Age- and Sex-Associated Differences in the Diet of the Asian Black Bear: Importance of Hard Mast and Sika Deer

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Abstract. In the context of reducing human–bear conflict, understanding potential foraging variation within a bear population yields insights into differences in foraging strategy according to an individual's sex and age. Stable isotope analyses reveal information regarding assimilated dietary components. To confirm the foraging variation of Asian black bears and assess its underlying factors, we conducted stable isotope analysis of hair samples. We constructed linear mixed-effect models to examine the effects of sex, age, and hard mast abundance on bear diet. Furthermore, we used stable isotope data on food resources to estimate bear diets from isotopic mixing models to evaluate differences in dietary components among age–sex classes. During the reproductive season, $\delta^{15}N$ values were positively correlated with bear age, and dietary deer fraction was the highest for adult males. Our results also showed that during the hyperphagia season, bears were mostly dependent on hard mast, regardless of its abundance. However, $\delta^{15}N$ values of bears were higher during poor mast years than when mast was plentiful, thus implying that bears consume increased proportions of deer and/or insects (e.g., Vespidae) in poor mast years. Our results indicate that feeding strategies in Asian black bears differ according to age–sex classes and seasons.

Key words: mast abundance, omnivore, stable isotope analysis, ungulates, *Ursus thibetanus*.

Food habits and foraging behavior provide basic information toward understanding the ecology of animals. Many studies of foraging ecology have been conducted at the population level; however, diet also differs within a population, mainly according to differences in sex, age, and body size among individuals. In particular, omnivores consume food items from multiple trophic levels, and omnivorous populations comprise individuals that differ from each other in their trophic positions, which range from herbivore to carnivore (Edwards et al. 2011).

Most members of the family Ursidae are omnivores, and some bear species exhibit foraging variation within populations [e.g., brown bear (*Ursus arctos*), Ben-David et al. 2004; Mowat and Heard 2006; Edwards et al. 2011; Costello et al. 2016; American black bear (*U. americanus*), Lesmerises et al. 2015; Costello et al. 2016]. For example, because of their larger body mass, adult male brown bears tend to consume more animal resources with high nutrient content, such as salmon (Mowat and Heard 2006; Matsubayashi et al. 2014) and ungulates (Milakovic and Parker 2013), compared with other members of the population. Similarly, compared with other members of the bear population, female American black bears with cubs more frequently consume hare and Vespidae to meet their additional nutritional requirements (Lesmerises et al. 2015). In addition, these intra-population

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variations in foraging items are strongly linked to differences in habitat selection within populations (Lesmerises et al. 2015). Studying foraging variation within a population may disclose associations between diet and foraging behavior, thus revealing the mechanism underlying the variation in foraging strategy among different sex and age classes of bears. However, because resource availability, which might influence bear behavior, changes annually; clarifying foraging variation within a population in the context of resource availability is important to quantify the relative values of resources.

Asian black bears (*Ursus thibetanus*) are omnivores. Although they sometimes capture sika deer (*Cervus nippon*) fawns opportunistically during early summer (Fujiwara et al. 2013), the bears are almost entirely dietarily dependent on plant materials (Hashimoto and Takatsuki 1997). In particular, hard mast is such an important food resource in autumn that bears change their food and behavior according to annual changes in hard mast production (Kozakai et al. 2011). Behavioral patterns in response to hard mast production varies by sex; during years of poor mast production, the proportion of increase in daily movement distance tends to be greater for females than for males (Koike et al. 2012).

In Japan, several thousand bears are killed annually as nuisances (Japan Bear Network 2006), and the sex ratio and age structure of killed bears vary seasonally and annually (Hayashi et al. 2008; Izumiyama et al. 2008), suggesting that the factors affecting nuisance activity might vary among sexes or ages (Hayashi et al. 2008). Although nuisance activity increases during autumn in poor mast years (Oka et al. 2004; Hayashi et al. 2008; Izumiyama et al. 2008), the sex and age compositions of killed nuisance bears do not follow any clear patterns consistent with mast production (Anezaki 2014). The mechanism underlying the issue may be associated with inter-individual variations in foraging strategy, including the response to resource fluctuation. Because food availability influences habitat selection by Asian black bears (Takahata et al. 2014, 2017), obtaining information regarding foraging variation within a population would help to clarify how diet availability modulates the behavior and habitat selection of bears and to facilitate the management of habitat conditions to preserve a suitable habitat for bears, to separate their habitats and human settlements, or both.

Stable isotope analysis is a suitable method for investigating inter-individual variation in diet within a population of Asian black bears. Unlike fecal analysis, stable isotope analyses of animal tissues reveal the foods assimilated by individuals (Kelly 2000). Various animal tissues (e.g., hair, blood cells, liver, and bone collagen) are suitable for this analysis; hair samples are particularly easy to collect, store, and prepare for analysis. In addition, analyzing hair growth enables the reconstruction of seasonal foraging habits because hair records the isotope signature of temporal changes in food (Schwertl et al. 2003).

In the current study, to identify factors affecting foraging variation among individuals that differ in age and sex, we examined foraging variation in a population of Asian black bears. We analyzed the stable carbon and nitrogen isotope ratios in bear hair samples to estimate the foraging histories during the summer (i.e., the reproductive season for bears) and autumn (i.e., the hyperphagia season for bears). In the reproductive season, bears' consumption of meat resources with high nutrient may differ according to their sex and age, because larger adult males may have access priority to their preferred resources like deer during competition with other members of the population. In the hyperphagia season, we focused on the effect of annual resource fluctuation on bear foraging variation. Trees that produce the hard mast that dominates the bear diet are distributed relatively homogeneously, and mast production is synchronized among individual trees in the study area (Tochigi et al. 2018). Given that the energy from fat accumulated during the hyperphagia season was used in the following hibernation (McLellan 2011), hard mast that contains high amounts of carbohydrates and fats is an essential food during this season. Therefore, the availability of hard mast species that are important for bear survival might influence the diet of the entire target population. On the basis of these considerations, we developed the following two hypotheses: (1) in the reproductive season, owing to their greater body mass, older bears—especially adult males—consume more deer than younger bears, and (2) in the hyperphagia season, all bears are likely to use hard mast to the same extent, but more animal materials are consumed in poor mast years than when mast is abundant. We tested these hypotheses by stable isotope analysis of individual bears.

Materials and methods

Study area

The study was conducted in the Ashio area of the southern Ashio–Nikko Mountains (approximately 460 km^2) in central Japan, where human–bear conflicts are

rare. Between 2003 and 2013, the annual ranges for precipitation and temperature in the study area were 1886.5–2976.0 mm and 6.6–7.9°C, respectively (Japan Meteorological Agency, http://www.data.jma.go.jp/obd/stats/etrn/, Accessed 01 Jul 2016).

The landscape is characterized by steep terrain ranging between 400 and 2400 m above sea level. The natural vegetation in this area is deciduous broad-leaved forest comprising Japanese oak (*Quercus crispula*), konara oak (*Q. serrata*), and maple (*Acer* spp.) up to 1600 m. Mixed forests comprising Japanese hemlock (*Tsuga* spp.) and birch (*Betula* spp.) occur above 1600 m. From 1000 to 1600 m, plantations of Japanese larch (*Larix kaempferi*) are dominant, whereas plantations of Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*) mainly occur below this zone.

The study area contains five hard mast species: Japanese oak, konara oak, Japanese chestnut (*Castanea crenata*), beech (*Fagus crenata*), and Japanese beech (*F. japonica*). Moderate or good mast production occurs every two or three years for Japanese oak, with synchrony among individual trees within several kilometers (Editorial Committee of Silvics of Japan 2009). Konara oak produces mast every three to five years, sometimes with asynchronous mast production among individual trees in the same forest stand, and Japanese chestnut produces mast biennially (Editorial Committee of Silvics of Japan 2009). Beech and Japanese beech produce mast every four to five years and every two to four years, respectively (Editorial Committee of Silvics of Japan 2009).

During spring, bears forage on green vegetation such as understory herbs and young leaves of trees. During summer, bears mainly consume social insects, such as ants (Formicidae), and soft mast (Fujiwara et al. 2013; Koike et al. 2016; Furusaka et al. 2017). In autumn (hyperphagia season), bears largely depend on hard and soft mast, but they sometimes also consume animal materials including insects (e.g., Vespidae and *Atachycines apicalis*) (Koike et al. 2012). In addition, in all seasons, bears fortuitously find and consume the carcasses of sika deer that have died naturally, and bears may attack fawns in early summer (Fujiwara et al. 2013).

Analysis of carbon and nitrogen stable isotope ratios

From 2003 to 2013, we collected hair samples from bears captured in the Ashio area between April and October. We captured bears by using barrel traps baited with honeycomb and immobilized them with tiletamine hydrochloride and zolazepam hydrochloride (Virbac,

Carros, France; 8 mg/kg estimated body weight). Whole guard hairs, including the root ends, were plucked from the back and shoulders of each trapped bear. Hair samples were placed in envelopes and stored at room temperature in the laboratory until analysis. In addition, we extracted a first premolar from each bear to determine its age by counting the cementum layers (Hachiya and Ohtaishi 1994). Bear capture and handling methods were performed in accordance with the Guidelines for the Procedure of Obtaining Mammal Specimens as Approved by the Mammal Society of Japan (http://www.mammalogy.jp/en/guideline.pdf).

Stable carbon and nitrogen isotope analyses were conducted on all hair samples. To remove dirt and lipids, the samples were rinsed with distilled water, soaked in a 2:1 chloroform:methanol solution, and then air dried. For each sample, we analyzed 10 to 30 hairs, which were cut into 5-mm segments (Mizukami et al. 2005). Bear hair grows at a relatively constant rate from mid-May to October (before hibernation), and hair molts mainly in July of the following year (Mizukami et al. 2005). In addition, hair that has finished growing represents the foraging history from June to October, from the tip to the root (Nakashita 2006), and the root end of the growing hair reflects the diet just before collection (Mizukami et al. 2005; Nakashita 2006). We identified the hair-growth year according to the hair length and sampling season (relative to molting): samples collected during the molting season contained both short hair that had grown during the sampling year and long hair that had grown during the previous year, whereas hair that was sampled before the molting season was all long hair that had grown during the previous year (Mizukami et al. 2005). In addition, we used only samples for which the hair-growth year could be determined; we excluded uncertain samples from all analyses.

In light of the mating season of the Asian black bear, we defined the reproductive season as June through July (Yamamoto et al. 1998). The hyperphagia season was defined as mid-September through October; during this season, bears in our study area consume mainly hard mast species regardless of annual variation in fruiting period (Nakajima et al. 2018). For each hair sample, we calculated the growth rate (mm/month) to associate hair segments with each reproductive and hyperphagia season. Stable isotope values for each sample and season were determined according to the assumption that hair began growing on 1 June, with growth ending on 31 October; this assumption was based on previous studies

reporting that hair growth began after mid-May and ended in late October (Bromlei 1972; Mizukami et al. 2005; Nakashita 2006). In the statistical analyses, we used the mean value of all hair segments grown in each season. Although bear hairs immediately reflect the current diet, there is a time lag before isotopic equilibrium is achieved, and the half-life of the metabolic pool is 19.5 days (Nakashita 2006). In our current study, we regarded each hair section as being representative of each season because there was 1.5 months (roughly 45 days) between the reproductive season (from June to July) and the hyperphagia season (from mid-September to October). The mean growth for 1.5 months (i.e., between the reproductive and hyperphagia seasons) likewise was 24 mm (range, 14–45 mm); these hair segments were not included in any hair sections.

Before the analysis, we oven-dried bear food samples at 60°C for at least 48 h. Deer meat samples were immersed in a 2:1 chloroform:methanol solution for 24 h, rinsed and decanted twice to remove lipids, and then air dried. Before analysis, all bear food samples were ground into a fine powder by using a mortar and pestle.

To determine the carbon and nitrogen isotope ratios, samples were enclosed in a tin cup and combusted in an elemental analyzer (FlashEA1112, Thermo Fisher Scientific, Bremen, Germany) interfaced with an isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage, Thermo Fisher Scientific, Bremen, Germany). Stable isotope values are expressed in δ notation as per mil (‰) or parts per thousand, according to the following equation (Bond and Hobson 2012):

$$\delta X = (R_{sample} / R_{standard}) - 1,$$

where X represents ^{13}C or ^{15}N, R_{sample} represents the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio for the sample, and $R_{standard}$ represents that of the international standard (Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen). The carbon and nitrogen elemental concentrations and isotope ratios were calibrated against laboratory standards (Shoko Science, Saitama, Japan), which are traceable back to international standards. The $\delta^{13}C$ and $\delta^{15}N$ values of the laboratory standards are –11.4‰ and –7.6‰ for L-histidine, –33.8‰ and 1.3‰ for glycine, –19.6‰ and 1.5‰ for L-alanine (1), –19.6‰ and 5.0‰ for L-alanine (2), and –19.6‰ and 10.1‰ for L-alanine (3), respectively. The analytical standard deviations of the stable isotope analyses were 0.2‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$.

Statistical analysis

To identify factors that influenced foraging variation within the study population, we examined the factors that affected the $\delta^{13}C$ and $\delta^{15}N$ values. We used linear mixed-effect models (LMEs) implemented in the 'lmer' function of the 'lme4' package of R software (version 3.5.3, R Core Team 2019). In the LMEs, which followed a Gaussian distribution, the $\delta^{13}C$ and $\delta^{15}N$ values of hair samples in each reproductive and season were used as response variables, and sex and age were used as explanatory variables. To account for the recapture of some individuals in different years, we included bear identity and year as random effects in the LMEs. We performed model selection by using the corrected Akaike Information Criterion (AICc) for small sample size; models with the smallest AICc values were considered the most parsimonious. We also conducted model averaging across our entire set of candidate models (Anderson et al. 2000) by using the 'model.avg' function within the 'MuMIn' package of R. We calculated the weighted unconditional standard error with its associated 95% confidence interval (95% *CI*) for each variable. We interpreted the significance of estimates for each variable by testing whether the 95% *CI* overlapped zero. By giving the estimates calculated from the models' assigned weights, model averaging allowed us to examine which variables were associated with variations in the $\delta^{13}C$ and $\delta^{15}N$ values for Asian black bears in the Ashio area.

To assess the relationship between dietary composition and the abundance of hard mast, we included mast abundance in autumn after 2005 as an explanatory variable in the LMEs. In the study area, changes in the mast production of Japanese oak, which is the dominant species, have the greatest influence on the behavior and food habits of bears during autumn (Kozakai et al. 2011). Given the mast production levels determined from surveys conducted in this area between 2006 and 2013 (Kozakai et al. 2017), we defined 2006, 2010, and 2012 as poor mast years and 2007–2009, 2011, and 2013 as moderate to good mast years. Details regarding the field survey and determination of hard mast production have been provided previously (Kozakai et al. 2017). We did not include the samples collected during the hyperphagia season before 2005 in the LMEs, because no information regarding mast production was available. Therefore, we used the samples collected in 2003–2013 and 2006–2013 for the reproductive and hyperphagia seasons, respectively.

Estimating dietary composition

We produced two mixing models to estimate the diet during each reproductive and hyperphagia season. Bears in the Ashio–Nikko Mountains exhibit a consistent seasonal foraging pattern (Koike et al. 2016); this allowed us to determine the food items corresponding to the hair-growth season. The bear food items in the Ashio–Nikko Mountains that we considered when analyzing the stable carbon and nitrogen ratios were based on a previous study (Koike et al. 2016), which classified food resources into three groups according to isotopic signatures: high δ^{13}C group (ants); high δ^{15}N and low δ^{13}C group (deer and insects such as Vespidae and *A. apicalis*, excluding ants); and low δ^{15}N and low δ^{13}C group (C3 plants). We used the major food items available in summer and autumn for analysis, because the hairs on the back and shoulders of bears grow from June to October, and their stable isotope ratios reflect the food items consumed during these seasons (Nakashita 2006).

Accordingly, we assigned the food resources available during each reproductive and hyperphagia season to appropriate food groups (Supplementary Table S1). Food groups and their component items during the reproductive season were: 1) ants (*Lasius flavus*, *L. japonicus*, and *Tetramorium tsushimae*); 2) C3 plants (soft mast: *Rubus phoenicolasius*, *Prunus grayana*, *Cerasus jamasakura*, and *Swida controversa*; leaves of trees: *Q. crispula*, *Malus toringo*, and *Salix caprea*); and 3) deer (*C. nippon*). In the hyperphagia season, the food groups and their component items were 1) C3 plants (soft mast: *P. grayana*, *S. controversa*, *Actinidia arguta*, and *Vitis coignetiae*; hard mast: *Q. crispula*, *Q. serrata*, and *F. crenata*) and 2) deer and insects (*C. nippon*, *A. apicalis*, and *Vespula flaviceps*). We did not include ants in any food group in the hyperphagia season, because bears consume them only infrequently during that season (Fujiwara et al. 2013; Koike et al. 2016).

We used the Bayesian isotopic mixing model available in R package (R Core Team 2019), Stable Isotope Analysis in R (SIAR; Parnell et al. 2010) to estimate the contribution of each food group to the bears' diets. Asian black bears were grouped into two age classes: young bears (age, 1–4 years) and adult bears (older than 4 years) according to their sexual maturation (Komatsu et al. 1994; Katayama et al. 1996). Because most Asian black bear cubs suckle until early August of the birth year (Bromlei 1972), weaning bears were not included in the young-bear group. We estimated the dietary contributions of three food groups during the reproductive season and of two food groups during the hyperphagia season for four age–sex bear classes (Table 1). For each model, we ran a burn-in of 100 000, followed by 1 000 000 iterations of Markov chain Monte Carlo (MCMC) with uninformative priors. SIAR accommodates the incorporation of uncertainty and variations in sources. Discrimination factors were designated as the differences in isotope values between animal tissues and the diet consumed, which arise during metabolic processes. We used the value for captive Asian black bears that were fed barley and corn (Nakashita 2006) to estimate the δ^{13}C discrimination factors because this was specific to our study species. We also applied discrimination factors for δ^{15}N that were obtained from the hair of captive rats (Kurle et al. 2014), because bears and rats, which are both monogastric mammalian omnivores, are assumed to discriminate with a similar magnitude (Hopkins and Ferguson 2012; Hopkins and Kurle 2016). Consequently, we used discrimination factors of 3.9 ± 0.1‰ for nitrogen and

Table 1. Stable isotope data and sample size of Asian black bears in the Ashio area

| Bear age–sex class | δ^{15}N value | | | | | | δ^{13}C value | | | | | |
| | Reproductive | | Hyperphagia | | | | Reproductive | | Hyperphagia | | | |
	Mean ± *SD* Range	(*n*)	Mean ± *SD* Range	(*n*)			Mean ± *SD* Range	(*n*)	Mean ± *SD* Range	(*n*)		
Young female	2.8 ± 0.8 1.2 to 4.2	(29)	2.5 ± 0.9 0.7 to 3.9	(26)			−20.9 ± 1.3 −23.0 to −17.9	(29)	−21.3 ± 0.9 −22.7 to −19.3	(26)		
Adult female	3.3 ± 0.7 1.4 to 4.7	(41)	2.1 ± 1.1 0.0 to 3.8	(28)			−21.4 ± 1.0 −23.2 to −19.5	(41)	−22.1 ± 0.7 −23.2 to −20.4	(28)		
Young male	2.7 ± 1.2 −0.7 to 4.5	(37)	2.0 ± 1.3 −0.7 to 4.3	(23)			−21.8 ± 1.4 −24.8 to −17.7	(37)	−22.1 ± 1.1 −24.3 to −18.8	(23)		
Adult male	3.5 ± 1.0 1.2 to 5.1	(41)	3.4 ± 1.0 1.1 to 4.9	(21)			−22.5 ± 0.6 −24.2 to −21.5	(41)	−22.3 ± 0.7 −23.3 to −20.4	(21)		

Table 2. Stable isotope values, trophic discrimination factors, and elemental concentrations incorpolated into SIAR models to estimate dietary contributions of Asian black bears in the Ashio–Nikko mountains

Food groups	Sample type	δ^{15}N (‰)	δ^{13}C (‰)	$\Delta\delta^{15}$N (‰)	$\Delta\delta^{13}$C (‰)	%N	%C
Reproductive season							
Ants	Adult ants	0.9 ± 0.9	-19.1 ± 3.6	3.9 ± 0.1	3.0 ± 0.2	7.7 ± 1.2	54.2 ± 0.8
C3 plants	Leaves and soft mast	-2.7 ± 1.4	-28.5 ± 2.5	2.4 ± 0.1	3.0 ± 0.2	2.8 ± 1.3	47.1 ± 4.2
Deer	Meat	1.7 ± 0.6	-26.3 ± 0.7	3.9 ± 0.1	3.0 ± 0.2	14.0 ± 0.0	44.8 ± 0.0
Hyperphagia season							
C3 plants	Hard mast and soft mast	-3.0 ± 1.8	-27.0 ± 2.4	2.4 ± 0.1	3.0 ± 0.2	1.0 ± 0.3	48.2 ± 6.3
Deer and insects	Meat, pupae and insects without ants	2.8 ± 0.9	-26.5 ± 0.4	3.9 ± 0.1	3.0 ± 0.2	11.1 ± 2.2	47.9 ± 2.1

Food composition of each food category was shown in Supplementary Table S1.
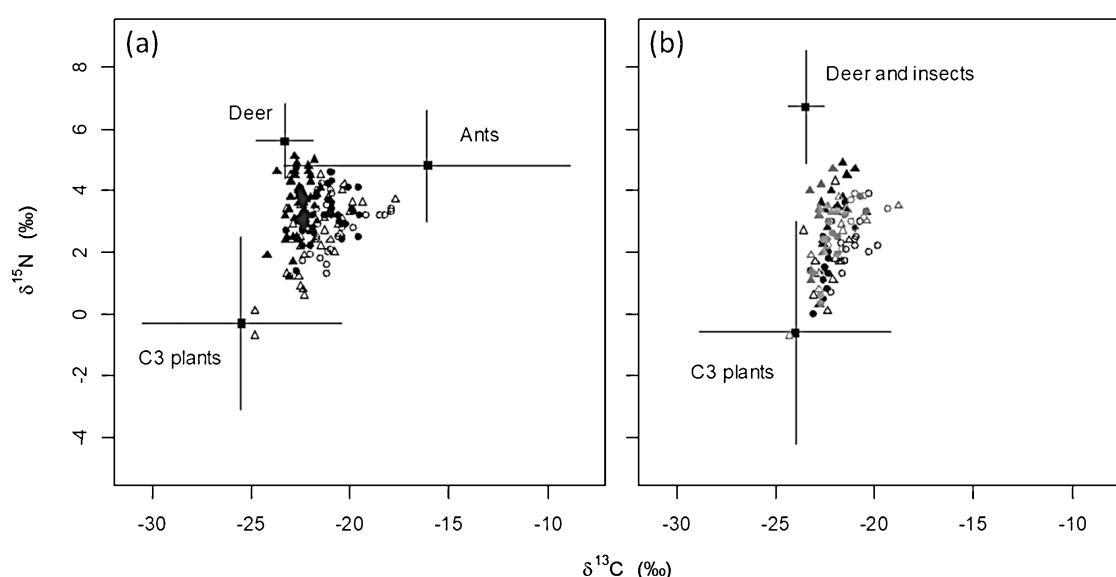
Fig. 1. Mixing diagrams of Asian black bears and their estimated food sources in the reproductive season (a) and the hyperphagia season (b). δ^{13}C and δ^{15}N values of bear hairs from samples collected during April to October, between 2003 and 2013 in the Ashio area. Open circles, solid circles, open triangles, and solid triangles represent young females, adult females, young males, and adult males, respectively. In the hyperphagia season, black and gray symbols denote bears during moderate to good mast years and those during poor mast years, respectively.

3.0 ± 0.2‰ for carbon when ants, deer, and insects were consumed and of 2.4 ± 0.1‰ for nitrogen and 3.0 ± 0.2‰ for carbon when C3 plants were consumed. Furthermore, we assigned elemental concentrations (%C and %N) because the C and N concentrations varied by the food items of Asian black bears (Supplementary Table S1). The information incorporated into the SIAR models is shown in Table 2.

Results

Between 2003 and 2013, we obtained data covering 148 bear-years from 59 individually captured bears: 41 bear-years from 20 adult males, 41 bear-years from 18 adult females, 37 bear-years from 20 young males, and 29 bear-years from 14 young females (Table 1 and Fig. 1). Because some of the young males and females were recaptured as adults, the sum of bears in all age–sex classes exceeded the number of individually captured bears. The low number of samples for the hyperphagia season was due to the exclusion of captured bears whose hair grew before autumn.

In the LME results for the reproductive season (Table 3), bear age was positively associated with the δ^{15}N value ($P = 0.016$, 95% $CI = 0.009$ to 0.086) and negatively associated with the lower δ^{13}C value ($P < 0.001$, 95% $CI = -0.144$ to -0.049), respectively. Therefore, older bears had significantly higher δ^{15}N values

Table 3. Parameters estimates, standard errors (*SE*), *P* values, and the 95% confidence intervals (*CI*) of δ^{15}N and δ^{13}C values in the reproductive and hyperphagia seasons estimated by model averaging for hair collected from Asian black bears in the Ashio area

| Season		δ^{15}N value					δ^{13}C value				
	Variables	Estimates	*SE*	*P* value	95% *CI*		Variables	Estimates	*SE*	*P* value	95% *CI*
Reproductive	Age	0.047	0.020	0.016	0.009	0.086	Age	−0.096	0.024	< 0.001	−0.144 −0.049
	Sex (male)	−0.055	0.221	0.805	−0.492	0.381	Sex (male)	−1.126	0.257	< 0.001	−1.633 −0.618
Hyperphagia	Age	0.088	0.030	0.004	0.028	0.148	Age	−0.035	0.021	0.101	−0.077 0.007
	Hard mast (poor)	0.604	0.284	0.036	0.040	1.169	Hard mast (poor)	−0.392	0.205	0.060	−0.799 0.016
	Sex (male)	0.302	0.295	0.312	−0.284	0.889	Sex (male)	0.137	0.166	0.417	−0.194 0.467

Table 4. SIAR mixing model estimates of the diets of Asian black bears during the reproductive season for the four bear age–sex classes in the Ashio area

Bear age–sex class	Ants		C3 plants		Deer	
	Mean	95% *CI*	Mean	95% *CI*	Mean	95% *CI*
Young female	0.37	0.32–0.43	0.61	0.56–0.66	0.01	0.00–0.04
Adult female	0.36	0.30–0.43	0.57	0.53–0.61	0.06	0.02–0.11
Young male	0.33	0.27–0.39	0.65	0.59–0.70	0.03	0.00–0.06
Adult male	0.23	0.18–0.29	0.59	0.53–0.64	0.18	0.11–0.25

Ants (*Lasius flavus*, *L. japonicus*, and *Tetramorium tsushimae*), Deer (*Cervus nippon*), and C3 plants (soft mast: *Rubus phoenicolasius*, *Prunus grayana*, *Swida controversa*, and *Cerasus jamasakura*, and leaves of trees such as *Quercus crispula*, *Malus toringo*, and *Salix caprea*).

and lower δ^{13}C values than younger bears. There was a significant influence of sex on the δ^{13}C values (*P* < 0.001, 95% *CI* = −1.633 to −0.618), such that the δ^{13}C values for male bears were lower than those for females. In the LME results for the hyperphagia season, hard mast production had a significant influence on the δ^{15}N value (*P* = 0.036, 95% *CI* = 0.040 to 1.169), indicating that δ^{15}N values in poor mast years were higher than those in moderate to good mast years. In addition, bear age was positively associated with the δ^{15}N value (*P* = 0.004, 95% *CI* = 0.028 to 0.148), but significant influences of sex, age, and level of mast production on the δ^{13}C values were not observed (Table 3).

The SIAR results for the reproductive season indicated that, for both sexes of bear, deer comprised a larger proportion of the diets of adults than of young bears, whereas dietary contribution of ants and C3 plants did not differ between any age–sex classes (Fig. 2). With increasing bear age class, the mean contribution of deer to the diet for males increased from 3% [0% to 6% (the lower to upper 95% credible interval ranges)] to 18% (11% to 25%), whereas that for females slightly increased: 1% (0% to 4%) for young females and 6% (2% to 11%) for adult females. Therefore, the age-associated difference in the dietary contribution from deer was substantial only for males (Table 4). In fact, the dietary contribution from
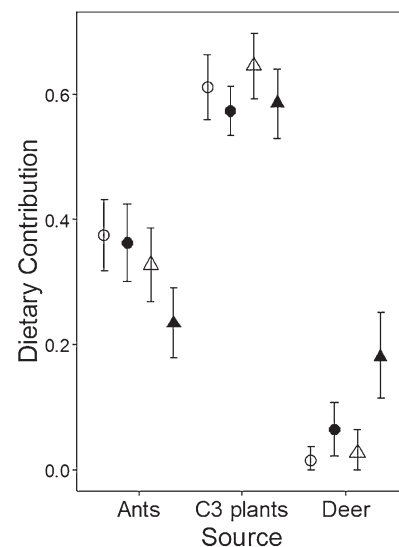
Fig. 2. The diet of each bear group in the reproductive season. Mean and 95% *CI*s of dietary contribution from ants, C3 plants, and deer for young females (open circle), adult females (solid circle), young males (open triangle), and adult males (solid triangle) estimated from SIAR.

deer for adult males was the highest and did not overlap with that of any of the other age–sex classes (Fig. 2).
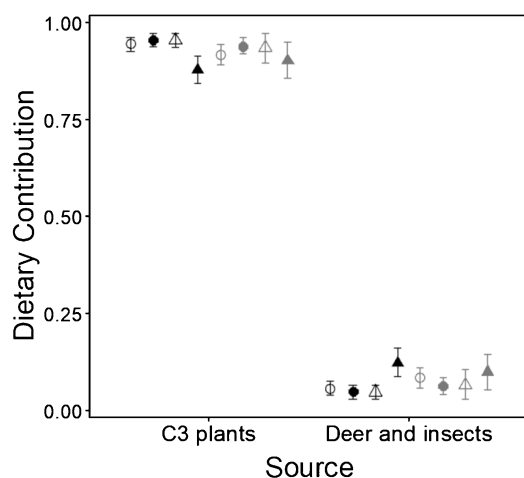
During the hyperphagia season, the dietary composition differed only slightly among age–sex classes, depending on the mast production level (Fig. 3). Comparison of

Table 5. SIAR mixing model estimates of the diets of Asian black bears during the hyperphagia season for the four bear age–sex classes and two of mast abundance categories in the Ashio area

Mast abundance	Bear age–sex class	C3 plants		Deer and insects	
		Mean	95% *CI*	Mean	95% *CI*
Moderate and good	Young female	0.95	0.93–0.97	0.05	0.03–0.07
	Adult female	0.96	0.94–0.98	0.04	0.02–0.06
	Young male	0.96	0.94–0.98	0.04	0.02–0.06
	Adult male	0.89	0.85–0.92	0.11	0.08–0.15
Poor	Young female	0.92	0.89–0.95	0.08	0.05–0.11
	Adult female	0.94	0.92–0.96	0.06	0.04–0.08
	Young male	0.94	0.90–0.98	0.06	0.02–0.10
	Adult male	0.91	0.86–0.97	0.09	0.03–0.14

Deer and insects (*Cervus nippon*, *Atachycines apicalis*, and *Vespula flaviceps*) and C3 plants (hard mast: *Quercus crispula*, *Q. serrata*, and *Fagus crenata*; soft mast: *Prunus grayana*, *Swida controversa*, *Actinidia arguta*, and *Vitis coignetiae*). Ants were not included in food groups during hyperphagia season.

Fig. 3. The diet of each bear groups in hyperphagia season. Mean and 95% *CI*s of dietary contribution from C3 plants and deer and insects of young females (open circle), adult females (solid circle), young males (open triangle), and adult males (solid triangle) in moderate to good mast years (black symbols and lines) and poor mast years (gray symbols and lines) estimated from SIAR.

dietary components between age–sex groups at each level of mast abundance revealed that deer and insects comprised relatively large proportions of the diets of adult males during moderate to good mast years, whereas the dietary contributions from each source overlapped with those of all bear groups in poor mast years. The dietary contribution of C3 plants remained similar (i.e., approximately more than 90%) among all age–sex classes, regardless of the level of mast production (Table 5).

Discussion

Our results revealed the presence of foraging variation within an Asian black bear population and suggest that age–sex class and temporal or spatial variation in food resources influence foraging variation among bears.

During the reproductive season, $\delta^{15}N$ values increased and $\delta^{13}C$ values decreased with age, suggesting that younger bears foraged more C3 plants and ants, whereas deer comprised a greater fraction of the diet of adult bears. According to the SIAR results for this season, the proportion of C3 plants was similar (approximately 60%) among all age–sex bear groups, and this food source contributed the largest proportion of each diet. Conversely, the dietary contribution of deer differed between age–sex classes; from young to adult, male bears exhibited a larger increase in the deer fraction, compared with females. In addition, young and adult female bears consumed more ants than did adult males. We offer two potential explanations for the age- and sex-associated differences in the diets during the reproductive season. First, foraging strategy may differ according to age–sex classes. In brown bears and American black bears, small bears are better able to meet their maintenance requirements by feeding on plants predominately. In comparison, large bears cannot gain or maintain their body mass feeding on plants and therefore select larger or clustered foods to maximize their foraging efficiency (Welch et al. 1997). Similarly, in our current study, large adult male bears consumed more deer as an adaptive foraging strategy, whereas smaller, female bears consumed more ants. A previous study indicated that bears in the Ashio area of

Japan obtained insufficient energy when their diet during the reproductive season comprised predominantly ants (Yamazaki et al. 2012). Therefore, during the reproductive season, if large bears need to feed more effectively, they may try to obtain additional food items, such as deer, that offer increased caloric content.

The second possible explanation for foraging variation among bear age–sex groups during the reproductive season is that the larger body mass of adult males may be advantageous for intraspecific competition in terms of obtaining animal foods. For example, young brown bears consume kokanee (*Oncorhynchus nerka*) as an alternative to anadromous salmon, which old and/or large bears tend to consume; this difference suggests a mechanism for decreasing conflict between young bears and larger, older bears (Mowat and Heard 2006). Because C3 plants and ants, which are the predominant food items at the population level according to fecal analysis, are widespread and abundant in our study area (Koike et al. 2016), female and young male bears can avoid competing with adult males by consuming these items. In addition, in the Ashio area, bears have been reported to attack newborn sika deer fawns in June and July (Fujiwara et al. 2013). Therefore, although we could not differentiate between adult deer carcasses and fawns, we presume that, compared with other groups, older and larger bears (i.e., the adult male age–sex group) may hunt more fawns, thus supporting our first hypothesis (i.e., because of their greater body mass and experience, older bears—especially adult males—consume deer more often than do younger bears in the reproductive season). Little detailed information regarding the behavior of Asian black bears during the reproductive season is available; future work that provides these data will help to reveal the features of, and explanations for, behavior variation within this population.

In the hyperphagia season, Asian black bears usually depend dietarily on hard mast, but they increase their consumption of other items during years of poor mast production (Koike 2010). In our LME results, δ^{15}N values were significantly higher during years with poor mast production, indicating that the diets of most bears had increased proportions of deer and insects and decreased C3 plants compared with consumption during years with moderate to good mast production. Asian black bears appeared to change their foraging habits in poor mast years; they consumed soft mast (Koike et al. 2012) and subordinate mast species for bears (Mizoguchi et al. 1996; Hashimoto et al. 2003; Mori et al. 2018) instead of

staple hard mast species, such as Fagaceae. Likewise, Takada (1979) noted that bears consumed more animal materials in poor mast years, thus supporting our results. Asian black bears might have different dietary responses to poor mast abundance depending on their habitat, because their characteristic food habits correspond to the resource availability of food items in each habitat (Hashimoto and Takatsuki 1997). However, the SIAR results that compared dietary components between age–sex groups in each mast year revealed that the diets of adult males contained high proportions of deer and insects in years when mast production was moderate to good, but dietary composition did not differ among age–sex classes during poor mast production years (Table 5 and Fig. 3). In moderate to good mast production years, adult male bears might consume additional deer and insects to help to maintain their body mass, similar to their foraging strategy in the reproductive season. In contrast, because δ^{15}N values in poor mast years were higher than those in moderate to good mast years, the similarity of dietary components between age–sex classes in poor mast years from SIAR suggests that all bears, except adult males, might have consumed increased proportions of deer and insects. Although the current analyses could not distinguish between deer and insects (e.g., Vespidae), because adult males are able to monopolize the terrestrial meat resources such as deer carcass, subordinate bears (i.e., adult females and young bears) might use insects to avoid competition with adult males. These combined results suggest that the diets of adult males included deer and insects regardless of the mast availability, whereas members of the other age–sex groups consumed a hard-mast–dominated diet in years with moderate to good mast production, but their dietary composition was similar to that of adult males when mast production was poor.

With regard to bear movement in response to mast production, both male and female movement patterns, such as long-distance movement, were similar in poor mast years, even though females usually moved less than males (Koike et al. 2012). The similarity in dietary components between adult males and the other groups in poor mast years may reflect the similar behavior patterns of males and females in poor mast years. Thus, our second hypothesis (i.e., in the hyperphagia season, all bears are likely to use hard mast to the same extent, whereas more animal materials are consumed in poor mast years) was partly supported. To our knowledge, our study is the first to reveal different dietary responses to hard mast production according to age–sex classes in Asian black bears.

Although we did not confirm the reproductive status of adult female bears in the current study, hard mast may be important for reproductive success (Costello et al. 2003; Seger et al. 2013). Therefore, assessing female reproductive status after hibernation simultaneously with their foraging variation would promote understanding of the complicated relationships between reproductive success and dietary composition according to annual resource variation.

A previous report regarding the sex composition of killed nuisance bears indicated that more males were killed than females in the reproductive season (Hayashi et al. 2008), which might reflect a sex-associated difference in dependence on anthropogenic food. In the current study, Asian black bears demonstrated different foraging tactics according to body size. In particular, compared with other members in the focal population, the diet of adult males included more deer (Fig. 2). Anthropogenic foods (i.e., crops, garbage, and livestock feed) are highly nutritious, as are potential meat sources such as deer. Because deer were more frequently a dietary component for adult male bears, they might also prefer anthropogenic food, thus increasing risk of human–bear conflict. In contrast, during the hyperphagia season, bears of all age–sex groups depended on hard mast but consumed animal materials as alternatives to hard mast in poor mast years. In Gunma prefecture, which included the study area, the sex and age composition of nuisance killed bears was unrelated to hard mast production (Anezaki 2014); that finding is confirmed by our current results that foraging tactics (i.e., bears depended on hard mast but consumed animal materials as alternatives to hard mast in poor mast years) might be similar in the population. Nevertheless, poor mast production leads to nuisance killing of bears (Oka et al. 2004), and the sex and age composition of culled bears varied between poor and good mast years in other areas (Izumiyama et al. 2008). Because distribution, abundance, and composition of food resources might all influence foraging variation in each population, it will be important to examine the characteristics and availability of foraging items for each population in a future study.

The dietary composition of Asian black bears varies depending on hard mast abundance and is related to their seasonal behavior. Our research supports the merit of further study of foraging variation within a population and provides important information regarding foraging strategy according to age–sex classes. However, this study had some limitations. First, some bears had higher $\delta^{13}C$ values than their diet in the hyperplasia season (Fig. 1b), which may indicate that (1) the trophic discrimination factors for $\delta^{13}C$ values did not match our data, (2) our model is missing some dietary items for the bears, or (3) food groups did not reflect the representative $\delta^{13}C$ values. Mixing models are sensitive to discrimination factors, which vary by species, tissue type, and the diet consumed (Caut et al. 2009). Given that we used trophic discrimination factor for the $\delta^{13}C$ specific to Asian Black bears (Nakashita 2006), and included all potential food groups of the species in this region (Fujiwara et al. 2013; Koike et al. 2016), options (1) and (2) are unlikely to be true. Animal materials such as insects can have different $\delta^{13}C$ values in different patches, and the $\delta^{13}C$ values of plants differ across various elevations (Mo et al. 2004). Individual bears likely consume food items with different $\delta^{13}C$ values because bears exploit a wide range of food sources in the hyperphagia season (Yamazaki 2015). As a result, the $\delta^{13}C$ values of the food items we collected probably did not completely recapitulate that of the assimilated diet of bears. Exclusion of a food source biases the dietary contributions of the other sources that are included in the analysis (Phillips and Gregg 2003; Phillips 2012). Given the possibility of misestimation regarding the diet of the bears, our results for the hyperphagia season must be interpreted with caution.

The second limitation of our study is that we could not assess the diets in spring and late autumn because the hair samples reflected the diet from June through October only (Bromlei 1972; Nakashita 2006). Hashimoto and Takatsuki (1997) reported that bears tend to scavenge on deer carcasses in spring. Other factors such as reproductive status (e.g., presence or absence of cubs) might also affect foraging variation in spring. Future researchers should collect additional animal tissues that have a rapid turnover rate, such as blood, to assess the spring diet of Asian black bears. Finally, demographic characteristics for our samples were limited to age and sex. According to Lesmerises et al. (2015), female American black bears with cubs tend to consume small animal species and insects to meet their physiological requirements. Therefore, future studies should consider the effect of reproductive status on the dietary composition of Asian black bears.

Supplementary data

Supplementary data are available at Mammal Study online.
Supplementary Table S1. Stable isotope values and

elemental concentrations for Asian black bear foods from Ashio–Nikko Mountains.

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