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Factors influencing lifespan dependency on agricultural crops by brown bears

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Abstract

Investigating factors underlying human-wildlife conflicts in agricultural landscapes is important for both preventing crop damage and wildlife conservation. Although environments surrounding crop fields are considered causal factors, incorporating individual aspects of animals, such as demographic and physical characteristics, into the investigation may aid the prediction of how nuisance control affects wildlife population structures. Here, we assessed the relationship of corn consumption by Hokkaido brown bears (*Ursus arctos*) with both demographic (sex and age) and physical (body size) characteristics and environmental factors (human presence and crop accessibility). We estimated the proportion of corn in the lifespan diet for both female ($n=61$) and male ($n=62$) bears using carbon and nitrogen stable isotope analyses. Then, we analyzed the factors correlated with corn consumption using a generalized linear model. Female and male bears consumed corn from 1.3% to 30.9% and 1.3% to 42.0% of their lifespan diet, respectively. Corn consumption by female bears was not correlated with any explanatory variables, whereas that of male bears was positively correlated with their body size and crop accessibility but negatively correlated with human presence. Large male bears were more likely to have consumed more corn than small male bears, but selective harvest of large bears may cause dwarfism of their overall population, impacting the local population dynamics. To reduce agricultural damage and population structure alteration of brown bears, the opportunity for them to learn to eat crops must be eliminated through border management between forests and agricultural fields and the relocation of agricultural fields when possible.

Keywords: agricultural landscape, body size, Hokkaido, human-wildlife conflict, stable isotope, *Ursus arctos*

Introduction

Agricultural damage by wild animals is widely reported globally and is one of the major drivers of human-wildlife conflicts (Wilson et al. 2006; Northrup et al. 2012; Ditmer et al. 2016). To control feeding damage, managers often capture and kill nuisance animals, but such temporary methods may not mitigate the problem and instead contribute to the decline and extinction of local animal populations (Woodroffe and Ginsberg 1998). To both prevent damage and conserve wildlife, it is important to investigate the factors underlying agricultural damage by wildlife.

Bears (*Ursus* spp.) are involved in human-wildlife conflicts in agricultural landscapes globally (Shivik et al. 2011; Elfström et al. 2014; Takahata et al. 2014) and are known for their opportunistic feeding behavior, which allows them to take advantage of their environment (Bojarska and Selva 2012). Brown bears (*U. arctos*) are large, omnivorous mammals that range widely from Eurasia to North America. In Hokkaido, Japan, these bears seasonally consume a wide variety of food, including herbaceous plants (from spring to late fall); ants (summer); berries (late summer to fall); nuts (fall); and deer (throughout the year) (Sato 2005). From late summer to early fall, brown bears have difficulty meeting their nutritional requirements through natural foods; thus, this time period is when Hokkaido brown bears most frequently invade agricultural fields and eat crops (Sato et al. 2005).

Such agricultural damage has recently been increasing in Hokkaido, causing estimated financial losses of 5,000,000–8,000,000 yen per year (Hokkaido Prefectural Government 2017a). Although countermeasure efforts, such as clearing the bush around crop fields and introducing electrical fences, are utilized to prevent the food-conditioning of bears, financial constraints and limited human resources preclude such management for all agricultural fields; thus, bears invading those fields are killed as nuisance control. Such bear harvest has also been increasing recently. One of the concerns about the management plan of Hokkaido brown bears is that while the maximum limit of bear harvest is determined by the Hokkaido Prefectural Government (2017a), the basal population used to consider the limit is known to have a wide confidence interval (Year 2012: $10,600 \pm 6,700$). Thus, the effect of increasing bear harvest on the regional population dynamics is not well understood.

Demographic and physical characteristics among individuals may be related to the nuisance behavior of bears. For example, males generally have larger home ranges (Mano 1994; Dahle and Swenson 2003a, 2003b) and may have more chances to invade crop fields than females (Ben-David et al. 2004). Moreover, younger bears are more likely to inhabit areas near artificial landscapes (Nellemann et al. 2007; Graham et al. 2010), and larger bears can dominate high-quality diets (Luque and Stokes 1976; Herrero 1983; Gende and Quinn 2004), which both apply to crop consumption. Since the reproductive success of bears is highly affected by demographic and physical characteristics (Zedrosser et al. 2007), bear harvests could have a substantial impact on the regional population structure through selective removal of specific individuals. However, the relationship between such characteristics and crop consumption has not been investigated.

Most previous studies that have investigated the factors underlying human-bear conflicts in agricultural landscapes have focused on environmental factors (Wilson et al. 2005; Nagasaka et al. 2011; Northrup et al. 2012; Hata et al. 2017). These studies indicated the effects of landscapes and human settlements surrounding crop fields on the human-bear conflict and provided management implications based on non-lethal practices. Incorporating individual aspects of bears into these investigations should enable an evaluation of how nuisance control may impact population structure and how non-lethal practices may instead be effective. Unveiling this relationship is likely to provide valuable insight into the management and conservation of Hokkaido brown bears.

Corn (dent corn and sweet corn) is the most frequently consumed crop by Hokkaido brown bears (Hokkaido Prefectural Government 2017a; Fig. S1) and is the only C_4 plant on which these bears forage. C_4 plants generally show significantly higher stable carbon isotope ratios than C_3 plants, so we can precisely evaluate the contribution of corn to the diet of each bear via stable isotope analyses.

Therefore, in this study, we aimed to investigate the relationship of corn consumption by bears with both individual factors, such as demographic (sex and age) and physical (body size) characteristics, as well as environmental factors (i.e., human presence and crop field accessibility). We expect that the age and body size of bears will be positively correlated with their crop consumption and that males will consume more crops than females.

Materials and methods

Study area

This study was undertaken on the Oshima Peninsula, South-Western Hokkaido, Japan (Fig. 1). The Oshima Peninsula comprises 6,560 km² (Hokkaido Prefectural Government 2016), and the size of its human population is 447,938 (Hokkaido Prefectural Government 2017b). The Oshima Peninsula is narrow in the west-east direction, and steep mountains cover a large part of the region. There are few flatlands in the region, and human residential areas closely adjoin or sometimes overlap with brown bear habitat. In 2012, the estimated brown bear population on the Oshima Peninsula was 1,400±600 (Hokkaido Prefectural Government 2017a). The mean number of brown bears killed for nuisance wildlife control annually in the region is approximately 100. Bears are often killed by guns when found on or around crop fields or captured by box traps or foot snares. The distribution of the financial damage among dent corn, beets, sweet corn, wheat and other crops throughout Hokkaido in 2014 has been estimated at 60%, 17%, 6%, 4% and 13%, respectively. Therefore, losses of corn represent two-thirds of the financial losses related to crop damage by bears (Hokkaido Prefectural Government 2017a).

Sample preparation

Since 1996, the Institute of Environmental Sciences of the Hokkaido Research Organization has collected biological samples of Hokkaido brown bears harvested as a result of nuisance control and game hunting. Among these collected samples, femurs were chosen for stable isotope analyses in this study because collagen from the entire compact bone thickness of femur reflects time-averaged isotopic information (Matsubayashi and Tayasu 2019), which enables an understanding of what each bear consumed throughout most of its lifespan. Additionally, the age, sex, femur size and harvest point were recorded for each individual. The ages of the bears were determined by counting the cementum annuli from an extracted tooth (Mundy and Fuller 1964). In this study, we selected 123 bears (female: $n=61$, male: $n=62$) harvested from 2000 to 2012 and stratified our sample to accurately represent variations in sex, age, femur size and harvest points. Most of these bears were considered nuisance bears because

they had invaded agricultural fields or human residential areas. We used only bears older than 4 years because the stable isotope ratios in juvenile bears, which mainly feed on their mother's milk, are affected by trophic enrichment (Bocherens et al. 2004). Femur length was used as an indicator of body size (Matsubayashi et al. 2016). Stable isotope ratios of 92 individuals were obtained from Matsubayashi et al. (2015), and we measured the stable isotope ratios of 31 additional individuals.

We determined 26 potential dietary items of the brown bears in our study area based on Sato et al. (2005) and collected 8 dietary items from the study site (Table 1). Additional isotopic data for those dietary resources were obtained from Matsubayashi et al. (2015), who sampled 18 dietary items at the same study site from 2009 through 2011.

Stable isotope analysis

We first drilled into the femurs using an electric drill to obtain bone powder (approximately 0.5 g), and we then immersed the samples in a 1:1 solvent of methanol and chloroform and extracted bone collagen using the experimental method of Schoeninger and DeNiro (1984). Briefly, bone samples were immersed in a 0.1 M NaOH for 12 h and then treated with 1.0 M HCl (12 h), heated in Milli-Q water (Millipore, Bedford, Massachusetts, USA) at 95°C for approximately 12 h, filtered through a 0.7-μm glass-fiber filter (GF/F, Whatman, Buckinghamshire, UK) and then freeze dried. We used approximately 0.4 mg of collagen for stable isotope measurements. Among the dietary items, we removed lipids from deer muscle using a 1:1 solvent of methanol and chloroform. Then, all the potential dietary samples were dried at 60 °C for at least 2 days and then ground in a mortar.

We measured stable carbon and nitrogen isotope ratios using a mass spectrometer (Thermo Finnigan Delta V advantage, Thermo Scientific, Waltham, MA, USA) connected to an elemental analyzer (Flash2000, Thermo Scientific, Waltham, MA, USA). Carbon and nitrogen isotope ratios are expressed in δ notations based on the international standard scale as follows:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}}) \quad (1)$$

where X is ^{13}C or ^{15}N ; R_{sample} corresponds to the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio of the measured sample; and R_{standard} is the Vienna Pee Dee Belemnite (VPDB) $^{13}\text{C}/^{12}\text{C}$ or the $^{15}\text{N}/^{14}\text{N}$ of atmospheric nitrogen. The overall estimated measurement error was <0.1‰ for $\delta^{13}\text{C}$ and <0.2‰ for $\delta^{15}\text{N}$.

Estimation of the contribution of corn to bear diets

We first performed a K nearest-neighbor randomization test (KNN test; Schilling 1986; Rosing et al. 1998) with Bonferroni *P*-adjustments to investigate whether the stable isotope ratios of all dietary items differed from each other. We combined dietary items whose stable isotope ratios were not significantly different.

We set trophic discrimination factors of $\delta^{13}\text{C}$ ($5.0 \pm 1.5\text{‰}$; Deniro and Epstein 1981; Minagawa and Wada 1984; Schoeninger and DeNiro 1984; Ambrose and DeNiro 1986; Sealy et al. 1987) and $\delta^{15}\text{N}$ ($3.0 \pm 1.5\text{‰}$; Vogel 1978; Von Schirnding et al. 1982; Schoeninger and DeNiro 1984; Lee-Thorp et al. 1989) for the bone collagen of brown bears (Table S1). We assumed that human processed foods had a negligible influence on the stable isotope value of each bear because a stomach content analysis of bears in our study area indicated low consumption at 4.8% (17 out of 354) of bears harvested from 2000 to 2009 (Mano and Tsuruga 2011). We then estimated the proportional contribution of each food resource to the diet of bears using the Bayesian isotopic mixing model Stable Isotope Analysis in R (SIAR; Parnell et al. 2010), and differences in the concentration of each element (C% and N%) were included in the analysis (Table S1). The estimated contribution of some dietary items can be inaccurate when the isotopic geometries of the dietary items are similar (Phillips et al. 2014). We expected corn, which is a C_4 plant, to show distinct and higher $\delta^{13}\text{C}$ values than other dietary items so that the contribution of corn could be accurately assessed. The mode of the distribution of the estimated contribution probability was used as the representative value of the dietary consumption rate in the latter statistical analysis.

Environmental factor quantification

To quantify the environmental factors within the habitats of individual bears, we used the software QGIS version 3.4 (QGIS Development Team 2020). The human population size, estimated corn field area, and estimated length of the edge between corn fields and forests (hereafter, edge length) were used as the potential environmental variables accounting for corn consumption. The human population size was used as an indicator of human presence in the

landscape, the corn field area was used as an indicator of corn availability, and edge length was used as an indicator for crop field accessibility by bears.

We established multiple buffers of different sizes around the harvest points of each bear and calculated the amount of each environmental variable in the buffers. We calculated the human population by summing the proportionate value of 1-km² vector grid population data (Ministry of Internal Affairs and Internal Communications 2015) that overlaid the buffers of each bear. Since the regional population changed from 2000–2012, we matched the population data with the years when the bears were harvested; we used 2000 data for bears harvested from 2000 to 2002, 2005 data for 2003–2007 bears, and 2010 data for 2008–2012 bears. Unfortunately, the spatial distribution of cornfields is not available in this region, but that of agricultural fields only. Alternatively, we estimated the corn field area as follows: i) the area in which agricultural fields are intersected with the buffers of each bear was calculated; ii) the proportion of the corn field area to the total agricultural field area was calculated; and iii) the corn field area was estimated by multiplying i) by ii). Similarly, we estimated the edge length using the following steps: i) the length over which agricultural fields and forests adjoined in the buffers of each bear was summed; ii) the proportion of the corn field area to total agricultural field area was calculated; and iii) the edge length was estimated by multiplying i) by ii). We used the vegetation map (scale 1:50000) provided by the Ministry of Environment (2015) for the spatial data of agricultural fields (including crop fields and pasture lands; Hata et al. 2017) and forests. We used multiple statistical sources based on administrative district listed in Text S1 to derive the area data of corn fields in our study area from 2000 to 2012. We assumed human population size would have a negative effect on corn use because brown bears tend to avoid humans (Elgmork 1978). Conversely, we assumed that the corn field area and edge length would have a positive effect on corn use because bears generally invade fields from the boundary zone.

Six buffers were used for females (radii=1.0, 1.5, 2.0, 2.5, 3.0, and 3.5 km) in accordance with the home range sizes of female brown bears in the study area (3.2 – 39.1 km², $n=18$; Mano 1994). Nine buffers were used for male brown bears (radii=1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, 4.5, and 5.0 km) because of their broader home range sizes in this study area (25.2–83.2 km², $n=10$; Mano 1994). Although a previous study showed that one male brown bear moved over an approximately 300-km² range (Tsuruga and Ishida 2011), we did not use buffers larger than 5.0

km because the previously recorded range seemed too large to be strongly associated with crop consumption. Harvest points were documented in the harvest report of each bear as the name of the district and an area mesh code ($n=107$), which were spatial codes used to describe 25-km² square grids defined by the Administrative Management Agency (1973), or a point on a geographical map ($n=16$). For bears reported with district names and area mesh codes, we first intersected the area of the district and mesh code. Then, we generated 15 random points inside the agricultural fields and forests in the intersected area since bears were most frequently harvested in these landscape elements. Then, we established multiple buffers from all points and calculated the mean value of the human population, corn field area, and edge length in each buffer. The mean area of uncertainty for the generated random points was 7.46 km² in females and 6.32 km² in males.

Statistical analysis

We used generalized linear models (GLM) and fit corn consumption as the response variable to predict the factors contributing to agricultural damage. The modeling procedure was conducted separately for females (female bear analysis) and males (male bear analysis). The model had a beta error distribution, which is employed when the response variable ranges from 0 to 1 such as with proportional values. The explanatory variables comprised individual information (age and femur length) and environmental information (human population, the corn field area, and the edge length within the buffer) for each bear.

Before GLM analysis, we employed Spearman's correlation analysis among the explanatory variables to avoid multicollinearity. When the correlation exceeded 0.7, we selected either variable from the pair for the statistical analysis. A high correlation ($r > 0.85$) was detected between the corn field area and edge length for both females and males (Table S2). We used the edge length for further analysis because it considers the connection between forests and corn fields, thereby incorporating finer information of the landscape configuration than the corn field area. High correlations were not found among other combinations of variables, and we used the four variables for GLM analysis.

Then, we constructed multiple models including all potential combinations of explanatory variables in both the female and male bear analyses. We used Akaike's information

criterion (AIC) for model selection. The model that had the lowest AIC score was selected as the best, and models with $\Delta\text{AIC} < 2$ were also selected as reasonable with substantial support. The analysis was performed using the betareg (Cribari-Neto and Zeileis 2010) and MuMIn (Bartón 2013) packages of program R version 3.4.0 (R Core Team 2018).

Results

The KNN tests showed significant differences in stable isotope values among C_3 herbs, C_3 fruits, and corn (Bonferroni adjusted $P < 0.005$). However, the values for ants and deer did not show significant differences, so we grouped them as terrestrial animals (Table S1). Among all the dietary items, corn, which is a C_4 plant, predictably showed the highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig. 2 and Table S1). The isotopic values of individual bears mostly ranged close to the values of C_3 herbs, C_3 fruits, and terrestrial animals. More male bears presented high $\delta^{13}\text{C}$ isotopic values that plotted close to corn (Fig. 2).

The Bayesian isotopic mixing model showed that both female and male bears consumed corn, which contributed a median of 7.8% and 5.6% to their lifelong diet, respectively (Fig. 3). The main diet components were naturally derived resources such as C_3 herbs and C_3 fruits, comprising a total of more than 70% of the diet in both sexes. The estimated contributions of corn to the individual bears' diets varied widely from 1.4% to 30.9% in females and 1.3% to 42.0% in males (Fig. 4). The number of bears that depend highly on corn (more than 20%) was larger among males (11 out of 62 bears) than females (1 out of 61 bears), but the number of bears with a low dependence (less than 5%) was also larger among males (27 out of 62 bears) than females (17 out of 61 bears).

In the female bear analysis, the best model was the null model, and other 14 competing models had $\Delta\text{AIC} < 2$ (Table 2). In the male bear analysis, the best model ($\Delta\text{AIC}_{\text{best-null model}} = 7.048$) included femur length, human population size, and edge length within a 2.5-km radius, and other 8 competing models had $\Delta\text{AIC} < 2$ (Table 3). All of these competing models included femur length and human population size, and most models included edge length. Both femur length and edge length were positively correlated with corn consumption. The human population size was negatively correlated with corn consumption. One model with the highest AIC in the competing models also included age, which had a positive effect on corn

consumption, although the SE of the coefficient was large. The radii of the buffers of the selected models varied from 2.0 km to 3.5 km.

Discussion

The stable isotope analysis showed that most Hokkaido brown bears did not consume corn as the main component of their diet, although some bears consumed a large amount of corn. Because the stable isotope ratios of bone collagen used in this study reflect the dietary information over the lifespan of the bears (Matsubayashi and Tayasu 2019), the variation in consumption could be interpreted as different crop-raiding patterns between individuals. For instance, bears with low corn consumption could have eaten relatively small average quantities of corn each year or relatively large quantities some years when natural foods were scarce but limited amounts in other years. In contrast, bears showing high corn consumption could have invaded crop fields yearly.

Female bear analysis indicated that no specific variables were correlated with corn consumption (Table 2), suggesting that the factors affecting female corn consumption remain unclear. This result also suggests that female bears do not always consume large amounts of crops even when their habitat includes accessible agricultural fields. Similar results were also reported in previous studies; some female bears never damaged crops despite the close proximity of their home ranges to agricultural land (Sato et al. 2008; Tsuruga and Ishida 2011). In addition, Ditmer et al. (2016) showed that captive female black bears that were born in the wild were more likely to eat natural foods than anthropogenic diets because of their taste familiarity and innate food preference. Considering that most female bears were found to consume corn but avoided using it as a major resource, female bears in our study area presumably recognized crops as a dietary choice but preferred natural resources. Thus, the patterns of female bear crop use in relation to individual and environmental factors remain unclear and may be related to factors not considered in this study, such as differences among individual bears in risk perception (Nellemann et al. 2007; Ordiz et al. 2012) and social learning (Breck et al. 2008; Mazur and Seher 2008; Hopkins 2013; Nielsen et al. 2013). We also believe that our analysis lacked female bear individuals with higher corn consumption to precisely account for the causal factors; therefore, further studies are needed to include such bears in the investigation.

The male bear analysis suggested that bears with longer femurs consumed greater amounts of corn, indicating that larger bears ate more corn than smaller bears. This result suggests that brown bears in Hokkaido might have higher growth rates due to corn consumption from late summer to early fall; therefore, it would have been highly advantageous for bears to invade corn fields instead of consuming a nutritionally insufficient natural diet during this season (Sato et al. 2005). Compelling evidence for this case is that sub-adult bears with higher corn consumption are as large as adult bears (Fig. S2), and it is likely that corn contributed to the high-quality initial growth of the sub-adult bears in our study area. Moreover, because bears intake high nutritive resources for a long duration, it is difficult for the bears to survive without them because of their high energetic demand (Robbins et al. 2004), suggesting endless consumption to avoid starvation and leading to habituation to anthropogenic resources. In this case, factors other than body size would have motivated bears to invade corn fields, ultimately leading to a larger body size for those individuals. For instance, social learning of dietary strategies that cubs learn from their mother could affect the behavior of the cub after becoming independent (Hopkins 2013). Since bears are believed to have a social advantage as determined by body size when competing for dietary resources (Luque and Stokes 1976; Herrero 1983; Gende and Quinn 2004), it is also likely that larger bears dominate corn fields and prevent smaller bears from consuming corn. Thus, we assume that bears in our study area are food-conditioned and therefore, invade agricultural fields yearly. Conversely, age showed limited support in relation to corn consumption. While other studies have shown a strong correlation between body size and age (Bartareau et al. 2011; Hilderbrand et al. 2018), the correlation coefficient between the variables in this study was relatively small ($r=0.394$, Table S2), which possibly resulted from our decision to include bears older than 4 years. Therefore, our analysis was able to separate the effects of body size and age, and the result implies that body size is a better explanatory factor for corn consumption than age.

Among the environmental factors studied, edge length had a positive effect on corn consumption by male bears, indicating that brown bears raid crop fields with greater accessibility from the forest and better escape cover, which is consistent with previous findings showing that agricultural lands with long zones of contact with forests tend to be more frequently damaged by bears (Nagasaka et al. 2011). Related studies also revealed that bears in Hokkaido often cross

boundaries between forests and agricultural fields to feed on crops (Sato et al. 2008; Tsuruga and Ishida 2011). The high correlation between the edge length and corn field area suggests the difficulty to distinguish the effect of the edge length (i.e., corn accessibility) and corn field area (i.e., corn availability) on corn consumption. However, we believe that accessibility is more valid than availability for explaining corn consumption considering that brown bears do not consume all available corn in the field and that they may detect corn even in a small amount given their high olfactory sensation. Human population size in the region had a negative effect on individual corn consumption, suggesting that bears invade agricultural fields where the human population is smaller. This result supports previous investigations that found that brown bears showed avoidance of human residential areas in Europe and North America (Mace et al. 1996; Ordiz et al. 2011; Sánchez et al. 2014). Although some brown bears habituate to human-dominated environments (Herrero et al. 2005; Martin et al. 2010), the bears in our study area foraged on crops by avoiding the risks associated with humans. The spatial configuration of the Oshima Peninsula roughly explains this pattern. Agricultural fields are located inland from human settlements toward mountainous forests that cover the peninsula and occupy a large area. Therefore, crop fields far from human settlements are in less populated areas, are connected to large areas of bear habitat, and are more vulnerable to raiding.

The male bear analysis showed the highest explanatory power at a radius of 2.0-3.5 km among the nine analyzed buffer sizes (radii from 1.0–5.0 km). Despite the knowledge that male bears generally have large home ranges and that no spatial relationship has been found between male bears and crop consumption in Eastern Hokkaido (Hata et al. 2017), studies have shown that habitat selection by male brown bears is related to smaller spatial scales (Ciarniello et al. 2007; Sánchez et al. 2014). However, these studies show that larger-scale variables also influence habitat selection, and they emphasize that multi-spatial-scale models have better predictive power than single-scale models and allow the relationships between environmental factors and habitat selection by an animal to be correctly interpreted. Thus, based on our multi-buffer models, 2.0-3.5 km should be an appropriate size range for testing the relationship between the environmental variables we used and crop consumption by male brown bears in our study area. Further investigation is needed to reveal the finer- and broader-scale factors contributing to agricultural damage by brown bears.

Our results demonstrated that larger male bears were more likely to have consumed corn than other bears, which suggests that such bears are more likely to be harvested. Larger bears not only have advantages in aforementioned dietary competition, but they are also reported to show higher reproductive success than smaller bears, possibly resulting from physical dominance among males or size-based selection among females (Andersson and Iwasa 1996; Zedrosser et al. 2007). Therefore, selective removal of larger bears may cause dwarfism of the overall population (Matsubayashi et al. 2016) and impact the local population dynamics, although actual assessments of such an impact remain challenging with the current population estimation methodology. Given that the dependencies on agricultural crops vary highly among the bear individuals, specifying food-conditioned individuals should be the key to effectively reduce agricultural damage and conserve brown bear populations near agricultural landscapes.

To reduce both agricultural damage and alteration of population structure of brown bears, the opportunity for bears to learn to eat crops must be eliminated through environmental management. As the results in this study and another previous study (Mano 2009) also suggested, constructing electrical fences and clearing bushes along the borders between forests and crop fields may be practical and effective actions that make it difficult for bears to invade agricultural lands. When possible, relocating agricultural fields closer to populated areas or away from forests may further reduce the chronic conflicts and, together, enable long-term conservation of local populations.

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Declarations

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405 ***Conflicts of interests***

406 The authors declare that they have no conflict of interest.

407

408 ***Ethics approval***

409 This article contains no studies performed by any of the authors involving animals.

410

411 ***Informed consent***

412 Informed consent was obtained from each participant included in the study.

413

414 ***Author contributions***

415 TS, Junko M, FN conceived the project. All authors designed the study. TS, Jun M, MK, HT,

416 TM contributed to the data collection. TS and YF conducted the GIS analysis. TS, Jun M

417 performed the experiments and data analysis. TS led the manuscript preparation. All authors

418 contributed to manuscript revisions and approval of the manuscript for publication.

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Figure captions

Fig. 1 Location of the study area and points where female (n=61, white) and male (n=62, gray) Hokkaido brown bears (*Ursus arctos*) were harvested between 2000 and 2012 in the Oshima Peninsula in Hokkaido, Japan. Note that harvest points were reported as geographical points or documentations of the district name and area mesh code; for the latter, the expected harvest points are depicted in the figure by generating centroids of the 15 random points generated in the intersected area of documentation

Fig. 2 Mean ($\pm$ SD) carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) of bone collagen from female (n=61, triangle) and male (n=62, square) Hokkaido brown bears (*Ursus arctos*) and their dietary resources harvested and collected between 2000 and 2012 and between 2009 and 2011. Stable isotope ratios of prey items have been corrected to account for isotope discrimination factors

Fig. 3 Median contributions of each dietary resource to the diets of both female (n=61, white) and male (n=62, gray) Hokkaido brown bears (*Ursus arctos*), 2000–2012. Boxes show 25% and 75% quartiles, and whiskers represent 1.5*IQR (interquartile range) below the 25% or above the 75% quartiles

Fig. 4 Histogram of corn consumption by both female (above) and male (bottom) Hokkaido brown bears (*Ursus arctos*), 2000–2012

Tables

Table 1. Species and sample sizes [*n*] of potential dietary resources of brown bears (*Ursus arctos*) used for the stable isotope analysis in Matsubayashi et al. (2015) and this study; these data were collected from 2009 to 2011 in Hokkaido, Japan.

Food Resources	<i>n</i> (Matsubayashi et al. 2015)	<i>n</i> (this study)
C ₃ herbs		
<i>Angelica edulis</i>	11	0
<i>Angelica genuflexa</i>	5	0
<i>Angelica sachalinensis</i> var. <i>sachalinensis</i>	10	0
<i>Angelica ursina</i>	12	0
<i>Coelopleurus gmelinii</i>	5	0
<i>Cryptotaenia canadensis</i> ssp. <i>Japonica</i>	10	0
<i>Heracleum lanatum</i>	0	2
<i>Ligusticum scoticum</i> ssp. <i>Hulten</i>	1	0
<i>Oenanthe javanica</i>	5	0
<i>Petasites japonicus</i> (buds)	6	0
<i>Petasites japonicus</i> (stems)	0	2
<i>Pleurospermum uralense</i>	1	0
<i>Urtica platyphylla</i>	0	2
C ₃ fruits		
<i>Actinidia argute</i>	0	2
<i>Actinidia polygama</i>	10	0
<i>Fagus crenata</i>	9	0
<i>Morus australis</i>	10	0
<i>Quercus crispula</i>	0	2
<i>Vitis coignetiae</i>	0	2
Corn		
<i>Zea mays</i>	0	5
Ants		
<i>Camponotus obscuripes</i>	4	0
<i>Formica japonica</i>	5	0
<i>Formica lemani</i>	5	0
<i>Formica yessensis</i>	10	0
<i>Paratrechina flavipes</i>	5	0
Deer		
<i>Cervus nippon</i>	0	4

Table 2. Model selection results of generalized linear model analysis to predict the relationship between individual and environmental factors and corn consumption of female Hokkaido brown bears (*Ursus arctos*) from 2000 to 2012.

	AIC ^a	Δ AIC ^b	Buffer size (km)	Coefficients of Explanatory Variables ($\pm$ Standard Error)				
				Intercept	Age	Femur Length	Edge Length	Human Population
Best	-212.349	0	-	-2.417 ($\pm$ 0.077)	-	-	-	-
2	-210.947	1.403	3.0	-2.419 ($\pm$ 0.077)	-	-	-	0.053 ($\pm$ 0.068)
3	-210.930	1.419	1.5	-2.419 ($\pm$ 0.077)	-	-	-	0.052 ($\pm$ 0.067)
4	-210.922	1.427	3.5	-2.419 ($\pm$ 0.077)	-	-	-	0.052 ($\pm$ 0.068)
5	-210.898	1.451	1.0	-2.419 ($\pm$ 0.077)	-	-	-	0.050 ($\pm$ 0.066)
6	-210.896	1.453	2.0	-2.419 ($\pm$ 0.077)	-	-	-	0.051 ($\pm$ 0.067)
7	-210.885	1.464	2.5	-2.419 ($\pm$ 0.077)	-	-	-	0.050 ($\pm$ 0.068)
8	-210.747	1.603	2.5	-2.418 ($\pm$ 0.077)	-	-	0.045 ($\pm$ 0.071)	-
9	-210.669	1.680	3.0	-2.418 ($\pm$ 0.077)	-	-	0.040 ($\pm$ 0.071)	-
10	-210.659	1.690	3.5	-2.418 ($\pm$ 0.077)	-	-	0.040 ($\pm$ 0.071)	-
11	-210.625	1.725	2.0	-2.418 ($\pm$ 0.077)	-	-	0.037 ($\pm$ 0.071)	-
12	-210.613	1.736	-	-2.418 ($\pm$ 0.077)	0.037 ($\pm$ 0.072)	-	-	-
13	-210.506	1.843	1.5	-2.418 ($\pm$ 0.077)	-	-	0.028 ($\pm$ 0.072)	-
14	-210.408	1.941	-	-2.418 ($\pm$ 0.077)	-	-0.019 ($\pm$ 0.072)	-	-
15	-210.388	1.961	1.0	-2.418 ($\pm$ 0.077)	-	-	0.014 ($\pm$ 0.072)	-

^aAkaike's information criterion score

^bDifference in AIC score from that of the best model

623 **Table 3.** Model selection results of generalized linear model analysis to predict the relationship between individual and environmental
624 factors and corn consumption of male Hokkaido brown bears (*Ursus arctos*) from 2000 to 2012.

	AIC ^a	Δ AIC ^b	Buffer size (km)	Coefficients of Explanatory Variables ($\pm$ Standard Error)				
				Intercept	Age	Femur Length	Edge Length	Human Population
Best	-165.365	0	2.5	-2.250 ($\pm$ 0.113)	-	0.282 ($\pm$ 0.108)	0.172 ($\pm$ 0.097)	-0.205 ($\pm$ 0.108)
2	-165.007	0.358	3.0	-2.248 ($\pm$ 0.113)	-	0.283 ($\pm$ 0.108)	0.175 ($\pm$ 0.099)	-0.203 ($\pm$ 0.108)
3	-164.652	0.713	2.0	-2.247 ($\pm$ 0.114)	-	0.274 ($\pm$ 0.108)	0.157 ($\pm$ 0.096)	-0.184 ($\pm$ 0.106)
4	-164.596	0.768	2.5	-2.232 ($\pm$ 0.115)	-	0.321 ($\pm$ 0.104)	-	-0.167 ($\pm$ 0.107)
5	-164.278	1.087	2.0	-2.231 ($\pm$ 0.115)	-	0.312 ($\pm$ 0.104)	-	-0.162 ($\pm$ 0.106)
6	-164.251	1.114	3.0	-2.231 ($\pm$ 0.115)	-	0.323 ($\pm$ 0.105)	-	-0.155 ($\pm$ 0.106)
7	-164.134	1.231	3.5	-2.245 ($\pm$ 0.114)	-	0.281 ($\pm$ 0.109)	0.171 ($\pm$ 0.101)	-0.189 ($\pm$ 0.107)
8	-163.604	1.761	3.5	-2.229 ($\pm$ 0.116)	-	0.320 ($\pm$ 0.105)	-	-0.135 ($\pm$ 0.105)
9	-163.421	1.943	2.5	-2.250 ($\pm$ 0.113)	0.025 ($\pm$ 0.104)	0.274 ($\pm$ 0.116)	0.172 ($\pm$ 0.097)	-0.208 ($\pm$ 0.108)

625 ^aAkaike's information criterion score

626 ^bDifference in AIC score from that of the best model

627

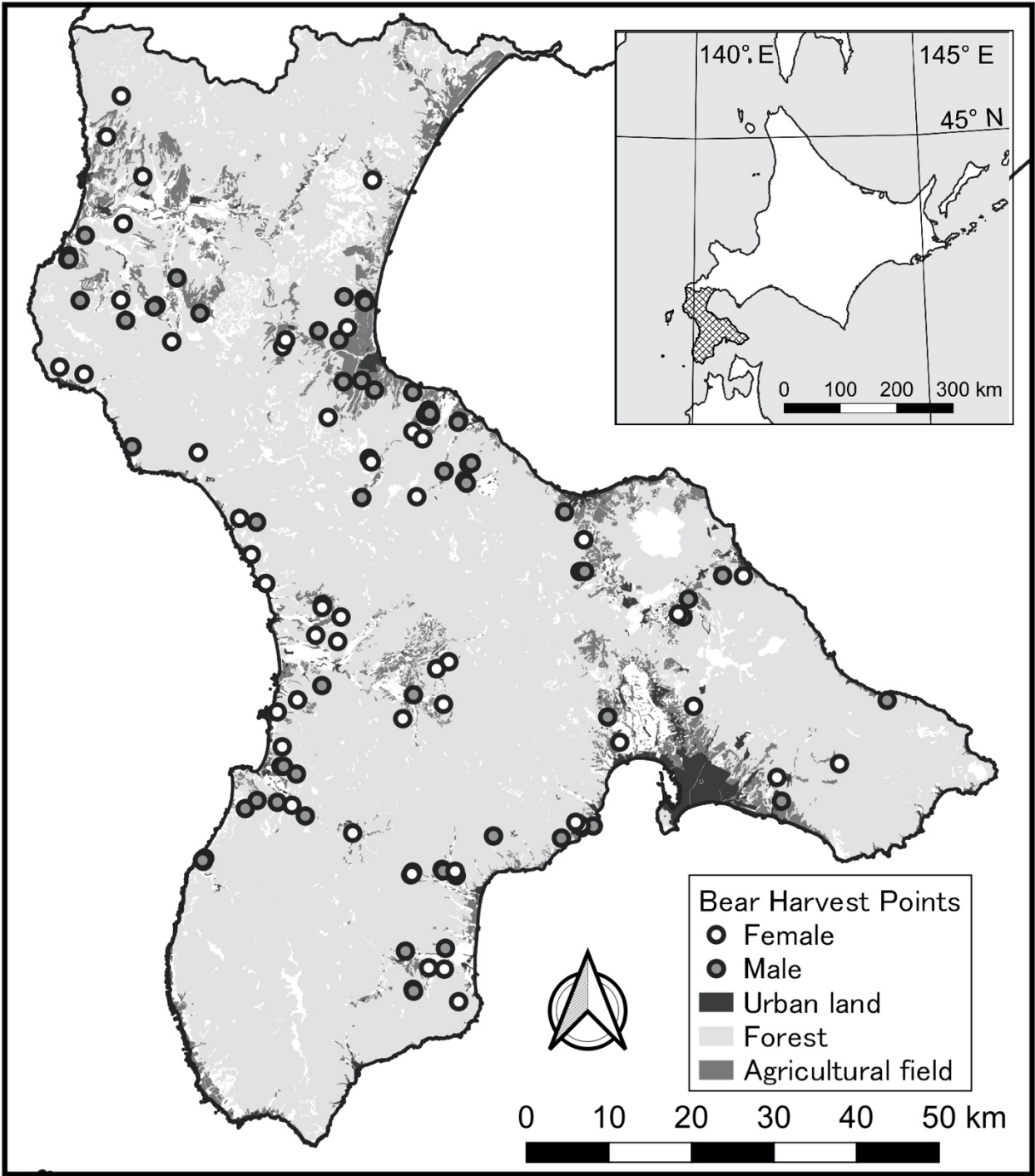


Fig. 1

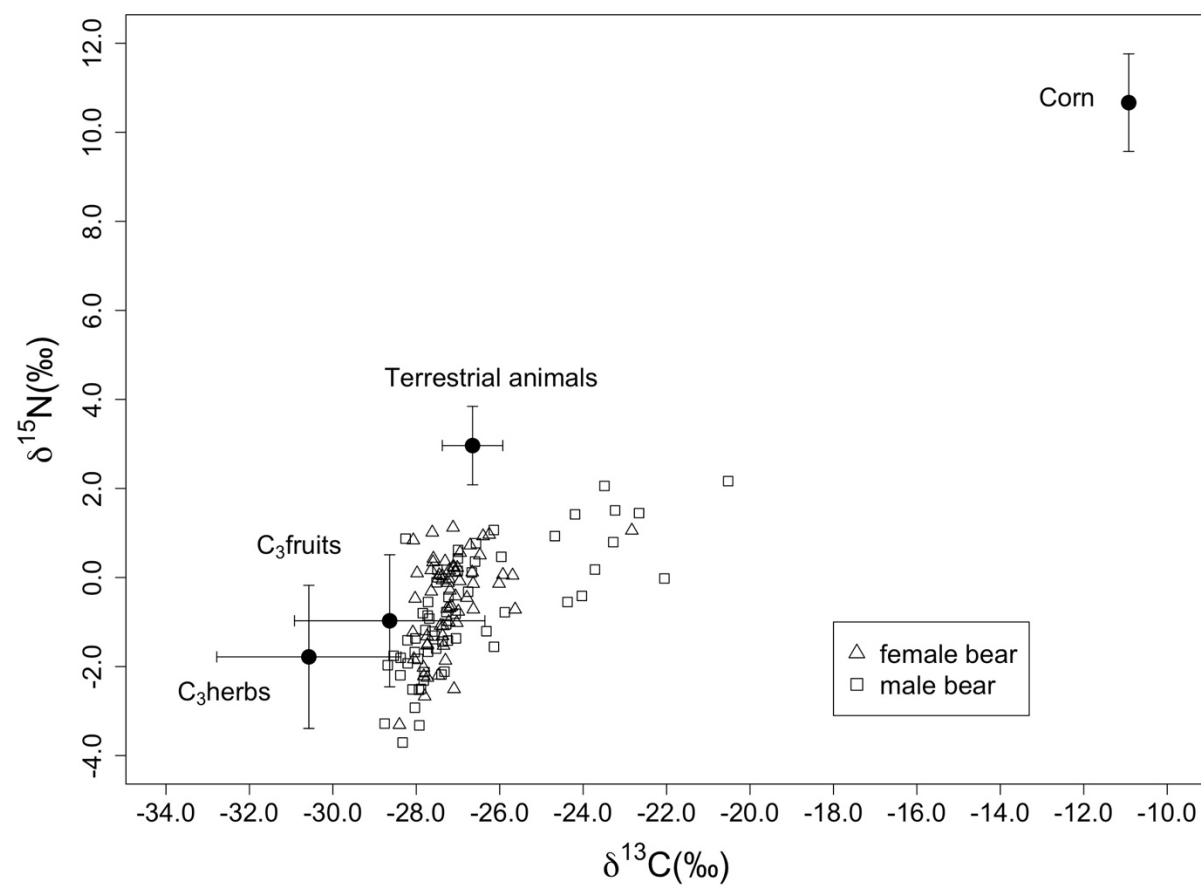


Fig. 2

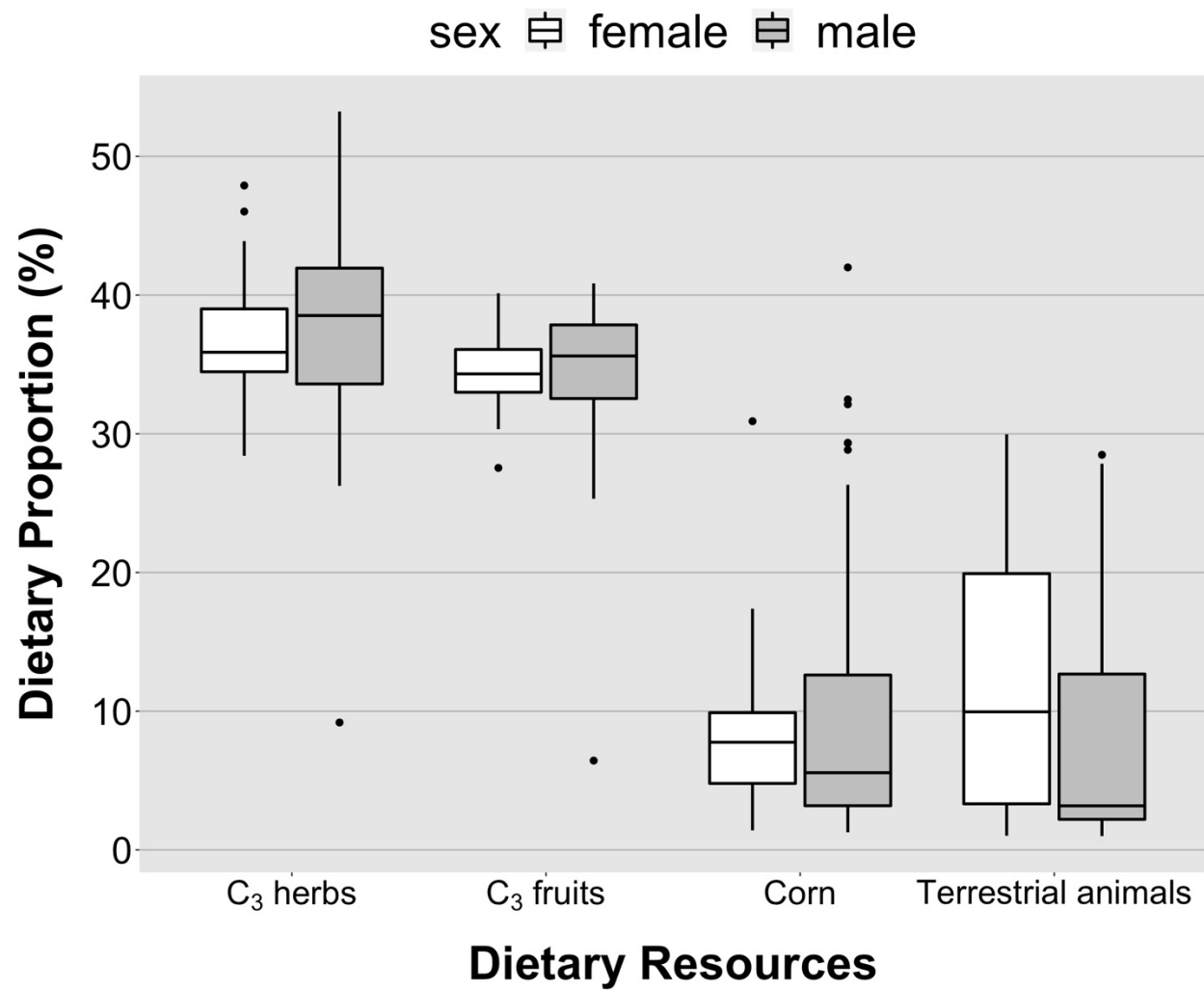
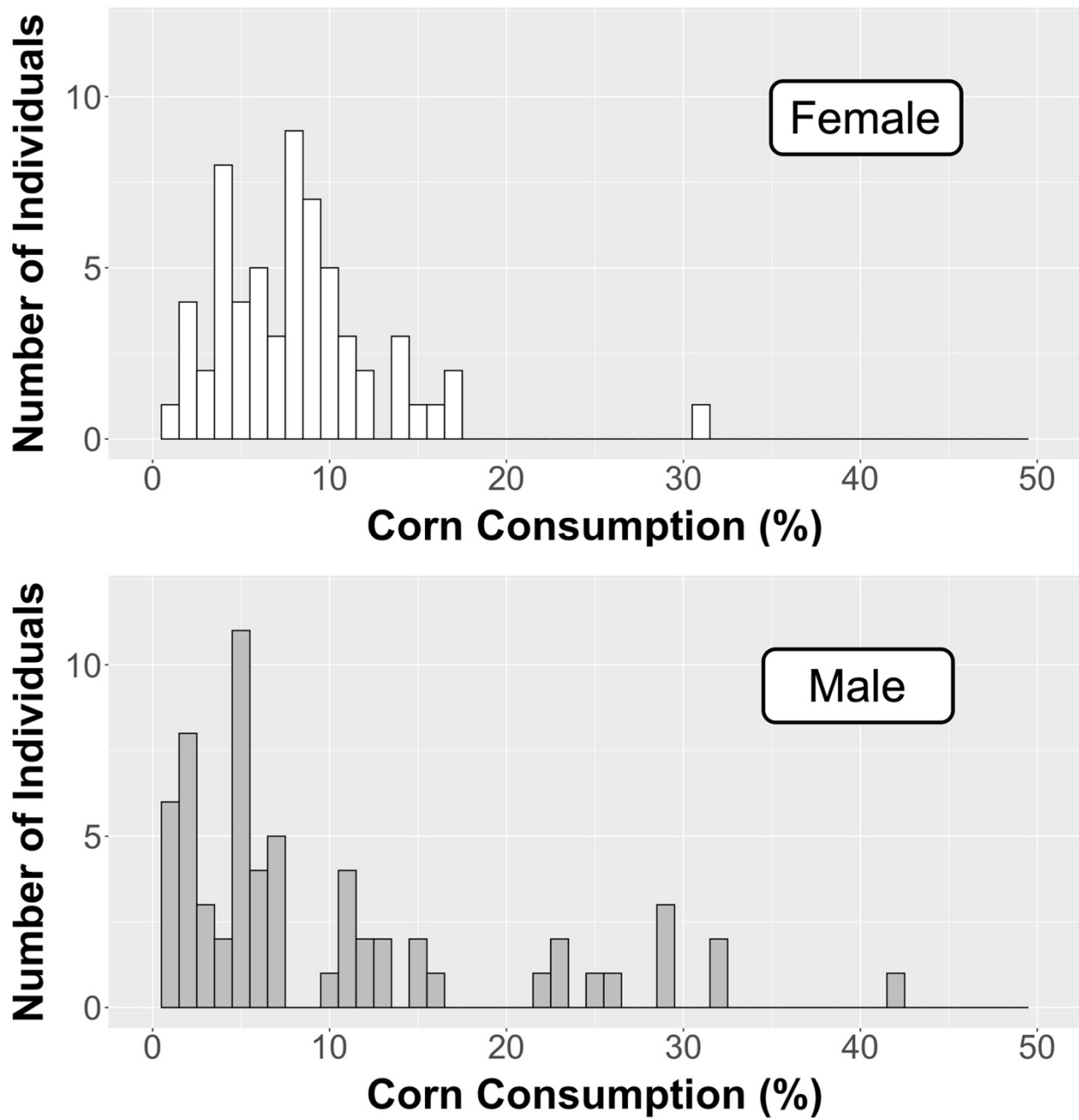


Fig. 3



638
639 **Fig. 4**