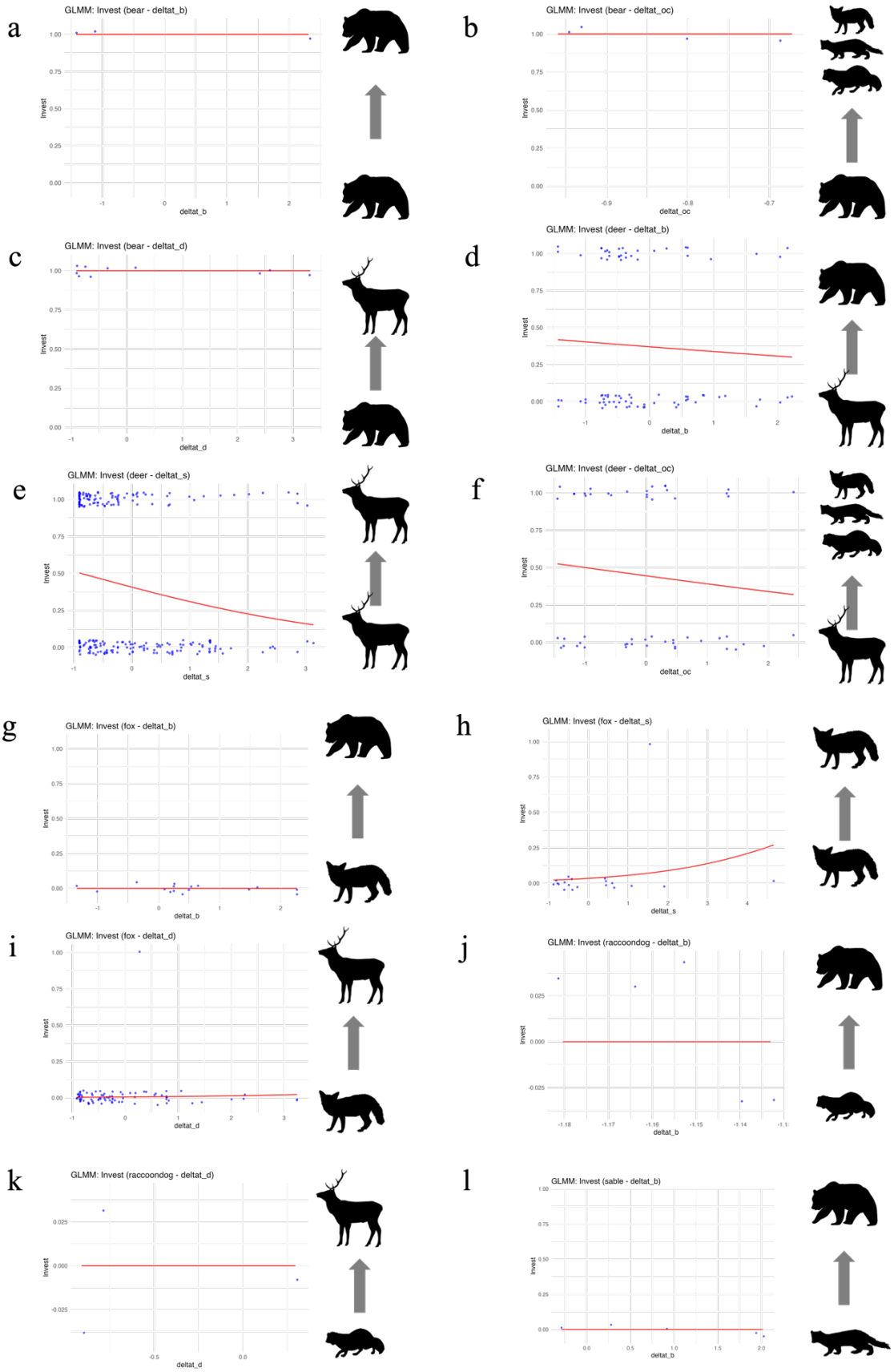


Figure 9. Time-dependency of mammal responses (leaving information behavior) to marking. This figure illustrates the behavioral responses of visitors to scents at 17 bear marking sites across species. The x-axis represents the elapsed time since the scent was deposited, while the y-axis indicated the behavioral response of visiting individuals, where 1 represents the occurrence of marking behavior, and 0 indicates the absence of this behavior. Panel **a** shows interactions where bears responded to scents left by other bears, while panel **b** highlights responses of bears to scents from mesocarnivores. Panels **c**, **d**, and **e** focus on sika deer, showing their responses to scents from bears, conspecifics, and mesocarnivores, respectively. Similarly, panels **f**, **g**, and **h** explore the responses of red foxes to scents from bears, conspecifics, and mesocarnivores. For raccoon dogs, panels **i**, **j**, and **k** present their behavioral responses to scents from bears, conspecifics, and mesocarnivores. The behaviors of raccoons are illustrated in panels **l** and **m**, highlighting their interactions with scents from bears and mesocarnivores. Lastly, the responses of sable are shown in panels **n**, **o**, and **p**, where their interactions with scents from bears, conspecifics, and mesocarnivores are analyzed. Each panel emphasizes how elapsed time since scent deposition influences marking behaviors across species.


a
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deltat_d
d
GLMM: Invest (deer - deltat_b)
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deltat_b
e
GLMM: Invest (deer - deltat_s)
Invest
deltat_s
f
GLMM: Invest (deer - deltat_oc)
Invest
deltat_oc
g
GLMM: Invest (fox - deltat_b)
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deltat_b
h
GLMM: Invest (fox - deltat_s)
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deltat_s
i
GLMM: Invest (fox - deltat_d)
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deltat_d
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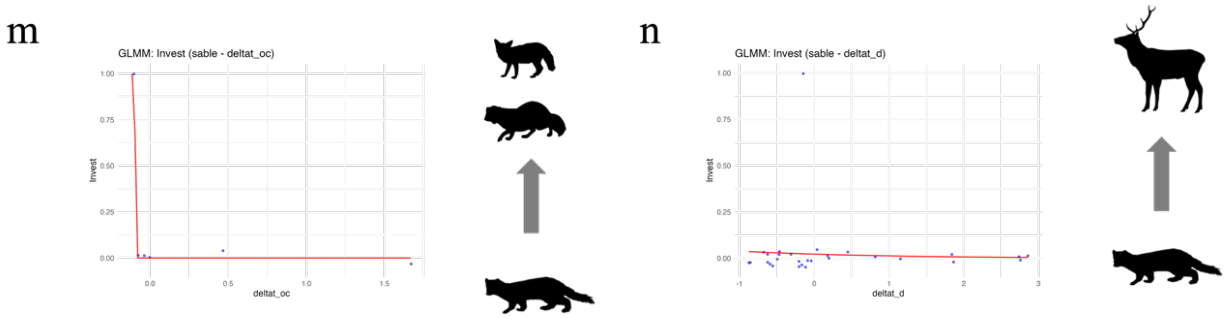
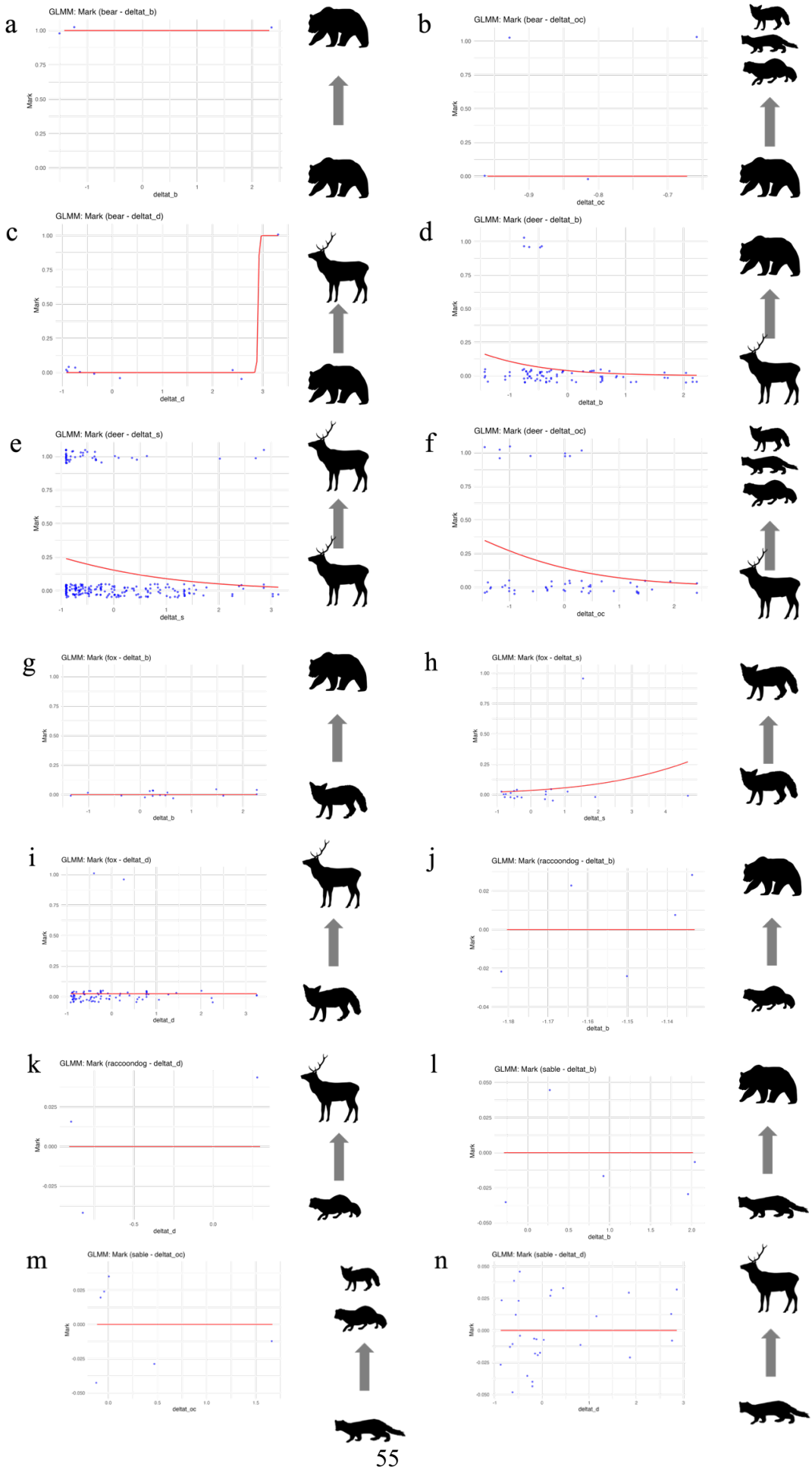


Figure 10 Time-dependency of mammal responses (receiving information behavior) to marking. This figure illustrates the behavioral responses of visitors to scents at 8 control sites across species. The x-axis represents the elapsed time since the scent was deposited, while the y-axis indicated the behavioral response of visiting individuals, where 1 represents the occurrence of sniffing behavior, and 0 indicates the absence of this behavior. Panel **a** shows interactions where bears responded to scents left by other bears, while panel **b** highlights responses of bears to scents from mesocarnivores. Panel **c** focuses on bear-to-sika deer interactions, while panels **d**, **e**, and **f** show the responses of sika deer to scents from bears, conspecifics, and mesocarnivores, respectively. Panels **g**, **h**, and **i** depict the behavioral responses of red foxes to scents from bears, conspecifics, and sika deer. Similarly, panels **j** and **k** explore the responses of raccoon dogs to scents from bears and sika deer. Finally, the responses of sable are presented in panels **l**, **m**, and **n**, highlighting their interactions with scents from bears, mesocarnivores, and sika deer.


a
GLMM: Mark (bear - deltat_b)
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GLMM: Mark (deer - deltat_b)
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GLMM: Mark (deer - deltat_s)
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GLMM: Mark (deer - deltat_oc)
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GLMM: Mark (fox - deltat_b)
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GLMM: Mark (raccoondog - deltat_b)
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deltat_d
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deltat_b
m
GLMM: Mark (sable - deltat_oc)
Mark
deltat_oc
n
GLMM: Mark (sable - deltat_d)
Mark
deltat_d

Figure 11 Time-dependency of mammal responses (leaving information behavior) to marking. This figure illustrates the behavioral responses of visitors to scents at 8 control sites across species. The x-axis represents the elapsed time since the scent was deposited, while the y-axis indicated the behavioral response of visiting individuals, where 1 represents the occurrence of marking behavior, and 0 indicates the absence of this behavior. Panel **a** shows interactions where bears responded to scents left by other bears, while panel **b** highlights responses of bears to scents from mesocarnivores. Panel **c** focuses on bear-to-sika deer interactions, while panels **d**, **e**, and **f** show the responses of sika deer to scents from bears, conspecifics, and mesocarnivores, respectively. Panels **g**, **h**, and **i** depict the behavioral responses of red foxes to scents from bears, conspecifics, and sika deer. Similarly, panels **j** and **k** explore the responses of raccoon dogs to scents from bears and sika deer. Finally, the responses of sable are presented in panels **l**, **m**, and **n**, highlighting their interactions with scents from bears, mesocarnivores, and sika deer.

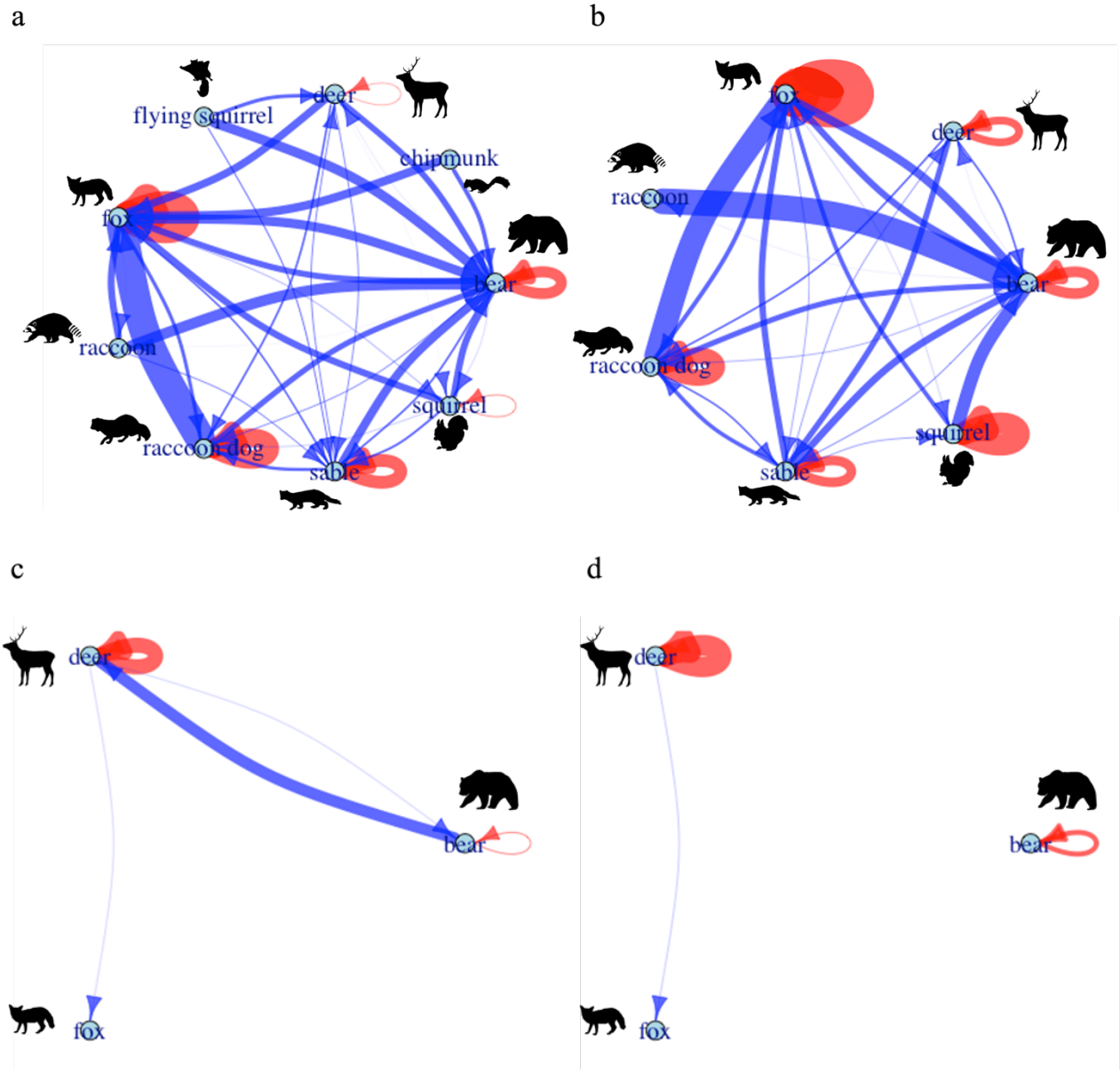

Figure 12. Social networks based on species-specific normalized frequency of receive information and leaving information. The panels illustrate the social networks constructed for receiving and leaving information behaviors at marking sites and control sites. **(a)** Receiving information network at marking sites, **(b)** leaving information network at marking sites, **(c)** receiving information network at control sites, and **(d)** leaving information network at control sites. Blue edges represent interspecific interactions, while red self-loops indicate intraspecific interactions. Each node represents a species that participated in the respective networks.

III. Use of bear scats by other animals: potential intra- and inter-species communication and food resources

Abstract

Scats are often avoided due to their strong odor and associated risks of infectious diseases and parasites. However, scats can serve as valuable resources for intra-specific communication and as a food source. Despite this, few studies have quantitatively assessed their ecological roles. Using camera trap surveys, I investigated the use of bear scats by various animal species. A total of 13 mammal species were observed, with 7 displaying behaviors such as sniffing, counter-marking, avoidance, and coprophagy. Additionally, 17 bird species were recorded, with 6 exhibiting coprophagy. Animal reactions to bear scats declined over time, persisting for approximately 30 days. Bears themselves engaged in sniffing, counter-marking, and occasional avoidance, suggesting roles in intra-specific communication. Deer showed avoidance behavior, possibly indicative of predator avoidance. Meso-carnivores, including foxes, raccoons, raccoon dogs, and sables, frequently marked bear scats with their own urine or scat, likely using them for chemical communication. Rodents commonly practiced coprophagy, likely consuming undigested plant seeds. Among birds, jays were the primary consumers of bear scats, with some tits also participating. This study highlights the diverse uses of bear scats as both a chemical information source and a nutritional resource. These findings underscore the ecological importance of scats and their multifaceted roles in inter- and intra-specific interactions, which warrant further investigation.

3.1. Introduction

Scats and urine are often perceived as unpleasant and intuitively repulsive due to their smell. This aversion likely stems from an evolutionary adaptation to avoid potential risks such as diseases and parasite infections (Cooper et al., 2000; Ezenwa, 2004; Garnick et al., 2010). However, in natural ecosystems, scats and urine play important roles as resources. For example, feces and urine are nutrient-rich, fertilizing soils and enhancing plant growth and primary production (Dhiman et al., 2020; le Roux et al., 2020; Powell et al., 1999). Additionally, scats of large animals often contain undigested materials such as seeds and vegetation, which can serve as food for smaller animals, including rodents, birds, and insects (Koike et al., 2012; Logiudice, 2001; K. Page et al., 2001). Thus, the utilization of animal scats is shaped by trade-offs between acquiring energy and avoiding infection risks (Weinstein et al., 2018).

Scats also play a significant role in intraspecific communication through chemical signaling. Certain mammals, such as rhinoceroses, ocelots, raccoons, badgers, raccoon dogs, and otters, create "communal latrines," where multiple individuals share specific sites for excretion (Buesching et al., 2016; Kaneko et al., 2009; T. W. King et al., 2017; Laurentino et al., 2023; Marneweck et al., 2018; L. K. Page et al., 1999; Weinstein et al., 2018; Yamamoto, 1984). These scats are often coated with secretions from anal glands, which contain chemical signals that convey information such as sex, maturity, dominance, and individual identity (Gosling & Roberts, 2001; Jordan, 2007; Leclaire et al., 2017). This allows animals to communicate effectively without direct encounters. However, little research has focused on the roles of solitary scats in intraspecific chemical communication. This lack of attention is surprising, as many mammals without

communal latrines possess anal glands capable of releasing chemical signals. Such chemical communication may be especially significant for solitary mammals.

The presence of excretions and their chemical signals can also influence interspecific interactions, particularly in predator-prey interactions. Fresh scats indicate recent activity by predators or prey, potentially influencing decision-making, such as escaping from predators or seeking prey. In fact, some ungulates exhibit strong avoidance behaviors when exposed to predator urine (Arnould et al., 1998; Kuijper et al., 2014). Additionally, certain animals engage in counter-marking or overmarking, where they deposit their scats or urine on the scats of other species (Apps et al., 2019; Paquet, 1991; Wikenros et al., 2017). While the exact function of counter-marking remains unclear, it may serve to facilitate intraspecific communication by utilizing conspicuous sites or to disrupt the chemical communication of competitors or predators (Apps et al., 2019; Cornhill & Kerley, 2020). Moreover, scats provide resource information in ecosystems; for example, the timing of food availability, such as fruits and seeds, can be inferred from scat contents. Thus, scats serve as valuable sources of information and food for both conspecifics and heterospecific.

In this study, I examined the potential roles of solitary scats of brown bears (*Ursus arctos*) in intra- and interspecific chemical communication and as a food resource. Brown bears are solitary, opportunistic predators inhabiting extensive areas in the northern hemisphere. They possess anal glands that are thought to deposit glandular secretions in their scats, which may vary by sex (Rosell et al., 2011), suggesting their potential role in intraspecific communication. Brown bears have a diverse diet, including plants, seeds, fruits, berries, insects, rodents, deer, moose, and salmon (Bojarska & Selva, 2012). Due to their omnivorous nature and generalized digestive systems, their scats often

contain undigested nutrients. Scats rich in fruit pulp and seeds may be particularly attractive to small granivorous animals. Therefore, brown bear scats may serve multiple ecological functions, supporting various animal interactions.

To examine these roles, I placed infrared cameras in front of bear scats to monitor the behavior of visiting animals. First, I hypothesized that brown bears use their scats for intraspecific communication, predicting that they would receive and leave information by sniffing and overmarking. I further hypothesized that some sympatric mammals use these chemical signals for interspecific communication. Specifically, sika deer (*Cervus nippon*), a potential prey species, were expected to avoid fresh bear scats. Meso-carnivores, such as red foxes (*Vulpes vulpes*), raccoon dogs (*Nyctereutes viverrinus*), and sables (*Martes zibellina*), might use bear scats for both intra- and interspecific communication by sniffing and overmarking. These meso-carnivores might also utilize bear scats to infer food availability. Finally, I hypothesized that rodents and birds would exploit bear scats containing seeds and fruits as a food resource. This study aims to elucidate the potential roles of brown bear scats in forest ecosystems.

3.2. Materials and methods

Study sites

I conducted field surveys in the Teshio Experimental Forest of Hokkaido University (45°N, 142°E), the Uryu Experimental Forest of Hokkaido University (44°N, 142°E), and Minami Furano (43°N, 143°E). The various forests supported a mixture of coniferous and deciduous broat-leaved trees with a ground cover of bamboo grass *Sasa* spp.. The mean annual temperature of Teshio Experimental Forest is 5°C (max. 35°C, min. –35°C) and annual precipitation is approximately 1000 mm. The mean annual temperature of Uryu

Experimental Forest is 3°C (max. >30°C, min. < –30°C) and the annual precipitation is approximately 1500 mm. The mean annual temperature of Minami Furano is 4.2°C (max. 20°C, min. –10°C) and annual precipitation is approximately 1300–1400 mm. Much of the precipitation falls as snow in winter, with snow depths exceeding 1 m every winter.

Scat collection and camera trap monitoring

I collected fresh scats, along the forest roads, observed some scats at the discovery points, and collected others to introduce to additional observation points. Age of scats varied between half a day old and up to less than 1 week old. The contents of the scats were classified into four categories: herbaceous plants (e.g., *Lysichiton camtschatcense*, *Petasites japonicus*), fruits and nuts (e.g., *Quercus crispula*, *Vitis coignetiae*), animal matter (e.g., *Cervus nippon*, *Oncorhynchus keta*), and dent corn (*Zea mays*). When scat contents spanned multiple categories, the scats were assigned to the category that constituted the majority of the content. Some scats were collected, leaving approximately the size of a clenched fist, to be used for another study. After collection, some scats were stored at -20°C until the experiment, and then introduced into the field after being thawed naturally.

A total of 58 scats were monitored using camera traps from September 2022 to November 2024. Two cameras were installed per scat: one was attached to a stake at knee height, and the other was mounted 110 cm above the ground in the opposite direction. However, only one camera was installed at some locations due to equipment limitations (**Fig. 1**). All cameras were set to record a 60-second video at 1-second intervals once movement was detected.

Behavioral observation

A series of consecutive videos, with an interval of less than 30 minutes between shots, were counted as independent events. Observed animal behaviors were classified into the following categories: exploration for scats (scent sniffing: continuous movement of the nose toward the scats, with the distance between the nose tip and the scats within one head's length), behavior using scats as a foraging resource (foraging, scat eating, pecking), counter-marking of scats (urination, scat marking, body rubbing), and avoidance after sniffing the scats (retreat and changing course). Each behavior was counted as one event when observed. If the behavior was not observed during a particular event, it was not counted.

Statistical analysis

Prior to the main analysis, I defined the time during which scats function as a source of information. Since scats serve as a temporary information source, they are excreted into the environment, then gradually weathered and returned to the soil. After the cameras were installed, the animals" behavior of obtaining information from the scats (sniffing) decreased over time, and by approximately 30 days (43,200 minutes) after installation, there was almost no response. Therefore, I defined the time during which scat functions as a source of information as approximately 30 days (**Fig. 2**).

A network analysis focusing on scats as central nodes was conducted. When visitors exhibited behaviors related to scats (receiving information=1, leaving information=1), the species that had performed marking behaviors during the preceding 43200 minutes were identified, and their frequency of marking was recorded to construct an edge list. For bear scats, the time of introduction to the field was considered as the

time when the bear performed the marking behavior. Based on the edge list, directed and weighted networks were constructed using the R package igraph (version 2.1.2; Csardi and Nepusz 2006). For each network, the following metrics were calculated: the number of nodes, the number of edges, graph density, average path length, local efficiency, global efficiency, proportions of intraspecific and interspecific edge weights, degree centrality, and betweenness centrality. All data were used for calculating general network metrics, such as node and edge counts. However, for identifying the top 5 heaviest weighted edges, data with a sample size of 10 or less were excluded. This exclusion applied only to the selection of the top 5 edges and did not affect the calculation of other network features. Edge weights were calculated by summing the number of observed behavioral events for each species and were subsequently normalized by the total number of observed events for that species. Finally, centrality indices and edge weights were visualized to examine the structures of the receiving information network and the leaving information network.

3.3. Results

Animals detected by camera traps

In total, I identified 2,966 unique events involving 13 mammal species and 222 events involving 17 bird species in and around bear scats (**Table 2**). Bats, shews, rabbits *Lepus timidus* and domestic cats *Felis catus* were also recorded but excluded from the counts because they were photographed infrequently. Brown bears exhibited scent sniffing in 28% of the cases, and urination and pedal marking (counter-marking) in 2%. One case (0.5%, adult female) also exhibited avoidance behavior. Deer, a prey species, were thought to respond strongly to scats. However, contrary to expectations, only 6% of all deer showed exploratory behavior. No counter-marking was observed in any case, and

avoidance behavior toward scat was observed in one case. The mesocarnivores—fox, raccoon dog, and sable—showed relatively strong behavioral responses, exhibiting scent sniffing in 15%, 34%, 20%, and 50% of cases, respectively. Three species, other than raccoons, exhibited urine and fecal counter-marking at scats (fox: urine 11%, scat 1%; raccoon dog: urine 10%, scat 1%; sable: urine 17%). Foxes showed fecal feeding in two events, one of which involved urination after the scats had been moved to the center of the forest path. After foxes, the next most commonly photographed medium-sized carnivore was the raccoon. Raccoons were generally either unattended or exhibited counter-marking behavior through urination. Because only a few sables were photographed, the use of scats would be rare. However, even in those few instances, they were photographed sniffing scats and urine-marking (see previous studies on butt flicking behavior). Raccoons exhibited only scent sniffing and did not engage in marking behavior in response to brown bear scats. They also cleverly avoided brown bear scats and did not step on them in any event. Rabbits were photographed in 36 instances, but all were unattended. A few squirrels and chipmunks were photographed, but all were unattended. Terrestrial rodents were observed sniffing in 10% of events and engaging in fecal feeding in 21% of events.

Use of scats as a foraging resource by birds and rodents

Birds and rodents were observed exhibiting significant foraging behavior primarily in scats containing fruits or seeds, with particularly notable foraging activity observed in scats containing dent corn (*Zea mays*) (**Fig. 3**). Foraging behavior was recorded for five bird species, among which the Eurasian jay (*Garrulus glandarius*) demonstrated the most frequent foraging activity, being observed during the day, and of the 104 total

photographed events, 86 occurred with dent corn scats. Foraging behavior was observed in 67% of these events. primarily exhibited foraging behavior during the nighttime, which was observed in three scats containing dent corn and two scats containing herbaceous plants.

Scat-centered networks

Receiving information and leaving information networks were constructed based on interactions observed around brown bear scats (**Fig. 4**). In the sniffing network, the highest degree centrality was observed for brown bears (Degree = 11), and brown bears also had the highest betweenness centrality. In contrast, in the marking network, both brown bears and foxes exhibited the highest degree centrality (Degree = 6) and betweenness centrality.

Regarding edge weights, the sniffing network showed strong weights for interactions such as fox-to-fox, deer-to-bear, and rodents-to-raccoon dog, highlighting diverse intra- and interspecific interactions. These findings suggest that brown bear scats serve not only as arenas for intraspecific interactions but also as hubs for interspecific interactions. In the marking network, brown bears, along with three mesocarnivora species (foxes, raccoon dogs, and martens), participated in marking behaviors. These species exhibited overmarking on both conspecific and heterospecific scents.

3.4. Discussion

Scats serve as a means of intraspecific communication for bears

For solitary large mammals with a clear marking tree, the role that randomly scattered scat in their habitat plays in intraspecific communication has often been overlooked. This

is likely because the sociality of solitary mammals has been considered less complex, with their communication primarily centered around a fixed marking sites. Scat scattered throughout the habitat and eventually fading away has been seen as unimportant. However, given that many solitary species have anal glands (presumably for secretion onto scats), it is possible that scats serve as a source of more information than previously imagined.

In this study, I demonstrated that brown bears respond behaviorally to scats, whose function in communication had been unclear until now. In addition to scent sniffing, brown bears also responded to scats by urinating and counter-marking with pedal marking. Pedal marking is a behavioral sequence specific to breeding males, in which the scent from the sole gland is rubbed on the ground, and it is observed as a straight line leading to the marking tree (Revilla et al., 2021; Sergiel et al., 2017) . During field surveys, the author often observed a series of footprint depressions typical of marking sites, even along forest roads where no marking sites were nearby (personal observation). Pedal marking was also observed while urinating immediately after sniffing scats. This behavioral sequence was also observed in captive individuals (both male and female), suggesting that scats function as a stimulus that triggers counter-marking and scent accumulation in visiting individuals (personal observation). These behaviors likely serve to supplement individual bear information as a temporary source of information that fills in the gaps between fixed marking sites along forest roads. All counter-markings were observed in adult males, not females or subadults. This pattern is similar to the general role division at marking sites during the breeding season (dominant adult males exhibit marking and counter-marking, while females and subadults only receive information and leave no scent of their own)(Clapham et al., 2014).

In terms of female responses to scats, avoidance behavior after sniffing was observed in only one case. This individual, which appeared to be an adult female, stopped after finding scats while walking along a forest road. After sniffing the scats, she appeared to change her course, possibly startled by the unexpected presence of the scats. This suggests that the scats may have indicated information about other individuals, such as males, that could pose a threat to this individual. Based on these observations, scats may serve as a source of information for females without leaving their own scent. However, I cannot conclude this with certainty due to the limited number of observations. To further examine this, experiments using fresh scats and sex-selected scats in captivity would be effective in evaluating their responses.

Response of potential prey to bear scats

Contrary to expectations, sika deer did not show much response to scats. Although scats may serve as a resource for deer to communicate immediate brown bear information and were thought to trigger significant responses to unexpected signals, scent sniffing occurred in only 6% of the total events, and avoidance behavior was exhibited by only 1% of the deer.

Although avoidance behavior was rare as a percentage, the behavior of the individuals that responded was evident. In most cases, they framed in while walking or foraging, stopped after sniffing the scats, and then retreated, either framing out or bypassing the scats. In the case of foraging, the individual would stop, sniff the scats, and then bypass them in the same manner. Although not defined as sniffing in this study, there were instances where animals sniffed at scats from a greater distance (e.g., 1 neck length) and bypassed them, as well as cases where they bypassed the scats even though no clear

sniffing behavior was observed. Considering this series of avoidance behaviors, it is reasonable to interpret that the scats propagated predator information that was unfavorable to the deer, and that the deer exhibited avoidance behavior in response.

On the other hand, scat may be more overlooked by deer than expected. Responses to scat were minimal, and even within 30 days, when scats are thought to function as a source of information for animals, trampling of scats by deer was observed. Several factors may explain why the deer did not respond as strongly as expected to bear scat.

First, the freezing process may have reduced the odor of the scats. Chemical signals, such as those used for interindividual communication, are often composed of low molecular weight volatile compounds and lipids (Brown & Macdonald, 1985; Charpentier et al., 2012). These compounds are depleted during frozen storage and degraded by the freezing and thawing process. In this experiment, both fresh scats and scats that were frozen after collection and then thawed were used, and it is possible that the thawed scats did not retain sufficient amounts of chemical components to effectively propagate information to brown bears. However, this is less likely because other animals responded to the same scats.

Second, sika deer might have overlooked the scats. The scats used in the experiment varied in size, ranging from those equivalent to the largest scats found in the field to those the size of a clenched fist. Therefore, it is possible that smaller scats were overlooked. Additionally, even for larger scats, they may not serve as visually or chemically prominent signals for deer, whose heads are positioned higher off the ground. However, it seems unlikely that size differences significantly affected the results, as some smaller scats were still responded to by deer.

Third, sika deer avoided scats during periods of high fecal freshness (when bear information is strongly propagated). Camera traps have the disadvantage of having a limited field of view due to their nature. Therefore, I do not know how the deer behaved outside the camera frame. It is possible that they smelled the scats from farther away than I could detect and chose not to approach the scats when they were fresh and outside the camera's sensor range. To investigate this, I compared the frequency of visits to scats by deer when the scats were fresh (during the first half of the informative period) with the second half of the informative period. If the deer had avoided approaching fresh scats, I would expect the frequency of visits during the first 30 days to be lower than in the second half. However, contrary to our prediction, the visit frequency was higher in the second half (**Fig. 3**). Therefore, the deer were not avoiding scats outside the camera frame.

Rejection of these three possibilities, therefore, support the conclusion that deer do not respond to bear scats in the way that was expected.

Intra- and inter-specific chemical communications by mesocarnivores

Scats functioned as a strong olfactory signal and a visually prominent site and were thought to be used by mesocarnivores for intraspecific communication. As predicted, three native mesocarnivores (fox, raccoon dog, and sable) exhibited scent-sniffing and urine counter-marking in response to brown bear scat. Foxes and raccoons also countermarked with scats. The fox additionally carried a piece of bear scat in its mouth, moved it about 50 cm to the center of the forest path, and urinated on it. This behavior involves attaching its own scent to a different location than the original bear scat. By using the bear's scent and the conspicuous object (scat), the fox may weaken the scent of the brown bear scat, thereby highlighting its own olfactory signals. At first glance, the act

of superimposing its own scat onto that of a higher predator might seem like a waste of resources. The scat of a top predator is a short-term resource and would not serve as a place for multiple individuals to visit and deposit their own scats for an extended period, as in a communal toilet. Therefore, investing in scats may not be an effective signaling strategy for other individuals. On the other hand, brown bear scats are located along forest roads that are also easily accessible to many medium-sized mammals, and counter-marking a top predator's scat with its own scent and visually prominent signal may be a way for the mesocarnivores to demonstrate dominance.

The non-native medium-sized carnivore, the raccoon, showed only scent sniffing and did not leave its own scent. As an introduced species, it is highly likely that its presence in this environment has triggered behaviors that were evolutionarily left behind, as its native habitat is dominated by top predators with strong carnivorous appetites. In its native habitat of North America, raccoons are potentially at risk of predation by coyotes (Albers, 2012). Visiting the scats of top predators to obtain predator-related information may be advantageous, while leaving its own scent there could be a disadvantage. Alternatively, since signals from the same species left in the scats of higher predators may not be important to raccoons, they may have cleverly assessed brown bear scats and conserved their limited resources (urine, scats) for their original intraspecific communication. Therefore, counter-marking may not have been an option for them.

Mesocarnivores were also predicted to use brown bear scat as a foraging resource, as brown bears and their foraging resources are included. This is particularly true for carnivorous foxes that consume animal matter found in scats, and for raccoons, which are fruit-eaters and utilize autumn scat as a foraging resource. Additionally, raccoons and other animals that use insects as a foraging resource were thought to also benefit from the

presence of insects such as centipedes, which are attracted to scat. Contrary to our prediction, very few scat feeders were observed. The few instances of foxes feeding on scat were associated with grass and sarcoptic scats. Regarding sarcoptic scat, it is likely that the foxes made secondary use of undigested foraging resources, as they were seen chewing. No utilization by insects, such as centipedes, was observed. Thus, scat does not seem to be an important foraging site for mesocarnivores.

Scats utilization as food resources by some birds and rodents

Seed dispersal is a crucial process for plant populations and community dynamics, and it has profound effects on ecosystem transitions (Wang & Smith, 2002) As bears are known seed dispersers, their scats are rich in undigested foraging resources and seeds. In this study, jays and rodents were the main scat feeders, with dent corn scat being particularly valuable as a foraging resource. In addition to dent corn, I presented scats containing undigested seeds and pericarp from monkey pear and pear, but no significant foraging behavior was observed.

Their foraging activity was most intense in the first few days after the cameras were installed, and during that time, the scats were mostly flattened and thinly dispersed. After the jays' usage decreased, other small birds began to use the scats. Presumably, jays and rodents act as predators (Janzen, 1986) immediately following the dispersal of excreted brown bear scat. Their flattening and clearing of the scat may also allow smaller animals access to the scat.

Dent corn is an agricultural crop that has been increasingly used by brown bears in recent years (Brown Bear Research Group of Hokkaido University, unpublished data). It is difficult for jays and rodents to directly utilize these crops on farmland, but it is likely

that a pathway exists in which brown bears spread the crops in the forest in the form of scat, which is then used by jays and rodents. After consuming the scat as temporary consumers, a cascade response was observed, in which smaller birds visited and foraged after the scat had been cleared into flat areas.

The treatment of scat as a foraging resource needs to be carefully considered. Although this study discusses scats other than dent corn scat in the same context, it is important to note that these scats may be perceived as very different resources by animals that use scat as a foraging ground.

Dual role of scats: communication hubs and feeding resources

This study showed the significant role of brown bear scats in mediating mammalian communication. In particular, the sniffing network revealed diverse interspecific interactions, suggesting that brown bear scats function as important hubs for facilitating interspecific communication. The presence of strong edge weights across various interspecific interactions further highlights the utilization of bear scats by a wide range of animal species. Conversely, the marking network primarily involved mesocarnivores, with behaviors such as overmarking observed on both conspecific and heterospecific scents. These findings indicate that brown bear scats play a critical role not only as sites for information exchange but also in shaping competitive interactions and resource use among carnivores.

Table 1. Target species and prediction

Taxon	Expected interactions with brown bears	Predicted response
Brown bear	Intraspecific communication	Attract
Sika deer	Prey	Avoid
Fox	Subordinal carnivora	Attract
Raccoon dog	Subordinal carnivora	Attract
Raccoon	Subordinal carnivora	Attract
Sable	Subordinal carnivora	Attract
Squirrel	No significant interaction	No interaction
Chipmunk	No significant interaction	No interaction
Other rodents	No significant interaction	Attract (feeding)
Birds	No significant interaction	Attract (feeding)

Table 2. Nine mammal species observed at brown bear scats captured by camera traps from 2022 to 2024 in the Teshio Experimental Forest, Uryu Experimental Forest, and Minami Furano. The percentage of each behavior relative to the total number of events.

Species	Events	Investigate	Urine	Scat	Coprophagy	Avoid
Bear	219	28%	2%	0%	0%	0.5%
Deer	1477	6%	0%	0%	0%	1%
Fox	464	15%	11%	1%	0.4%	0%
Raccoon dog	189	34%	10%	1%	0%	0%
Raccoon	115	20%	0%	0%	0%	0%
Sable	6	50%	17%	0%	0%	0%
Squirrel	22	0%	0%	0%	0%	0%
Chipmunk	8	0%	0%	0%	0%	0%
Rodents	91	10%	0%	0%	21%	0%

Table 3. Eighteen bird species observed at brown bear scats captured by camera traps from 2022 to 2024 in the Teshio Experimental Forest, Uryu Experimental Forest, and Minami Furano. The percentage of each behavior relative to the total number of events.

Family	Species	Events	Feeding
Phasianidae	*Tetrastes bonasia*	9	0%
Columbidae	*Streptopelia orientalis*	19	0%
Scolopacidae	*Scolopax rusticola*	6	0%
Corvidae	*Garrulus glandarius*	104	67.3%
Paridae	Poecile spp.	2	0%
Sittidae	*Sitta europaea*	2	50%
Turdidae	*Geokichla sibirica*	2	0%
	Turdus obscurus	1	0%
	Turdus pallidus	9	22.2%
	Turdus chrysolaus	7	0%
	Turdus eunomus	46	4.3%
	Turdidae spp.	2	0%
Muscicapidae	*Larvivora cyane*	1	0%
	Larvivora akahige	1	100%
	Tarsiger cyanurus	1	0%
Motacillidae	*Anthus hodgsoni*	1	0%
Fringillidae	*Spinus spinus*	2	0%
Emberizidae	*Emberiza personata*	4	50%

Table 4. Key Metrics of Four Interaction Networks. The table summarizes key metrics of four interaction networks, including network size, total edge count, intraspecific and interspecific weights, the node with the highest degree centrality (node name, centrality value, and edge percentage), the node with the highest betweenness centrality (node name and value), and the five strongest weighted edges (from, to, and weight).

Metric	receiving information	leaving information
Network Size	8	4
Number of Edges	25	9
Intraspecific_Weight	2.87	2.12
Interspecific_Weight	15.88	3.75
Highest Degree Centrality		
Node	Bear	Bear, Red fox
Centrality Value	11	6
Edge percentage (%)	44	67
Highest Betweeness Centrality		
Node	Bear	Bear, Red fox
Centrality Value	5	2
Top 5 heviest weighted Edges (From -> To, weight)		
1st	Red fox -> Red fox, 1.44	Red fox -> Red fox, 1.60
2nd	Sika deer -> Bear, 1.12	Red fox -> Bear, 1.01
3rd	Rodents -> Raccoon dog, 1.11	Raccoon dog -> Bear, 1.00
4th	Bear -> Bear, 1.07	Raccoon dog -> Red fox, 0.38
5th	Raccoon -> Bear, 1.06	Raccoon dog -> Raccoon dog, 0.33

Figure 1. Camera trap monitoring system.

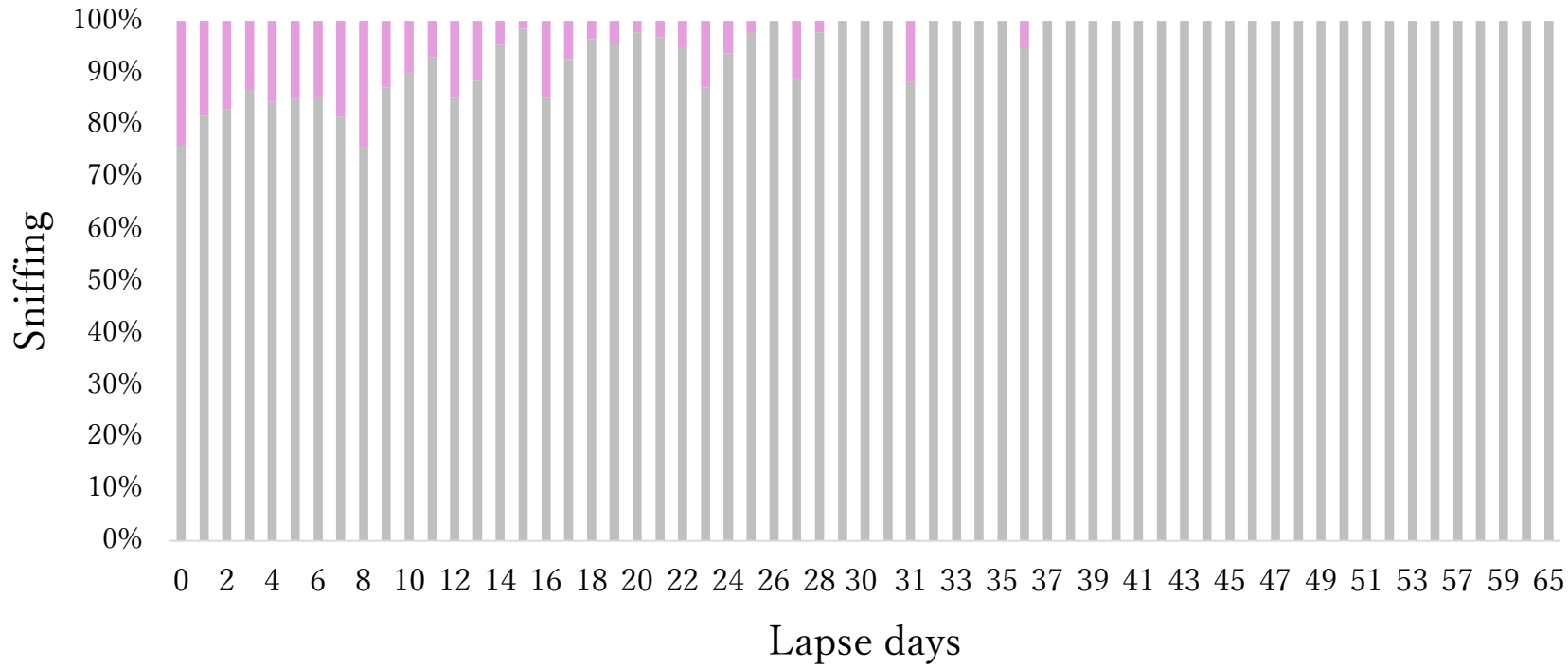

Figure 2. This figure illustrates the temporal decline in sniffing response to scats across all recorded mammal species. The x-axis represents the number of days elapsed since the onset of observation (Lapse days), while the y-axis denotes the proportion of events in which sniffing behavior was detected. The pink bars indicate the percentage of events in which sniffing was observed. Over time, the probability of sniffing responses exhibited a progressive decline, with detections becoming negligible beyond 30 days post-deposition.

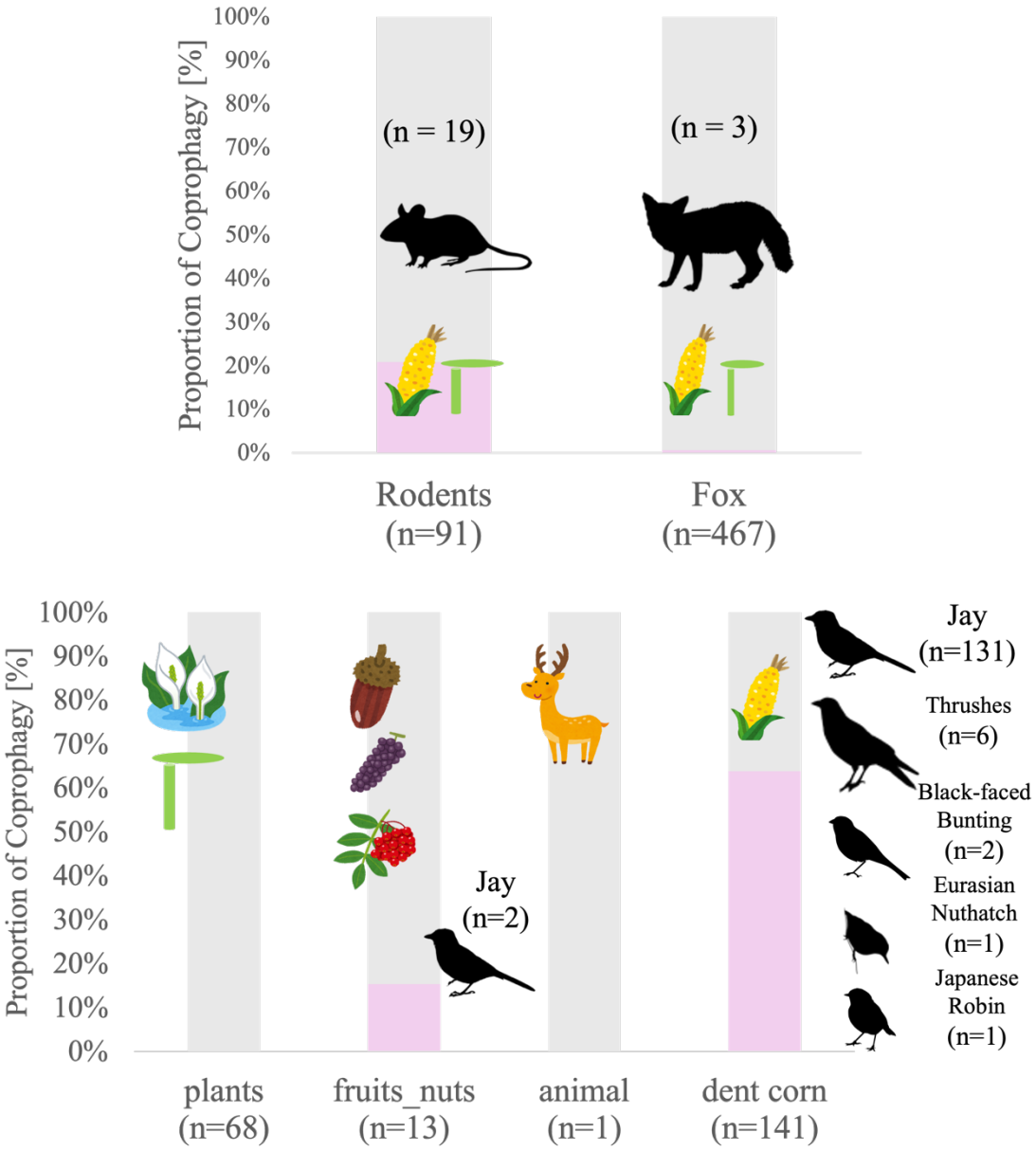

Figure 3. The figure illustrates the number of coprophagy events and the scat contents consumed by animals. The upper graph represents the proportion of coprophagy events in mammals, showing the percentage of coprophagy events relative to the total observation events for each animal group (rodents and foxes). The bar graph aggregates all foraging resource events. The lower graph represents the proportion of coprophagy events in birds**,** showing the percentage of coprophagy events relative to the total observation events for each scat content category (plant material, fruits and nuts, animal material, and dent corn).

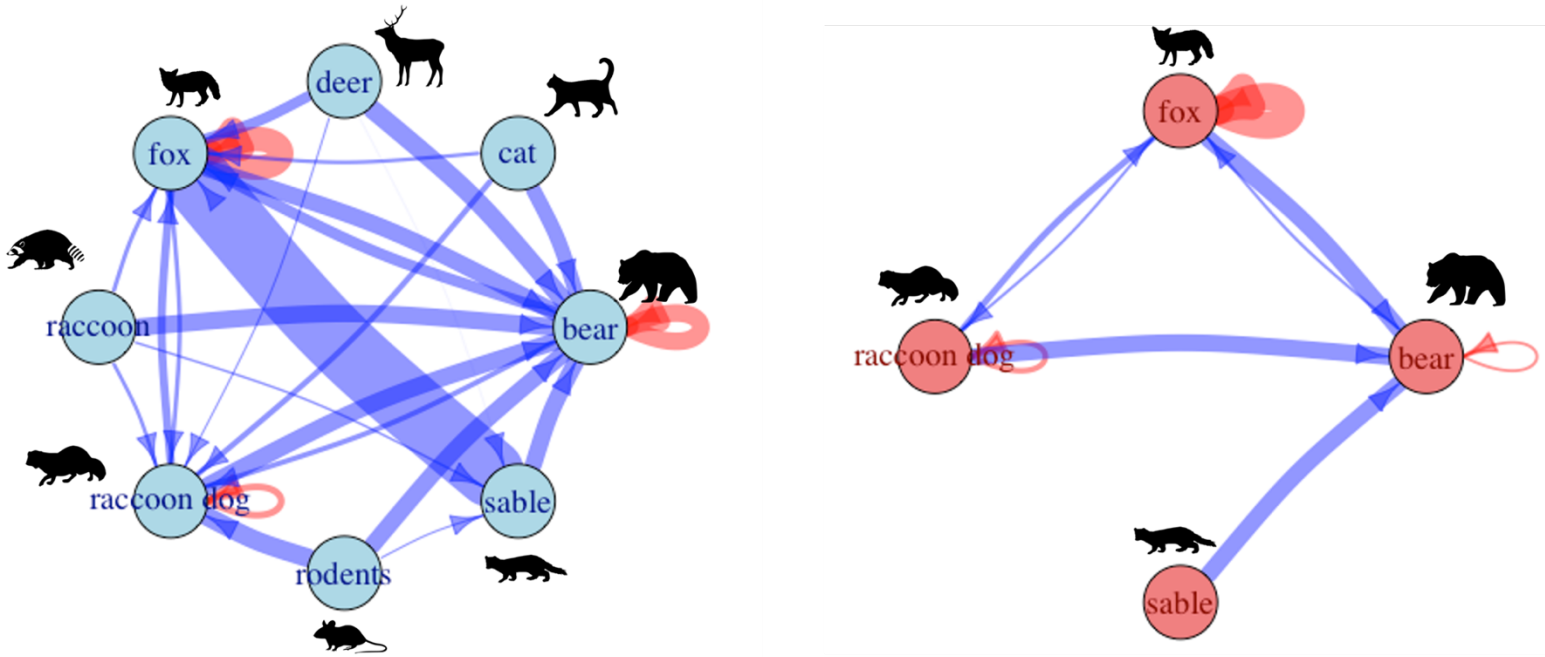

Figure 4. Intra- and interspecific networks centered on brown bear scats. The networks represent interactions centered on brown bear scats, highlighting intra- and interspecific behaviors. The left panel illustrates the network for "receiving information" behaviors, while the right panel depicts the network for "leaving information" (overmarking) behaviors. Blue edges indicate interspecific interactions, while red self-loops represent intraspecific interactions.

IV. General Discussion

4.1. Networks in forest communities: "societies" formed by mammalian and avian populations

In this doctoral thesis, I examined the intra- and inter-specific networks centered around brown bear marking sites, which function as key ecological structures within forest communities. Additionally, I investigated the potential role of bear scat as a more ephemeral network hub, providing an alternative mode of information transfer. The results revealed that a wider range of species than previously recognized utilize these hubs for both communication and resource acquisition.

Both bear marking sites and scat serve as visually and chemically prominent multimodal signals that mediate interactions among various taxa. These hubs play crucial roles in predator-prey interactions, such as sika deer "eavesdropping" on brown bear information and dominant breeding males overmarking sites to assert their status. Within carnivore guilds, subordinate mesocarnivores access information, overmark, or rub to signal dominance or to mitigate predation risk. Rodents occasionally engage with these sites, potentially for predator avoidance or to utilize scent resources left by bears. Additionally, birds are also drawn to these locations, likely for foraging purposes. These findings highlight that brown bear marking sites function as ecological interaction hubs, structuring the broader network of species interactions within Hokkaido's forest communities (**Fig. 1**).

Mammals exhibit a remarkable diversity of social structures, including solitary lifestyle, pair bonding, extended family groups, and cooperative or communal breeding (Burda et al., 2000; Clutton-Brock, 1997). Understanding the evolution of these social systems has been a major focus in behavioral ecology, as it also provides insights into the

dynamics of human society (Lukas & Clutton-Brock, 2017; Thierry et al., 2000). Traditionally, a "society" has been defined as "a group of individuals belonging to the same species and organized by a community"(Wilson, 1975). However, recent studies have increasingly shown that carnivores and ungulates communicate with different species through diverse signals (Jones et al., 2016; Parsons et al., 2018). These interspecific interactions may be as significant—if not more significant—than intraspecific interactions, suggesting that carnivores form a "society" that transcends species boundaries (Apps et al., 2019). While the full ecological benefits of these interactions remain unclear, it is plausible that they enhance survival by providing access to predator information, reducing predation pressure, and increasing reproductive opportunities.

Furthermore, carnivores, ungulates, birds, rodents, and other species that appear to lack direct interactions were also found to engage in indirect communication. Visiting brown bear sites may provide these species with chemical signals and foraging resources, thereby enhancing their adaptability. The interplay between communication networks and food webs likely contributes to the complex structure of forest communities. These findings suggest that sympatric mammals and birds are not just neighbors but may actively respond to each other's presence, shaping their interactions bared on shared environmental cues and resources. The "society" within each species may thus interact dynamically to sustain the broader ecological network.

Many of these interactions involve one-way information transfer, such as "eavesdropping". It remains debatable whether such one-way information transfer constitutes true communication. Communication is generally defined as a process in which a sender transmits a signal that influences the recipient's potential for subsequent

action (Dudzinski et al., 2009). However, diverse and complex communication systems exist in nature, and evidence from terrestrial and aquatic taxa strongly suggests that various forms of one-way information transfer occur through acoustic, visual, and chemical cues or signals (Apfelbach et al., 2005; Clapham et al., 2014; Doyle et al., 2011; Herman, 2017).

4.2. Scat as an immediate signal supplementing fixed-site communication

Scat, as a transient remnant, functioned as an important communication tool for brown bears and other species. Unlike fixed marking sites, which are revised and reinforced over time, scat is dispersed throughout the environment, enabling more immediate and flexible communication. While the use of latrines as olfactory information sources has been well-documented across various species (Buesching et al., 2016; Kaneko et al., 2009; T. W. King et al., 2017; Marneweck et al., 2018; L. K. Page et al., 1998; Vitale et al., 2020; Yamamoto, 1984), the roles of randomly dispersed scats, such as those of brown bears, in natural setting remains poorly understood. Scats likely function as ephemeral chemical signals, conveying information that influences interactions among both conspecific and sympatric species.

Despite its role in chemical communication, scat represents a transient resource, and its significance as an informational cue may not be as strong as that of fixed marking sites. For example, sika deer, a primary prey species expected to show strong responses, exhibited minimal reactions to scat compared to marking sites. They often passed by scat without noticing it and only stopped when their noses were close to it. While bear scats may be large enough to be noticeable to humans, they may not always be sufficiently prominent to consistently capture the attention of animals.

Scat, while functioning as a source of information, is also rapidly consumed by certain taxa, particularly rodents and birds, thereby limiting its longevity as a chemical signal. This suggests that the secondary resource use by rodents and birds may inhibit scat-mediated interactions among carnivores and ungulates. Scat with high foraging value likely degrade more quickly than those with lower foraging nutritional content. Understanding how animals respond to different types of scat —whether through counter-marking, selective avoidance, or immediate consumption—could offer deeper insights into the role of feces in mammalian communication networks.

4.3. Scat as a vector for nutrient transfer

Beyond its role in communication, brown bear scat serves as a pathway for nutrient transfer between agricultural lands and forest ecosystems. In the study area, brown bears heavily rely on dent corn as a primary food source in autumn, consuming large quantities in agricultural fields before retreating to forested areas. As a result, their scats contained substantial amounts of undigested corn, effectively transporting high-energy resources from farmland to the forest. This movement of nutrients via scats represents a critical, yet often overlooked, ecological function of brown bears.

The deposition of nutrient-rich scats in forest environments may have cascading effects on local wildlife. Birds and rodents, already known to forage on undigested seeds within carnivore scats (Koike et al., 2012; K. Page et al., 2001), likely benefit from the introduction of dent corn into forest habitats, This secondary resource use may after their foraging behaviors, distribution patters, and even population dynamics. Furthermore, the spatial redistribution and plant community structure mediated by seed dispersal (Johnson

et al., 2018; Perea et al., 2021; Seidler & Plotkin, 2006), potentially supporting the growth of opportunistic plant species.

Although bears have long been recognized as seed dispersers, their role in transporting cultivated crops into natural ecosystems highlights an anthropogenic dimension to this process. The increasing reliance of brown bears on agricultural food sources raises important questions about ecological consequences of this interaction, particularly in regions where human-wildlife conflicts are intensifying. Understanding the extent to which bear-mediated nutrient transfer affects forest communities could provide valuable insights for both conservation and land management strategies.

4.4. Interspecies communication in forest ecosystems

4.4.1. The role of brown bears and the forest environment in facilitating interactions

Resent advances in mammalian semiochemistry have highlighted the widespread presence and ecological significance of interspecific communication. These interactions play a critical role in shaping ecosystem processes and structures, suggesting their relevance for conservation and management strategies (Apps et al., 2019).

Forest environments, characterized by limited visibility compared to open habitats such as savannas and grasslands (Edwards et al., 2022), may promote the development of interactions mediated through chemical signals rather than visual cues. Marking sites and scats, in particular, act as key sources of olfactory information in such environments, facilitating interspecific communication.

This study detected more interspecies interactions compared to previous studies (Edwards et al., 2022), not only among birds and small rodents but also involving carnivores and even-toed ungulates. These interactions may be driven in part by the

behavioral ecology of brown bears, which, unlike apex predators, exhibit relatively low predation pressure on sympatric species. While apex predators create strong risk-averse behaviors among mesocarnivores and prey species, the primary prey of brown bears in the study area is sika deer, reducing direct predation threats to smaller carnivores and rodents. As a result, species that would typically avoid large carnivores may utilize brown bear marking sites with greater frequency.

Additionally, brown bears are behaviorally versatile omnivores that occupy a broad range of habitats across the Northern Hemisphere. Their marking behaviors, dietary preferences, and site selection strategies may influence the structure of interspecific interactions in different ecosystems. In Hokkaido, brown bear marking sites served as central hubs where multiple taxa converge, utilizing these locations for both communication and resource acquisition. A comprehensive assessment of marking site use across various environments and ecological communities would provide deeper insight into the role of brown bears in forest ecosystems.

4.4.2. Beyond Information exchange: the microbiome and physiological interactions

Interspecific interactions at marking sites and scat and latrine locations could extend beyond the mere exchange of chemical signals and resource use; they may also facilitate microbial transmission between species. The microbiome, particularly gut and skin-associated microbial communities, plays an increasingly recognized role in animal metabolism, immunity, and overall health. Through physical contact, olfactory investigation, and coprophagy, microbial communities can be exchanged among individuals, forming interconnected microbial metacommunities (Sarkar et al., 2020).

Both positive and negative aspects of microbiota transmission can be anticipated.

On the positive side, the acquisition of advantageous gut bacteria may enhance digestive efficiency, expand dietary flexibility, and strengthen immune responses (Koch & Schmid-Hempel, 2011; Sarkar et al., 2024). Additionally, the transmission of symbiotic microbiota might contribute to the evolution of sociality, as seen in primates where physical contact among social partners influences gut microbiome composition (Amato et al., 2017; Lombardo, 2008; Troyer, 1984)

Conversely, microbial exchange also raises the risk of pathogen transmission (Sarkar et al., 2020, 2024; Stephens et al., 2019). Unlike intraspecific pathogen spread, interspecific transmission can lead to broader disease outbreaks, potentially impacting multiple taxa simultaneously (Craft et al., 2008; Mollentze et al., 2020). This raises concerns that pathogens originating from brown bears may negatively affect visiting species, reducing their fitness (Sepúlveda et al., 2014) Interestingly, species with higher pathogen resistance may frequent these high-risk sites more often, while more vulnerable species tend to avoid them (Weinstein et al., 2018). Testing this hypothesis by analyzing pathogen prevalence in species utilizing these sites could offer new insights into disease ecology and interspecific network dynamics.

4.5. Future directions in understanding interspecific communication

4.5.1. Investigating micro-olfactory environments

One critical approach involves investigating the spatial distribution of scent cues at marking sites. Odor accumulation is likely non-random, with certain locations acting as scent hotspots. The choice of marking locations may depend on factors such as odor detectability, persistence, and diffusion patterns (P. Apps et al., 2019; Maja Mohorović & Miha Krofel, 2021; Nie et al., 2012). Future studies should assess how different species

interact with these scent deposits, examining which areas of marking sites are most frequently visited and how species-specific behaviors influence scent accumulation.

Based on the spatial distribution of scent-marking behaviors, I hypothesize that even within the confines of a brown bear marking site, micro-olfactory landscape likely exists, with distinct odors dispersed across different substrates. Pedal marks (Revilla et al., 2021; Sergiel et al., 2017) and urine scent trails on the ground may signal the presence of marking tree before direct interaction with the trunk. The tree itself, discolored and scented due to dorsal gland secretions (Tomiyasu et al., 2018), carries strong olfactory cues that could persist over time (Clapham et al., 2013; Green & Mattson, 2003). Behavioral observations indicate that brown bears follow a sequential marking routine—sniffing the ground, inspecting the tree from its base upward, and engaging in overmarking behaviors such as rubbing, urination, and pedal marking (Clapham et al., 2014). In contrast, mesocarnivores tended to approach trees in a linear manner, primarily sniffing at nose level and counter-marking at similar heights (personal observation). Foxes, raccoons, and sables frequently defecated near marking trees (personal observation), creating additional scent layers that may influence subsequent visitors.

4.5.2. Time-series analysis of cross-specific interactions

A second approach involves time-series analysis to decipher the dynamics of interspecific communication. Determining whether counter-marking and scent-sniffing behaviors are triggered by the scent of a preceding visitor (interspecific response) or an individual of the same species (intraspecific response) can clarify the functional role of brown bear marking sites. Identifying the sequence of visitors and their interactions could provide

insights into whether chemical signals trigger cascade effects, where one species' behavior influences subsequent interactions by others.

For instance, observations of raccoon dogs and foxes sniffing and counter-marking sable scat suggest hierarchical scent-mediated interactions at bear marking sites. However, distinguishing the full sequence of interactions in natural settings remains challenging, as prior visitors often leave undetectable traces. This limitation could be addressed through controlled experiments—introducing cleaned trees with artificially applied brown bear scents to replicate natural marking sites and examining animal responses under controlled conditions.

4.5.3. Captive experiments: unrevealing the complexity of olfactory communication

Captive experiments provide an opportunity to investigate the nuances of scent communication under controlled conditions (Janda et al., 2019; Swaisgood et al., 2002). I hypothesize that behavioral assays could provide insights into captive animals' responses to scent samples collected from wild marking sites, allowing researchers to measure reactions such as scent-sniffing duration, counter-marking frequency, and avoidance responses.

These experiments could also clarify the function of counter-marking in different species. By presenting brown bear scent to mesocarnivores and prey species (e.g., owls, foxes, and squirrels), it may be possible to determine whether brown bear odor serves as an antipredator cue or influences mate selection. Such findings would enhance our understanding of how chemical signals chape social interactions across taxa (e.g., Kobayashi, 2000).

4.5.4. Advances in chemosensory research

Recent studies have adopted integrative approaches, combining genetic, cellular, and behavioral analyses to deepen our understanding of olfactory and gustatory systems (e.g., Murata et al., 2014; Uenoyama et al., 2021; Katsushima et al., 2024). Beyond behavioral assays, molecular techniques such as metabolomic analyses of gland secretions and excretions, are essential for identifying the neural mechanisms underlying scent-mediated behaviors (Clapham et al., 2023; Sergiel et al., 2017; Tomiyasu et al., 2018). These methodologies will help clarify the chemical components foundations of heterospecific interactions.

4.5.5. Automated monitoring of olfactory communication

A final approach involves refining the use of automatic cameras and remote sensing technologies to monitor animal behavior at scent sites (Apps et al., 2019). Unlike direct visual observations, which are limited in scope, automated systems allow researchers to track how scent cues influence animal movements over time. However, improved camera placement and scent-tracking methodologies are necessary for optimized these studies (Apps et al., 2019).

To supplement static camera data, the deployment of GPS collars and accelerometers on animals (Barwick et al., 2018; Lesmerises et al., 2015) could provide additional insights into delayed behavioral responses to olfactory cues. By analyzing post-scenting activity, researchers can determine whether scent detection alters movement patterns, territory usage, or interactions with other species. This integrative approach would provide a more comprehensive picture of how olfactory signals shape ecological interactions across different taxa.

4.6. Implication for large mammals' managements

Conflicts between large wild animals and humans have increased globally in recent decades. Due to their substantial body size and high energy demands, large carnivores serve as the most influential apex predators, playing a critical role in regulating ecosystem functions (Ripple et al., 2014). Large carnivores are also particularly vulnerable to human activities (Darnell et al., 2014; Löe & Röskaft, 2004; Woodroffe et al., 2005), and bears are no exception. Of the nine bear species, six are threatened with extinction due to habitat and food competition with humans (Penteriani & Melletti, 2020). The global population and distribution of the brown bear have declined by more than 50% since the mid-1800s due to overexploitation, habitat loss, and the fragmentation of remaining populations into small, isolated groups (Servheen, 1990)

In Hokkaido, the focus area of this study, human-bear conflicts have risen sharply over the past decade (Sato, 2017). Identifying and preserving the new ecological functions created by these animals' behaviors is critical for maintaining rich ecosystems before these functions are irreversibly lost (Tomita & Hiura, 2020; Tomita & Hiura, 2024). In the context of mammalian ecological roles, brown bears function as apex predators, exerting top-down control on prey populations (Dorresteijn et al., 2015; Levi et al., 2012; Tallian et al., 2017). As large-bodied omnivores, they also consume substantial biomass of herbaceous vegetation during spring and summer, influencing plant community dynamics (García-Vázquez et al., 2018; Rode et al., 2001). The findings of this study further highlight their roles as ecosystem engineers, creating foraging sites and communication hubs that structure interspecific interactions (Chapter 2, 3). Additionally, brown bears contribute to seed dispersal, both directly by transporting seeds and indirectly by facilitating secondary seed predation by other species (Chapter 3, Koike et

al., 2012). Furthermore, their movement between agricultural landscapes and forests mediates nutrient transfer, redistributing high-energy resources and potentially influencing trophic interactions and ecosystem nutrient cycling (Chapter 3). Forest managers can help protecting forest biodiversity by conserving key sites such as marking sites and other areas critical for interspecies communication (Zyśk-Gorczyńska et al., 2015).

Understanding wildlife distribution patterns across various spatial and temporal dimensions is essential for identifying ecological hotspots and advancing effective conservation strategies (Hu et al., 2025). Retaining trees during logging to conserve biodiversity is becoming an increasingly common practice in forestry (Gustafsson et al., 2012, 2020). Prioritizing the conservation of hotspots, such as brown bear marking sites, could significantly contribute to maintaining biodiversity by preserving critical locations for animal interactions within the environment.

Biodiversity assessments often rely on indicator species or species assemblages whose populations can be reliably quantified and monitored (Landres et al., 1988; Simberloff, 1998; Thomson et al., 2005) Brown bear marking sites, which have been found to attract multiple phylogenetically distinct species (e. g., woodpecker: Drever et al., 2008), may provide a quantitative assessment of mammal and bird diversity within a forest community. Additionally, the aggregation of multiple species at brown bear marking sites presents a potential strategy for population management. These sites could function as natural "super-lures" (Linklater et al., 2013), attracting brown bears and other target species to facilitate conservation efforts, ecological monitoring, or controlled interventions. Conversely, chemical cues collected from these sites could be strategically deployed to other locations to manipulate the spatial distribution of species that exhibit

avoidance responses to bear-associated odors, thereby contributing to habitat management and mitigating human-wildlife conflicts.

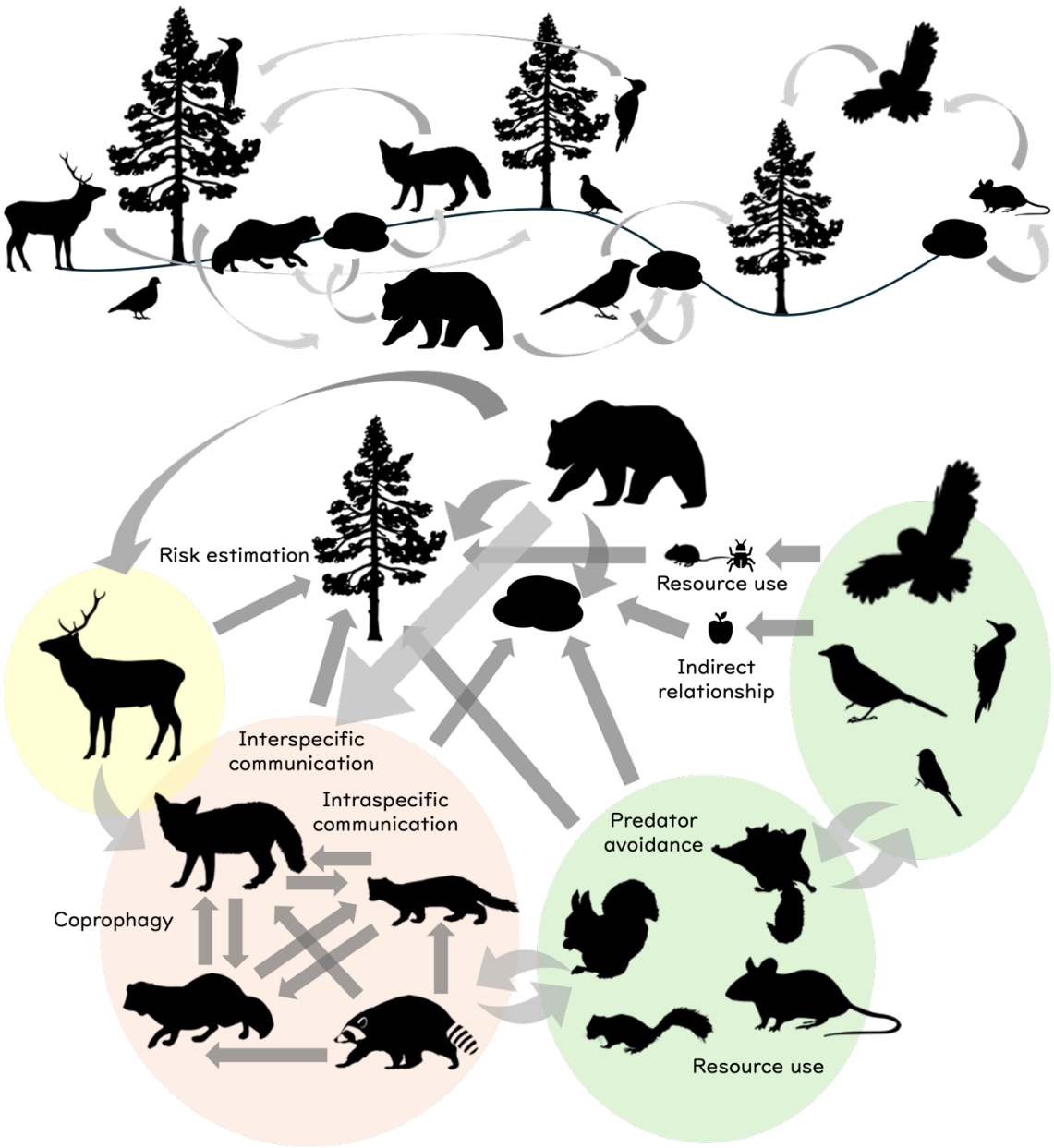

Figure 1. Conceptual diagram illustrating the communication and resource network facilitated by brown bear marking sites and scats.

V. Summary

Mammals create specific marking sites, such as rubbing trees and communal latrines, for intraspecific communication. By leaving chemical signals through scent gland secretions or scats and urine, as well as visual signals through body rubbing or claw marks, they exchange information with spatially and temporally distant individuals. This is particularly important for solitary carnivores, functioning as essential strategies for maintaining social structures, including mate selection and dominance hierarchies. These conspicuous sites facilitate energy-efficient communications among conspecifics.

Recent technological advancements and reduced costs of automatic camera traps have led to an increase in reports of different species visiting marking sites created by other species. However, many of these reports are fragmented and descriptive, and few studies have quantitatively assessed the purpose of visits by different species. Traditional observations have mainly focused on interactions within carnivore guilds or between apex predators and their prey, while the use of marking sites by a broader range of species, such as small mammals and birds, has been overlooked. The purposes of visits by different species are likely to be multifaceted, involving both communication and the use of foraging resources. Therefore, it is essential to broaden the scope to include groups that are expected to visit for foraging purposes and to detect a wide range of interactions. Furthermore, past observations have primarily focused on fixed sites, such as marking trees communal latrines, but the role of typical isolated scat—a resource with similar functions, scattered incidentally in the environment—has not been given much attention. Interspecific interactions around carnivore marking sites and isolated scats may be more common than previously thought and may have cascading effects on ecosystem processes and structure.

This doctoral thesis used the brown bear, the largest terrestrial mammal in the Northern Hemisphere, as a model species to elucidate the roles of marking sites and isolated scats in forest communities from the perspectives of chemical communication and resource use. The conspicuous marking sites and scats created by brown bears are easily observable. Given that their expansive home ranges overlap with various taxa such as ungulates, mesocarnivores, rodents, and birds, it is expected that these interactions can be detected.

In Chapter 2, a field experiment was conducted using artificial control sites similar to marking sites to investigate how brown bear marking sites were utilized by animals in the forest. Over two years of automatic camera trapping, a total of more than 4,900 events from 15 mammal and more than 39 bird species were recorded. It was found that all mammal species obtained some form of information from the marking sites. Sika deer, a potential prey of brown bear, obtained information about the predator, and mesocarnivores like red foxes and raccoon dogs used the sites, probably for intraspecific communication through scent marking and counter-marking. Additionally, rodents exhibited scent sniffing behavior only at the marking sites. Though rare, red foxes and Ezo squirrels were observed rubbing their bodies on the sites shortly after brown bear visits. This behavior may help them gain benefits, such as predator avoidance or mate selection, by acquiring the scent of brown bears. Moreover, a network analysis showed much higher species interactions at bear marking sites compared to control sites. Birds also visited the marking sites more frequently than control sites, primarily for foraging purposes. Foraging behavior was observed at the trunks and on the ground by a variety of bird species, including jays, thrushes, woodpeckers, and owls. These observations suggest a cascade reaction, where the landscape created by brown bears (e.g., bark

stripping, exposed ground, ammonia buildup) becomes an attractive foraging environment for insects and rodents, thus attracting birds as well.

In Chapter 3, a field experiment was conducted by placing brown bear scats and automatic camera traps to investigate whether the scats are utilized as a resource for intraspecific and interspecific communication, as well as for foraging. Over a period of three years, more than 3,000 events by at least 13 mammal species and 17 species from 11 bird families were recorded. Brown bear often sniffed and counter-marked on the scats, suggesting that they use the chemical signals of scats for intra-specific communication. Although infrequent, deer were observed obtaining information about the predator (brown bear) from the scat, exhibiting avoidance behavior. Mesocarnivores, such as red foxes and raccoon dogs, frequently sniffed the scat and engaged in counter-marking behaviors using urine and scats, suggesting that they also use brown bear scat for intraspecific communication. Rodents and jays frequently utilized the scat as a foraging resource. The high value of the scat, particularly due to the presence of undigested seeds, was highlighted. Additionally, red foxes were also observed consuming small amounts of scat.

Based on these findings, it has become clear that brown bear marking sites in the forests of Hokkaido function as a hub for interactions among a broader range of taxa than previously thought. By visiting these sites for both information acquisition and resource use, apex predators, their prey (e.g., ungulates), medium-sized carnivore, rodents, and even birds all intersect at these marking sites. This suggests that brown bear marking sites act as a central hub for cross-species interactions.

Additionally, scat was indicated to serve as an important communication tool for maintaining both brown bear and other species' social structures. Scat, with its random

and temporary nature, may play a complementary role in communication by supplementing the interactions that occur at fixed sites, such as marking sites.

This thesis has revealed the extensive animal community associated with brown bear marking sites; however, the complex interactions within this community remain unclear. Future research should include detailed time-series analyses of the behavior of the species that perform the marking and the individuals that visit afterward. Additionally, controlled scent presentation experiments in captive settings are expected to help clarify the behavioral response mechanisms to odors. Furthermore, to complement the field of view of automatic camera traps and investigate broader and more delayed effects, combining remote monitoring via GPS with these cameras will allow for a deeper understanding of animal decision-making and interspecific communication.

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VII. References

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