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Increased brown bear predation on sika deer fawns following a deer population irruption in eastern Hokkaido, Japan

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Abstract By the 1970s, brown bears (*Ursus arctos*) in Hokkaido, northern Japan, were opportunistic omnivores that mainly depended on plant materials. Because the sika deer (*Cervus nippon*) population irrupted in eastern Hokkaido in the 1990s, we expected that brown bears might prey on sika deer fawns. First, we developed a simple and cost-effective method of monitoring possible bear predation on deer fawns by analyzing the widths of deer hairs remained in bear scats. Based on hair thickness standards, we distinguished the brown bear consumption of deer fawns from adults by analyzing bear scats ($n = 108$) collected during the deer birthing season (late May–late July) in 1999–2008. To evaluate the importance of fawns to bears, we compared the occurrence of fawn and adult deer hairs in bear scats among three periods (I, 1999–2000; II, 2003–2005; III, 2006–2008) in eastern Hokkaido. The occurrence of fawn hairs in bear scats increased from 12.5 to 27.3 % in volume and from 6.3 to 33.6 % in frequency from period I to period III, whereas adult hairs in scats decreased from 42.8 to 26.1 % in volume and from 34.4 to 22.7 % in frequency during the same time. These data suggest that bears increasingly preyed on deer fawns after the deer population irruption and decreasingly used adult carcasses because of the enforcement of deer carcass treatment by the Hokkaido government.

Keywords *Cervus nippon* · Predation · Neonates · Food habit · *Ursus arctos*

Introduction

Omnivores are generalist consumers that can feed on animals with dynamic distributions and on plants with static distributions (Bastille-Rousseau et al. 2011). As such, they can adjust to the changing availability of food resources, unlike obligate herbivores and carnivores (Zager and Beecham 2006). This ecological plasticity of omnivores allows them to occupy different trophic positions depending on environmental conditions (Stenroth et al. 2008).

Ursidae, with the exception of polar bears (*Ursus maritimus*), have a wide range of feeding habits, including herbivory, omnivory, and insectivory (Christiansen 2008). More than other ursids, the brown bears (*Ursus arctos*) have broad ecological plasticity and the ability to adapt to changing ecological conditions; therefore they range more widely than any other bear species (Servheen 1990; Stirling and Derocher 1990). Until the 1980s, brown bears had not been considered to be aggressive predators (Herrero 1985) but rather opportunistic omnivores, feeding mostly on plant matter and carcasses (Craighead and Craighead 1972; Mealey 1980; Servheen 1983). In recent studies, changes in the foraging behavior of brown bears were reported. For example, in northeastern Norway, bears attacked adult moose (*Alces alces*) as their most important food item under conditions of deep snow in spring, and yearlings in poor condition and pregnant cows (Persson et al. 2001). However, most studies on bear ecology in North America and Europe have revealed that brown bears were important predators of ungulate neonates, and bear predation could be a significant greater source of neonate than adult mortality (Ballard 1992; Ballard and Van Ballenberghe 1998; Persson et al. 2001; Zager and Beecham 2006; Swenson et al. 2007; Blanco et al. 2011). In North America, significant increases of prey

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populations and changes in the learned behavior of bears were suggested to have caused the changes foraging behavior (French and French 1990; Gunther and Renkin 1990).

On Hokkaido, the northern island of Japan, brown bear and sika deer (*Cervus nippon*) occur in the same habitat. Wolves (*Canis lupus*) were extirpated from the island by 1890 (Inukai 1993), and the brown bear is now the only large carnivore and is a potential predator on sika deer. Bears range over about 60 % of Hokkaido (Hokkaido Institute of Environmental Sciences [HIES] 2004), an area that roughly corresponds to the island's forested area (55,400 km²). Population numbers in the 1990s were estimated at 1,771–3,628 based on interviews with hunters (HIES 2000).

By the mid-1880s, the deer population had declined to threatened levels and its distribution shrank to a limited area due to overharvest and heavy snowfalls. However, the population recovered rapidly and by the 1990s had expanded into its former range and become well established in eastern Hokkaido. The population's rebound can be attributed to long-term legislative protection and favorable habitat alterations, such as the creation of conifer plantations and pasture (Kaji et al. 2000). Recently, the deer population has been irrupting in eastern Hokkaido with range expansion and a rapidly increasing population in western Hokkaido as well (Uno et al. 2009; Kaji et al. 2010). This deer range expansion has led to increased agricultural and forest damage. In response, starting in 1998, the Hokkaido government has promoted aggressive population control (Kaji et al. 2010). However, hunters often left the deer carcasses, with meat and fur, in the fields after shooting them (HIES 2000; Lead Poisoned Eagles Network 1999, 2000, 2001).

Until the 1980s, brown bears in Hokkaido were considered to be opportunistic omnivores that mainly depended on plants and used little or no meat materials (Ohdachi and Aoi 1987; Yamanaka and Aoi 1988). Sato et al. (2004, 2005), however, suggested that bears began to consume deer carcasses throughout the year in eastern Hokkaido in the mid-1990s. We would expect that bear predation on fawns might occur in eastern Hokkaido in response to the range expansion and population irruption of sika deer, as has been shown in similar circumstances in North America (French and French 1990; Gunther and Renkin 1990). By monitoring bear predation on sika deer fawns, we can address changes in an omnivore's foraging behavior.

Studies of bear predation on ungulates in North America and Europe were based on direct observations (French and French 1990; Gunther and Renkin 1990; Blanco et al. 2011), observations of carcasses eaten by radio-collared bears (Bull et al. 2001), or the monitoring of neonatal mortality caused by bears (Zager and Beecham 2006; Swenson et al. 2007). However, direct observations are labor-intensive and extremely difficult with Hokkaido brown bears, because these bears inhabit dense forests with poor visibility, and monitoring the

causes of neonatal mortality costs a great deal. Therefore, we needed to develop a simple and cost-effective method for continually monitoring the possibility of bear predation on fawns.

The objectives of our study were (1) to develop a simple and cost-effective method of monitoring possible bear predation on deer fawns, and (2) to address whether there was a relationship between the deer population irruption and the bear predation on deer fawns.

Study area

The Urahoro region is a district forest belonging to the Hokkaido government and is located at the foot of Shiranuka Hill (100–700 m above sea level) in eastern Hokkaido, Japan (Fig. 1; 42°N and 143°E; 431 km²). From 1999 to 2008, the mean annual temperature was 6.4 °C, annual precipitation, including snowfall, was 966.4 mm, and the maximum snow depth was 54 cm in the center of the town of Urahoro, southwest of the study area (Japan Meteorological Agency 2011). Natural forest covered 81.4 % of the area, while 12.6 % was coniferous plantations (Sato et al. 2008). The entire study area was crisscrossed with a high density of trails (21 km/ha) and we established transect routes for sampling bear scats along them. The Urahoro region was used for agricultural field crops to the west of Urahoro Town and pasture to the east of Onbetsu in Kushiro City and Shiranuka Town.

The study area has had abundant sika deer since the 1990s (HIES 2006). Parturition of sika deer mainly occurred from the end of May to the end of June (Suzuki et al. 1996). Female deer typically gave birth to a single fawn and had pregnancy rates higher than 90 % (Kaji et al. 2010). In eastern Hokkaido, nuisance control occurred from the beginning of April to the end of October and hunting took place from the end of October to the end of March to prevent agricultural damage and to manage the deer population. The deer population increased from 1992 to 1998 and peaked around 1998. Afterwards, it decreased temporarily but recovered to almost to 1993 levels by 2005 (Kaji et al. 2010).

In the summer of 1978, brown bears in the study area depended on herbaceous plants, with no evidence of deer or crop consumption (Sato et al. 2004). By 1999–2000, while herbaceous plants were still common, crops such as sugar beets and corn became common in the study area; deer carcasses left in these fields from nuisance control and hunting became available to bears year round (Sato et al. 2004).

Materials and methods

Discriminating between fawn and adult sika deer based on hair thickness

Studies on the diets of wolves were able to distinguish between neonate and adult ungulate remains in wolf

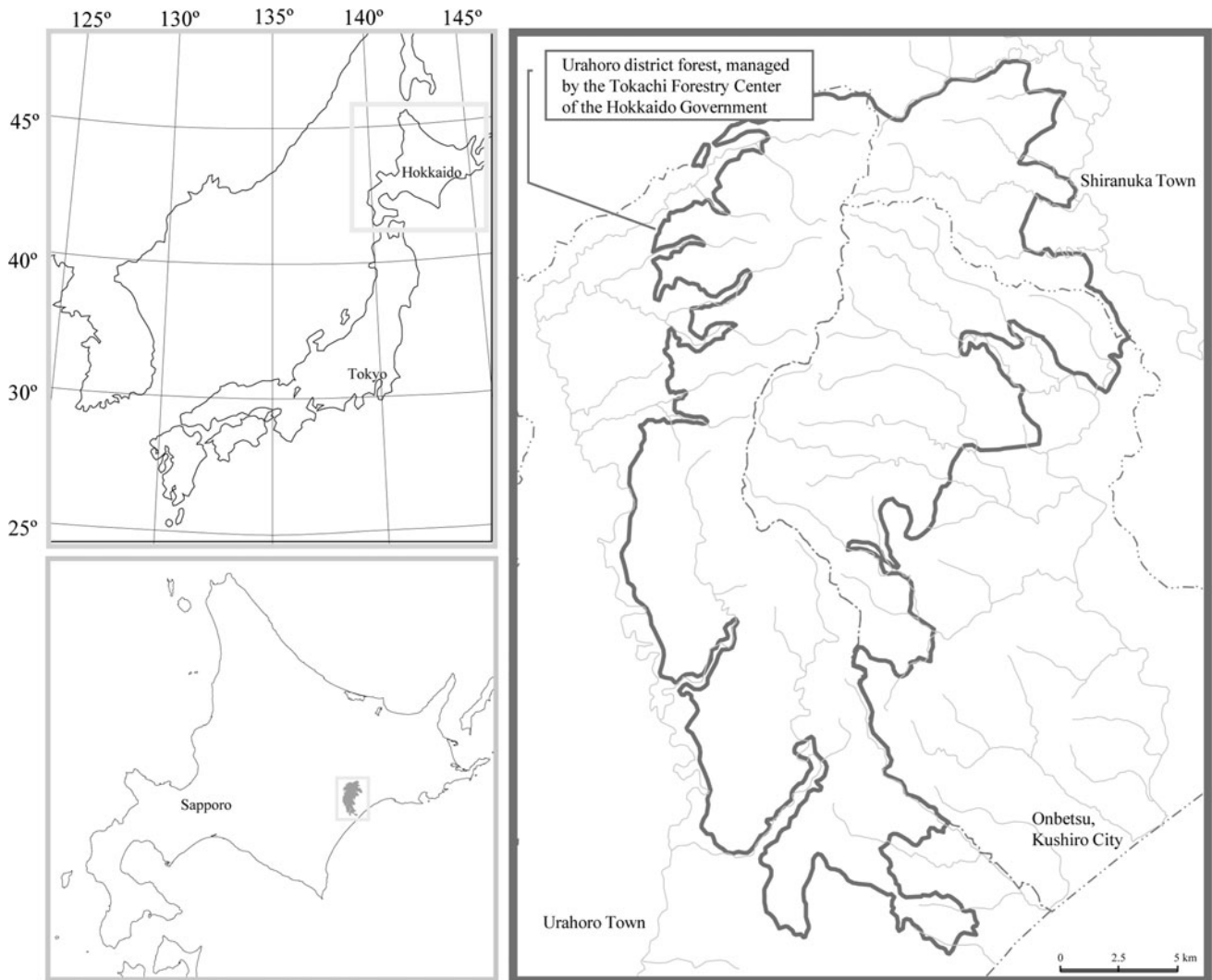


Fig. 1 Location of the study area. The *black solid line* in the right-hand figure indicates the Urahoro District Forest, which is managed by the Tokachi Forestry Center of the Hokkaido

government. *Gray lines* indicate major rivers. Transect routes were established throughout the study area

scats based on hair length, thickness, shape, or color, as well as the degree of bone fusion and closure of epiphyses aided the analysis (Gauthier and Theberge 1985; Capitani et al. 2004; Mattioli et al. 2004). Therefore, we analyzed deer hairs found in bear scats to monitor bear predation on fawns. We divided deer into two age classes, fawns and adults (yearlings and older). To distinguish between fawns and adults, we compared hair thickness between fawns and yearlings, which should have the thinnest hairs among the adult age classes. We collected hairs from the forelegs, backs, and abdomens of yearlings ($n = 3$) and fawns ($n = 4$) during the deer parturition period (end of May–end of June) in 2009–2010. Both guard hair and underfur may be consumed when bears eat deer. We used only guard hair for analysis of yearlings because the underfur of yearlings is as thin as that of fawns. On the other hand, we used both hair types for fawns because they could not be distinguished with certainty. Hairs were rinsed with

water and air-dried before analysis. We took more than 15 hairs from each part of each individual and measured the width midway between the root and tip of the hair with a tabletop microscope scanning electron microscope (Miniscope TM-1000, HITACHI). We compared the width of hairs of fawns and yearlings to establish standards for discriminating deer age classes in bear scats.

Evaluation of the importance of sika deer fawns in bear diets

Bears prey on most ungulate neonates within the first month after birth (Swenson et al. 2007; Barber-Meyer et al. 2008; Blanco et al. 2011). Because the main parturition season for sika deer in Hokkaido is late May to late June (Suzuki et al. 1996), we collected bear scat samples defecated from late May to late July.

In 1999–2008 (except 2001 and 2002), we established census routes along paths (58 km in 1999–2004 and approximately 120 km in 2005–2008) and walked or drove through them once or twice in each study year. We collected 108 bear scats and froze them for further analysis. To compare fawn consumption by bears with trends in deer availability over the past decade, we divided the study into three periods based on population indices and harvest numbers (Kaji et al. 2010) as follows: in period I (1999–2000), the deer population had decreased from its 1998 peak but remained abundant with high harvest numbers; in period II (2003–2005), the population had recovered almost to 1993 levels and harvest numbers had decreased; and in period III (2006–2008), the population increased further and harvest numbers were as in period II, but hunters were encouraged to collect carcasses (Fig. 2).

We analyzed all samples collected by the point-frame method (Sato et al. 2000) to quantitatively evaluate their contents. After thawing, we washed samples on a sieve (1.0- or 2.0-mm mesh aperture) with tap water. We then spread approximately 500 g of the remaining material onto a stainless-steel tray (38 × 33 cm). The bottom of the tray was marked with a 1 × 1 cm grid, and the points of intersection were regarded as point frames. We counted over 400 points for seven food categories (fawns, adult deer, herbs, berries, ants, insects other than ants, and crops) and recorded their frequencies of occurrence and volumes in each sample. Sato et al. (2000) confirmed that the point-frame method reflected dry weight. To distinguish fawns from older deer, we used hair thickness standards obtained in the above analysis.

Animal materials in bear scat tend to be underestimated relative to plant materials because of the bear's digestive physiology (Pritchard and Robbins 1990; Hewitt and Robbins 1996). We therefore re-estimated the volumes of the seven dietary categories using the following correction factors as proposed by Hewitt and Robbins (1996): 3.0 for deer, 0.25 for herbs, 1.2 for berries, 1.1 for ants and other insects, and 1.0 for crops.

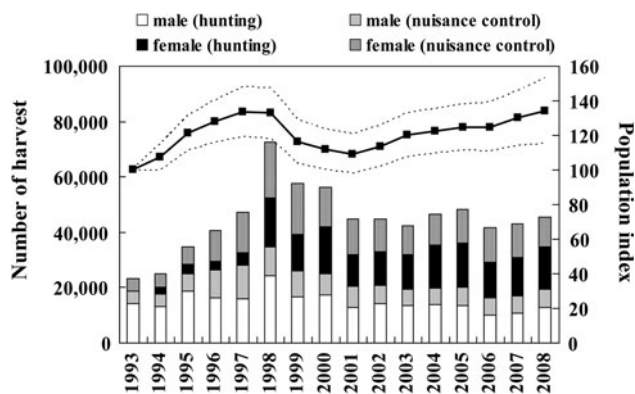


Fig. 2 Bayesian estimates of population indices obtained from the state-space model based on the stage-structured model (Yamamura et al. 2008) and number of deer harvested from 1993 to 2008. The bold line indicates the estimates of population indices. The dotted lines indicate the standard error (Kaji et al. 2010, fig. 6a)

We performed a Pearson Chi-square test of equality on the corrected volumes for overall seven diet compositions and on the frequency of occurrence of fawns to test for differences between period I and III using the statistical environment R version 2.13.0 (<http://www.r-project.org/>).

Results

Differentiation between fawns and adult sika deer based on hair thickness

The mean (\pm SD) of the thickness of yearling guard hairs was $129.5 \pm 14.4 \mu\text{m}$ (range 100–155 μm) on forelegs, $131.9 \pm 19.0 \mu\text{m}$ (97.7–172 μm) on backs, and $142.6 \pm 19.0 \mu\text{m}$ (102–178 μm) on abdomens. Fawn hairs were $77.2 \pm 18.4 \mu\text{m}$ (51.5–122 μm) on forelegs, $63.1 \pm 11.2 \mu\text{m}$ (22.1–81 μm) on backs, and $62.2 \pm 15.2 \mu\text{m}$ (20.3–86.8 μm) on abdomens. The mean thickness including all parts of yearling hairs was $134.9 \pm 18.5 \mu\text{m}$ and fawns' was $67.8 \pm 16.8 \mu\text{m}$ (Table 1; Fig. 3). The widest fawn hair found was 122 μm , and there were no fawn hairs wider than 130 μm in this experiment. Most of the yearling hairs were wider than 130 μm . Therefore, we concluded that hairs wider than 130 μm in bear scat were belonged to yearlings (or older) deer and that scats with only hairs narrower than 130 μm indicated that the bear had consumed fawns.

Evaluation of the importance of sika deer fawns in bear diets

We collected 32, 32, and 44 scats in periods I, II, and III, respectively. In all three periods, herbs occurred in scats at the highest frequency ($> 71\%$) of all food sources, and roughly half of the bear diet, as measured by both frequency and volume, consisted of deer (including both fawns and adults) (Table 2). Among the three periods, the overall diet compositions across the seven major categories differed significantly ($df = 12$, $\chi^2 = 93.4962$, $p < 0.0001$). The proportions of deer (fawns and adults) versus other foods in the bear diets did not differ

Table 1 Mean thickness and standard deviation of yearling and fawn hairs collected in eastern Hokkaido, Japan, in 2009–2010

	Thickness (μm)	SD
Yearling ($n = 3$)		
Foreleg ($n = 45$)	129.5	14.4
Back ($n = 46$)	131.9	19.0
Abdomen ($n = 49$)	142.6	19.0
All ($n = 140$)	134.9	18.5
Fawn ($n = 4$)		
Foreleg ($n = 76$)	77.2	18.4
Back ($n = 68$)	63.1	11.2
Abdomen ($n = 71$)	62.2	15.2
All ($n = 215$)	67.8	16.8

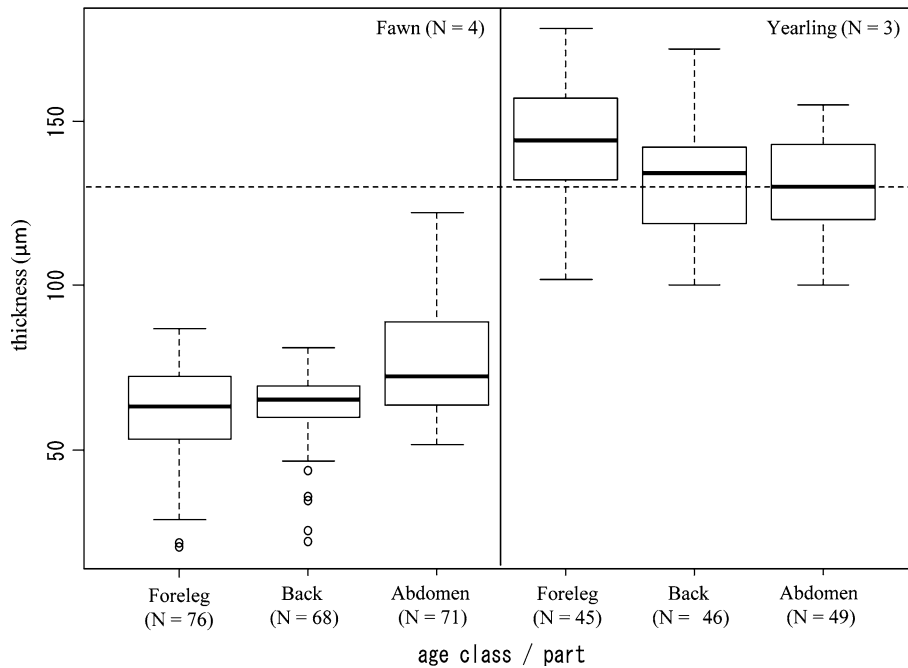


Fig. 3 Hair width data for yearling and fawn hairs collected in eastern Hokkaido, Japan, in 2009–2010. The dotted line at 130 μm indicates the criterion for distinguishing fawns from adults

significantly ($df = 2$, $\chi^2 = 2.4603$, $p = 0.2923$), but the proportions of fawns versus adult deer were significantly different ($df = 2$, $\chi^2 = 52.2443$, $p < 0.0001$).

The frequency of occurrence of adult deer in bear diets decreased from 34.4 % ($n = 32$) in period I to 22.7 % ($n = 44$) in period III, while that of fawns increased from 6.3 to 27.3 % over the same time (Table 2). The frequency of occurrence of fawns in bear diets differed significantly between the two periods (fawn: $df = 1$, $\chi^2 = 4.1393$, $p = 0.0419$).

Discussion

We developed a simple and cost-effective method for differentiating between fawn and adult sika deer using hair thickness. This enabled us to evaluate the importance of sika deer fawns in brown bear diets and to monitor changes in bear feeding behavior toward neonate ungulate by scat analysis. Yearling hairs averaged 130 μm or more and fawn hairs were always narrower than 130 μm , so we were able to monitor the relationship between bear feeding ecology and deer abundance continuously and on a large scale.

Scat analysis indicated that bears consumed fawns during the deer population irruption of 1999–2008 and that the number fawns in their diets increased proportionally to the increasing deer population in eastern Hokkaido at that time. This result supported our hypothesis that bears increasingly preyed on fawns as the deer population increased.

Also, we considered three possibilities for the increasing predation on fawns: brown bears had begun

Table 2 Frequency of occurrence (F) and volume (V) for each diet category in brown bear scats collected in the Urahoro region, Hokkaido, Japan, in 1999–2008

	Period I ($n = 32$)		Period II ($n = 32$)		Period III ($n = 44$)	
	F (%)	V (%)	F (%)	V (%)	F (%)	V (%)
Deer (fawns)	6.3	12.5	12.5	19.9	27.3	33.6
Deer (adults)	34.4	42.8	34.4	35.9	22.7	26.1
Herbs	75.0	14.3	71.9	8.5	75.0	11.2
Berries	0.0	0.0	6.3	0.6	6.8	2.0
Ants	50.0	11.5	71.9	22.1	54.5	12.3
Insects	25.0	4.6	46.9	5.3	9.1	3.0
Crops	15.6	14.3	18.8	7.6	18.2	11.0

to prey on fawns more aggressively than before, bear hunting skills had improved (French and French 1990), or the proportion of bears using fawns in bear population had increased. In Shiretoko National Park, in northeastern Hokkaido, which had a high density of sika deer (Kaji et al. 2004), we observed a female bear with cubs searching for fawns in grasslands during the June birthing season (Kobayashi and Yamanaka, pers. obs.). That area was an ideal birthing area for sika deer and most fawns were hidden in vegetation and did not move far after birth (Suzuki 2000). Based on this observation, female bears could become specialists at hunting fawns. Festa-Bianchet et al. (2006) reported that cougars (*Puma concolor*) in Canada had become highly successful at preying on bighorn sheep by learning the predictable space-use patterns of these sheep. For bears, predation on ungulates is apparently a learned behavior (Zager and Beecham 2006), and much of the feeding

behavior was acquired during the period of mother-cub association (French and French 1990; Gilbert 1999; Mazur and Seher 2008). Therefore, the percentage of bears actively preying on fawns may increase as more bears learn to hunt from their mothers. Because the deer distribution has been expanding in western and northern Hokkaido (Kaji et al. 2010), bear predation on fawns might soon extend throughout Hokkaido. In the future, DNA analysis of scats, in parallel with content analysis, will help to elucidate how many bears feed on deer fawns and what the sex ratio of fawn prey is.

Moreover, we expect that fawns born in early summer might be more important in bear diets for another reason. High densities of sika deer reduced some important vegetation resources for bears. In the study area, fences were constructed between farmland and mountainous areas in 1997–2000 to prevent deer invasion into farmland. Comparison of vegetation inside and outside of the fences revealed the effects of overgrazing by deer. Some perennial herbs, like Apiaceae, *Artemisia* spp. and *Petasites japonicas*, that were important spring and summer resources for bears, on the mountain-side, had decreased by 2009 because of the deer grazing pressure (Kawamura, unpublished data). Under limited food conditions in summer, bears were obliged to obtain alternative resources, such as deer fawns. These plastic feeding habits might allow bear populations to persist in landscapes modified by humans.

Management implications

Because the deer population of Hokkaido irrupted during the 1990s, causing significant agricultural and forest damage and changes in the natural vegetation, deer population management is the most critical wildlife management issue throughout Hokkaido (Kaji et al. 2010). Although adult female survival is the most important factor in ungulate population dynamics, neonate survival may play a major role (Gaillard et al. 1998; Miura and Tokida 2009). Juvenile deer are most susceptible to mortality, so obtaining reliable estimates of their survival rates is important for population modeling and management planning (Roseberry and Woolf 1991; Bowden et al. 2000). For large herbivores sympatrically inhabiting an area with predators, the most common cause of neonatal mortality is predation (Singer et al. 1997; Sinclair et al. 2003; Pojar and Bowden 2004; Owen-Smith et al. 2005). Our findings demonstrated that brown bear could be an important factor causing fawn mortality in Hokkaido. In further research, we must quantitatively evaluate the fawn mortality caused by brown bears by directly monitoring fawn mortality, as Blanco et al. (2011) have suggested.

On the other hand, Schwartz and Franzmann (1991) demonstrated that increased consumption of moose calves by black bears (*Ursus americanus*) could contribute to superior growth and reproduction of bears. Therefore, we should evaluate how fawn use influences

bear growth and reproductive to better understand bear population dynamics.

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References

- Ballard WB (1992) Bear predation on moose: a review of recent North American studies and their management implications. *Alces Suppl* 1:162–176
- Ballard WB, Van Ballenberghe V (1998) Predator/prey relationships. In: Franzmann AW, Schwartz CC (eds) *Ecology and management of the North American moose*. Smithsonian Institution Press, Washington, D.C., pp 247–273
- Barber-Meyer SM, Mech LD, White PJ (2008) Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildl Monogr* 169:1–30
- Bastille-Rousseau G, Fortin D, Dussault C, Courtois R, Ouellet J (2011) Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? *Ecography* 34:588–596
- Blanco JC, Ballesteros F, García-Serrano A, Herrero J, Nores C (2011) Behaviour of brown bears killing wild ungulates in the Cantabrian Mountains, southwestern Europe. *Eur J Wildl Res* 57:669–673
- Bowden D, White GC, Bartmann RM (2000) Optimal allocation of sampling effort for monitoring a harvested mule deer population. *J Wildl Manag* 64:1013–1024
- Bull EL, Torgersen TR, Wertz TL (2001) The importance of vegetation, insects, and neonate ungulates in black bear diet in northeastern Oregon. *Northwest Sci* 75:244–253
- Capitani C, Bertelli I, Varuzza P, Scandura M, Apollonio M (2004) A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystems. *Mamm Biol* 69:1–10
- Christiansen P (2008) Feeding ecology and morphology of the upper canines in bears (Carnivora: Ursidae). *J Morphol* 269:896–908
- Craighead FC Jr, Craighead JJ (1972) Grizzly bear prehibernation and denning activities as determined by radiotracking. *Wildl Monogr* 32:1–35
- Festa-Bianchet M, Coulson T, Gaillard J, Hogg J-MT, Pelletier F (2006) Stochastic predation events and population persistence in bighorn sheep. *Proc R Soc B Biol Sci* 273:1537–1543
- French SP, French MG (1990) Predatory behavior of grizzly bears feeding on elk calves in Yellowstone National Park, 1986–88. *Int Conf Bear Res Manag* 8:335–341
- Gaillard JM, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol Evol* 13:58–63
- Gauthier D, Theberge J (1985) Wolf predation in the Burwash caribou herd, southwest Yukon. *Rangifer Spec Issue* 1:137–144
- Gilbert BK (1999) Opportunities for social learning in bears. In: Box HO, Gibson KR (eds) *Mammalian social learning*. Cambridge University Press, London, pp 225–235
- Gunther KA, Renkin RA (1990) Grizzly bear predation on Elk calves and other fauna of Yellowstone National Park. *Int Conf Bear Res Manag* 8:329–334
- Herrero S (1985) *Bear attacks: their cause and avoidance*. Lyons and Burford, New York

- Hewitt DG, Robbins CT (1996) Estimating grizzly bear food habits from fecal analysis. *Wildl Soc Bull* 24:547–550
- Hokkaido Institute of Environmental Sciences (2000) Results of a survey related to sika deer and brown bear sighting on Hokkaido (IV) (in Japanese). Hokkaido Institute of Environmental Sciences, Sapporo
- Hokkaido Institute of Environmental Sciences (2004) Results of a survey related to brown bear sighting on Hokkaido (in Japanese). Hokkaido Institute of Environmental Sciences, Sapporo
- Hokkaido Institute of Environmental Sciences (2006) Results of survey related to sika deer in Hokkaido (in Japanese). Hokkaido Institute of Environmental Sciences, Sapporo
- Inukai T (1993) Review on extirpation of wolves on Hokkaido (in Japanese). *Shokubutsu to Dobutsu (Plants Anim)* 1:1091–1098
- Japan Meteorological Agency (2011) Climate statistics in Japan (in Japanese). <http://www.data.jma.go.jp/obd/stats/etrn/index.php>
- Kaji K, Miyaki M, Saitoh T, Ono S, Kaneko M (2000) Spatial distribution of an expanding sika deer population on Hokkaido Island, Japan. *Wildl Soc Bull* 28:699–707
- Kaji K, Okada H, Yamanaka M, Matsuda H, Yabe T (2004) Irruption of a colonizing sika deer population. *J Wildl Manag* 68:889–899
- Kaji K, Saitoh T, Uno H, Matsuda H, Yamamura K (2010) Adaptive management of sika deer populations in Hokkaido, Japan: theory and practice. *Popul Ecol* 52:373–387
- Lead Poisoned Eagles Network (1999) Annual report 1998 (in Japanese). Lead Poisoned Eagles Network, Kushiro
- Lead Poisoned Eagles Network (2000) Annual report 1999 (in Japanese). Lead Poisoned Eagles Network, Kushiro
- Lead Poisoned Eagles Network (2001) Annual report 2000 (in Japanese). Lead Poisoned Eagles Network, Kushiro
- Mattioli L, Capitani C, Avanzinelli E, Bertelli I, Gazzola A, Apollonio M (2004) Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in north-eastern Apennine, Italy. *J Zool* 264:249–258
- Mazur R, Seher V (2008) Socially learned foraging behavior in wild black bears, *Ursus americanus*. *Anim Behav* 75:1503–1508
- Mealey SP (1980) The natural food habits of grizzly bears in Yellowstone National Park, 1973–74. *Int Conf Bear Res Manag* 4:281–292
- Miura S, Tokida K (2009) Management strategy of sika deer based on sensitivity analysis. In: McCullough DR, Takatsuki S, Kaji K (eds) *Sika deer: biology and management of native and introduced populations*. Springer, Tokyo, pp 453–472
- Ohdachi S, Aoi T (1987) Food habits of brown bears in Hokkaido, Japan. *Int Conf Bear Res Manag* 7:215–220
- Owen-Smith N, Mason DR, Ogutu JO (2005) Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. *J Anim Ecol* 74:774–788
- Persson I, Wikan S, Swenson JE, Mysterud I (2001) The diet of the brown bear *Ursus arctos* in the Pasvik Valley, northeastern Norway. *Wildl Biol* 7:27–37
- Pojar TM, Bowden DC (2004) Neonatal mule deer fawn survival in west-central Colorado. *J Wildl Manag* 68:550–560
- Pritchard GT, Robbins CT (1990) Digestive and metabolic efficiencies of grizzly and black bears. *Can J Zool* 68:1645–1651
- Roseberry JL, Woolf A (1991) A comparative evaluation of techniques for analyzing white-tailed deer harvest data. *Wildlife Monographs* 117
- Sato Y, Mano T, Takatsuki S (2000) Applicability of the point-frame method for quantitative evaluation of bear diet. *Wildl Soc Bull* 28:311–316
- Sato Y, Aoi T, Kaji K, Takatsuki S (2004) Temporal changes in the population density and diet of brown bears in eastern Hokkaido, Japan. *Mammal Study* 29:47–53
- Sato Y, Mano T, Takatsuki S (2005) Stomach contents of brown bears *Ursus arctos* in Hokkaido, Japan. *Wildl Biol* 11:133–144
- Sato Y, Kobayashi Y, Urata T, Takatsuki S (2008) Home range and habitat use of female brown bear (*Ursus arctos*) in Urahoro, eastern Hokkaido, Japan. *Mammal Study* 33:99–109
- Schwartz CC, Franzmann AW (1991) Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildl Monogr* 113:1–58
- Servheen C (1983) Grizzly bear food habits, movements, and habitat selection in the Mission mountains, Montana. *J Wildl Manag* 47:1026–1035
- Servheen C (1990) The status and conservation of the bears of the world. *Int Conf Bear Res Manag Monogr Ser* 2:311–316
- Sinclair ARE, Mduma S, Brashares JS (2003) Patterns of predation in a diverse predator-prey system. *Nature* 425:288–290
- Singer FJ, Harting A, Symonds KK, Coughenour MB (1997) Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *J Wildl Manag* 61:12–25
- Stenroth P, Holmqvist N, Nystrom P, Berglund O, Larsson P, Graneli W (2008) The influence of productivity and width of littoral zone on the trophic position of a large-bodied omnivore. *Oecologia* 156:681–690
- Stirling I, Derocher AE (1990) Factors affecting the evolution and behavioral ecology of the modern bears. *Int Conf Bear Res Manag* 8:189–204
- Suzuki M (2000) Hokkaido sika deer (in Japanese). In: Museum Shiretoko (ed) *Mammals of Shiretoko I*. Hokkaido Shinbun Press, Sapporo, pp 27–48
- Suzuki M, Kaji K, Yamanaka M, Ohtaishi N (1996) Gestation age determination, variation of conception date, and external fetal development of Sika Deer (*Cervus nippon yesoensis* Heude, 1884) in eastern Hokkaido. *J Vet Med Sci* 58:505–509
- Swenson JE, Dahle B, Busk H, Opseth O, Johansen T, Söderberg A, Wallin K, Cederlund K (2007) Predation on Moose Calves by European Brown Bears. *J Wildl Manag* 71:1993–1997
- Uno H, Kaji K, Tamada K (2009) Sika deer population and their management on Hokkaido Island, Japan. In: McCullough DR, Takatsuki S, Kaji K (eds) *Sika deer: biology and management of native and introduced populations*. Springer, Tokyo, pp 405–420
- Yamamura K, Matsuda H, Yokomizo H, Kaji K, Uno H, Tamada K, Kurumada T, Saitoh T, Hirakawa H (2008) Harvest-based Bayesian estimation of sika deer populations using a state-space model. *Popul Ecol* 50:131–144
- Yamanaka M, Aoi T (1988) Brown bears (in Japanese with English abstract). In: Ohtaishi N, Nakagawa H (eds) *Animals of Shiretoko*. Hokkaido University Press, Sapporo, pp 181–223
- Zager P, Beecham J (2006) The role of American black bears and brown bears as predators on ungulates in North America. *Ursus* 17:95–108