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Research article

Do ingredient and nutrient intake reveal individual dietary specialization in an omnivorous carnivore, the brown bear?

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Generalist populations often harbor individual dietary specialists. Whether using a narrower set of resources than the population (= specialization) affects specialists' nutrient intake remains underexplored. We evaluated variation in ingredient and nutrient specialization in a European brown bear *Ursus arctos* population via the Proportional Similarity Index (PS*i*, from 0 = highly specialized to 1 = not specialized) and assessed associations of specialization with year, season and reproductive class. Different methodologies concerning the organization of raw data for PS*i* calculations were evaluated (i.e. the resolution of diet compositional data (feces vs the average of all feces per individual) and temporal restrictions for the population (year-round vs within-season). Overall, a tendency for ingredient specialization (PS*i* 0.37 ± 0.14) and absence of nutrient specialization (PS*i* 0.79 ± 0.10) was observed. Ingredient specialization was mainly influenced by the proportion of berries, graminoids, oats and moose in the diet. Annual, seasonal and reproductive class effects were moderate and did not strongly affect PS*i* for both ingredients and nutrients. Organizing diet compositional data from a 'feces resolution' to 'individual resolution' decreased specialization. Changing the comparative population in PS*i* calculations from 'all-year-round' to 'within year and season' also resulted in less pronounced specialization. The degree of specialization was not caused by individuals exhibiting consistent ingredient preferences over the years (low repeatability of PS*i*) except in spring. Our results suggested absence of nutrient specialization and mild ingredient specialization, which appeared to be an outcome of the ecological circumstances rather than specific individual traits. Additionally, we demonstrated that the methods applied can have substantial influence for the calculation of specialization indices.

Keywords: brown bear, dietary specialization, nutrient

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Introduction

The use of dietary resources is commonly described as a population property, which indirectly implies that the diet of conspecifics within a population is similar or equal (Bolnick et al. 2003). Nonetheless, individualism in resource use within a population has been reported several decades ago, i.e., a set of (dietary) resources is available to and used by the population, but certain individuals only use a subset of these resources (reviewed by Bolnick et al. (2003)). The latter is commonly referred to as individual dietary specialization – defined as realized (variation in resource consumption) and not evolutionary specialization (an evolved physiological phenotype to use specific resources) (Devictor et al. 2010) – and occurs in many vertebrate and invertebrate species (Bolnick et al. 2003). Such dietary individual specialists are often 'hidden' in more generalist populations. For instance, in the great tit *Parus major*, which is considered a dietary generalist, dietary specialization was observed among breeding pairs, with more specialized pairs having larger broods (Pagani-Núñez et al. 2015). Similarly, a red fox *Vulpes vulpes* population in eastern France included individuals that specialized on free-ranging domestic Bresse chickens (Jacquier et al. 2020a).

Intrapopulation dietary variation is often explained with factors such as year, season, age, sex and morphology, which can be modelled statistically (often mixed effects regression models, i.e. diet composition ~ year, season, age, sex, morphology), but it does not equal individual specialization; rather, individual specialization contributes to intrapopulation dietary variation (Bolnick et al. 2003). As reviewed by Bolnick et al. (2003), individual specialization can be perceived as the variation in the residual error term in a statistical model which allows to fine-tune the definition: individuals whose dietary niche is substantially narrower than the population's niche for reasons not attributable to sex, age, morphology or temporal effects. To quantify the degree of individual specialization, indices of 'intrapopulation dietary variation' or 'individual specialization' can be used (Bolnick et al. 2002), as they typically compare individuals with the population. After calculating such indices, effects of temporal or other intrinsic or extrinsic factors on the index can be evaluated. For example, in a population of the seabird Brünnich's guillemot *Uria lomvia*, diet specialization was observed although the difference in specialization between age and sex groups was limited, suggesting that some individuals specialized independent of their sex or age (Woo et al. 2008). The determinants of individual dietary specialization are complex interplays between the environment (resource characteristics and abundance) and the individual (reviewed by Bolnick et al. 2003). An ecological approach to specialization is to consider it as a mechanism of within-population resource partitioning. Herbivores and carnivores showed fundamental differences in the (daily) amount of food required (De Cuyper et al. 2020), which resulted in differences in time devoted to foraging due to differences in the distribution of forage and prey resources. This suggests that herbivorous species should be less likely to show within-population resource partitioning compared to carnivores. An isotope-based study of herbivore and carnivore populations in African savannas supported this assumption, where herbivorous species showed lower levels of isotopic differentiation across individuals than carnivores (Codron et al. 2016).

Obtaining a balanced nutrient intake is an important driver for foraging behavior (Raubenheimer et al. 2009, Erlenbach et al. 2014, Kohl et al. 2015, Remonti et al. 2016) and has been linked to fitness (Lee et al. 2008, Erlenbach et al. 2014, Solon-Biet et al. 2014). Individuals can regulate nutrient intake by foraging for different food items with similar nutritional properties or by combining foods of varying nutrient composition in the required proportion (Raubenheimer and Simpson 1997, Raubenheimer and Jones 2006, Mayntz et al. 2009). For instance, in a white shark population *Carchardon carcharias*, variation in resource use was observed with some individuals using only subsets of specific prey, making them dietary specialists. However, overall nutrient intake was similar among individuals in the population (Grainger et al. 2023). This raises the question whether a similar nutrient intake for specialists and non-specialists can always be assumed within the same population. Among populations of the same species, dietary variation is well documented. For instance, a higher degree of carnivory has been described for omnivores (brown bear *Ursus arctos*, European badger *Meles meles*, European pine marten *Martes martes*) living in more northern latitudes compared to their southern conspecifics (Vulla et al. 2009). The diet of wild boars (*Sus scrofa*) was highly variable across its global range in terms of food items, but dietary nutrient profiles were also distinct between geographical regions (Senior et al. 2016).

Brown bears are omnivorous carnivores that have been extensively studied in terms of foraging behavior, including the food items and nutrient composition of the diets (Fortin et al. 2007, Bojarska and Selva 2012, Stenset et al. 2016, Coogan et al. 2018, De Cuyper et al. 2023). They experience a strong seasonality in their diets, which in many populations fluctuate from protein-rich animal-based diets in spring and summer to carbohydrate-rich fruit-based diets in fall (Stenset et al. 2016, Coogan et al. 2018). In recent years, it has been observed that bears specifically foraged for a low protein to non-protein ratio in the fall diet (Robbins et al. 2007, 2022, Erlenbach et al. 2014), which led to an efficient accumulation of adipose tissue for hibernation (Erlenbach et al. 2014). Dietary specialization in ursid populations has been studied to some extent via quantitative measures of diet variation, but only at the level of food items, not nutrients. In the Asian black bear *Ursus thibetanus*, dietary specialization was observed but was mainly associated with seasonal food fluctuations: individuals were more specialized in summer (low food abundance) and less specialized in spring and fall (high food abundance) (Mori et al. 2019). Adult male polar bears *Ursus maritimus* have been described as specialized on bearded seals *Erignathus barbatus* compared to adult females and subadults in the Hudson Bay area, Canada (Thiemann et al. 2011). This suggests that although dietary specialization was observed, this was mainly caused by

temporal effects or intrinsic effects such as age, sex and reproductive class. However, Hertel et al. (2023) reported on individual dietary specialization in European brown bears within a single population (ranging from omnivorous to carnivorous diets) and found that it was strongly determined by social learning from the mother, the environment (resource abundance or habitat composition) and other maternal effects (genotype or maternal environment that shape similar phenotypes of the offspring). Further examination of individual dietary specialization in terms of resource use and the associated nutrient intake can provide more insight into whether species-specific nutrient specialization exists alongside ingredient specialization, and whether specialization exists regardless of sex, age, morphology or temporal effects.

Omnivorous species, with their broad dietary spectrum, should be ideal model candidates to evaluate intra-population resource partitioning. We used individuals from the Swedish brown bear population, of which the ingredient and nutrient intake profiles per year (2015–2018), season, and reproductive class have been previously described in De Cuyper et al. (2023), and assessed: 1) the degree of individual dietary specialization in terms of ingredient and nutrient intake. We calculated the proportional similarity index (PSi) for the ingredient and nutrient intake based on i. fecal depositions (PSi_{feces}) and ii. the individual averages of the latter (PS$i_{\text{individual}}$). We expected less pronounced specialization for PS$i_{\text{individual}}$, and tested 2) whether year, season and reproductive class affected PS$i_{\text{individual}}$ values. We expected ingredient and nutrient specialization to be most strongly influenced by season, i.e. more specialization in fall because the 'berry-binging' that occurs in that season will be most distinct from the annual population average. We further predicted differences in specialization between reproductive classes in terms of ingredient but not nutrient intake since De Cuyper et al. (2023) reported that different reproductive classes in this population varied in ingredient but not nutrient intake, and tested 3) whether the PS$i_{\text{individual}}$ should rather be calculated within smaller year-season datasets. Examining within-year-season specialization might be more meaningful in a species whose diet is characterized by strong seasonal fluctuations (Jaeger et al. 2010, Carneiro et al. 2017). We predicted less specialization for both ingredients and nutrients when PSi was calculated within smaller year-season datasets because it eliminates temporal fluctuations in food availability, and tested 4) the temporal consistency of foraging behavior within individuals (Stewart et al. 2022). A high degree of specialization of a species across years can be caused by individuals showing consistent foraging behavior, although it may as well be caused by different individuals in every year.

Material and methods

Brown bear monitoring

Brown bears in southcentral Sweden (61°5′N, 15°05′E) were monitored by the Scandinavian Brown Bear Research Project (SBBRP) via GPS-GSM collars from 2015 to 2018 (40 to 50 tags annually; Vectronic Aerospace GmbH; approved by the Animal Ethical Committee in Uppsala, Sweden (C18/15) and the Swedish Environmental Protection Agency (NV-00741-18)). Diet composition was studied annually from April/May until late October via feces collection. In 2015, one feces per individual was collected weekly, and from 2016 on, one feces per individual was collected every two weeks. The GPS location of every bear was recorded every hour. Whenever GPS signals clustered (min. 3 consecutive GPS locations within a 30 m-radius for more than 1.5 h) (Ordiz et al. 2011, Rauset et al. 2012), a resting event was deduced, and sites were visited for feces collection. Bears typically defecate close to their resting site or beds (Steyaert et al. 2019), which are defined as a 1–2 m^2 dents in the ground and identified based on the presence of bear hair (Ordiz et al. 2011). Feces within a 5 m radius of the bed were collected. During the mating season, only single-bed-locations were sampled to avoid sampling unknown individuals. Every fecal sample can be characterized by the following parameters: GPS coordinates, bear ID, sex (female (F), male (M)), age and/or age group (subadult (until three years) or adult (from four years on)), reproductive class (adult lone female, adult male, adult female with yearlings, adult female with cubs of the year, subadult female, and subadult male), year and date of feces deposition, season of feces deposition: spring from den exit to moose calving season (until 20 May) (Swenson et al. 1997), summer from 21 May until the first berry ripening (31 July), and fall from the 1 August until late October (Friebe et al. 2001)). This dataset included bears that were followed for 1, 2, 3 (both consecutively and non-consecutively) or 4 years, but with the majority followed for 3 or 4 consecutive years (524 feces from 17 bears). Note that for the classification into reproductive classes, individuals can change status within a season, e.g. females with yearlings become lone females after separation from the yearlings, or females with cubs of the year can become lone females when cubs die. Additionally, some females with yearlings will keep their offspring for an additional year, i.e. 2.5 year olds (Van De Walle et al. 2018).

Ingredient and nutrient composition of brown bear diets

Fecal samples from the years 2015 to 2018 were used to estimate the volume percentage of ingredients via the methods described in Hamer and Herrero (1987), Dahle et al. (1998) and Stenset et al. (2016). Ingredients were identified visually (and microscopically for ants) and ingredient categories were: berries (bilberry *Vaccinium myrtillus*, lingonberry *Vaccinium vitis-idaea*, crowberry *Empetrum nigrum*, raspberry *Rubus idaeus*, other berries [unidentified]); other fruit (unidentified); vegetation (graminoids, oats *Avena sativa*, horsetail *Equisetum arvense*, maize *Zea mays*, mushrooms [unidentified], leaves and twigs, bilberry bushes, grains/cereals [unidentified], other vegetation [unidentified]); invertebrates (ants [*Formica* spp, *Camponutus* spp. and other ants {unidentified}], other invertebrates [unidentified]); vertebrates (moose *Alces alces*,

other vertebrate species, bear hair); miscellaneous (material that could not be identified or attributed to any of the aforementioned food item categories)); bird eggs. The proportion of ingredients in the actual diet was estimated via the estimated dietary content (EDC) calculation (% DM) following Hewitt and Robbins (1996) and Bojarska and Selva (2013). The nutrient composition of all diet ingredients (crude protein (CP), crude fat (EE), digestible carbohydrates (NfE), fiber (TDF including animal fiber) and ash) was extracted from the literature and the proportional nutrient composition of bear diets (% DM) was calculated as the sum of all multiplications of each ingredient EDC with the nutrient concentration of each ingredient. Calculations of ingredient and nutrient composition are described in detail in De Cuyper et al. (2023) and can be found in the online Dryad data repository De Cuyper (2023). In total, dietary ingredient and nutrient profiles were estimated from 886 feces (325 in 2015, 163 in 2016, 157 in 2017 and 241 in 2018) from 55 bears (36 in 2015, 23 in 2016, 24 in 2017 and 33 in 2018). The average ingredient and nutrient profiles were then calculated for every individual for every year – season - reproductive class combination which led to a total of 258 individual ingredient and nutrient profiles for 55 bears. The total number of feces used per bear individual to calculate individual profiles ranged from min. 2 to max. 47 feces with an average of 16 (± 11 SD) feces. The total number of feces used per bear – year – season – reproductive class combination ranged from min. 1 to max. 10 feces with an average of 3 (± 2 SD) feces (Supporting information).

Dietary specialization

Dietary specialization was evaluated using the proportion similarity index (PSi) (reviewed by Bolnick et al. 2002) (Eq. 1):

$$PSi = 1 - 0.5 \sum_j \left| p_{ij} - q_j \right| = \sum_j \min \left(p_{ij}, q_j \right)$$

with p_{ij} representing the proportion of the jth ingredient/nutrient in the diet of individual or feces i, and q_j representing the proportion of the jth ingredient/nutrient in the overall 'diet' of the population (i.e. comprising all animals, years, and seasons). Individuals or 'feces' that would specialize on a single ingredient/nutrient j, would have a PSi of q_j. In individuals or 'feces' that would have similar ingredient/nutrient proportions as the population, PSi will equal to 1. The population wide prevalence of specialization can be calculated as the average of all individuals' or feces' PSi (Bolnick et al. 2002). PSi values calculated with feces as the experimental unit are termed PSi_{feces}, and PSi values calculated for individual bears (individual-year-season-reproductive class combination) are indicated with PS$i_{individual}$. Additionally, PS$i_{individual}$ values were recalculated with the comparative base of the 'population's diet' now restricted per year and season (PS$i_{individualYS}$) to evaluate within-year-season specialization (Fig. 1).

Data analysis

All statistical analyses were performed in RStudio (ver. R4.3.1). PSi was calculated via the R individual specialization 'RInSp' package (Zaccarelli et al. 2013). p-values for the probability of PSi outcomes were obtained via the Monte Carlo resampling simulation (999 replicates). Normality of both PSi_{feces} and PS$i_{individual}$ data for ingredients and nutrients were evaluated and confirmed via Q–Q plots, boxplots, and Shapiro Wilk W ≥ 0.95. A Levene's test for homogeneity of variance allowed assumption of equality of variance. PSi_{feces} and PS$i_{individual}$ were compared with an independent samples t-test, for both ingredients and nutrients. The PSi value difference between ingredients and nutrients was compared with a paired samples t-test, for both fecal units and individuals.

A linear mixed model (LMM) was used with PS$i_{individual}$ as the response variable and year, season, and reproductive class and all possible two-way interactions as explanatory variables. Bear ID was inserted as random factor on the intercept. Variable selection was performed by stepwise backward elimination of non-significant interactions and variables until a minimal model with only significant (α ≤ 0.05) variables was retained. Model residuals were normally distributed and homogeneity of variance was assumed, as evidenced by residual plots (residual versus fitted plot and normal Q–Q plot) and Shapiro–Wilk W values ≥ 0.95, allowing a Gaussian error distribution. For post-hoc identification of significant differences between factors in the linear mixed effects models, we used 'lsmeans' from R package 'emmeans' (Lenth 2021), resulting in Tukey-adjusted p-values. The season spring was omitted from the LMM analysis because it was neither represented in every year nor were sufficient bear reproductive classes represented in spring.

Since not all normality and homogeneity of variance assumptions were met for ingredient and nutrient PS$i_{individualYS}$, a non-parametric Wilcoxon test was performed to evaluate the difference between PS$i_{individual}$ and PS$i_{individualYS}$. PS$i_{individualYS}$ values were plotted against single ingredient and nutrient intakes (% EDC and % DM, respectively) to explore which ingredients and nutrients caused dietary specialization.

Repeatability of ingredient and nutrient PSi_{feces} values was tested via the 'rptR' package (Stoffel et al. 2017) for each season and reproductive class over years for every individual. PSi_{feces} was used to allow for more repetitions per individual in every year, season, and reproductive class. The following cut-off values were applied: R < 0.2 low to no repeatability; 0.2 < R < 0.6 moderate repeatability; R > 0.6 high repeatability (Corsini et al. 2019). The statistical significance of the repeatability was tested via likelihood ratio tests (LRT).

Results

Ingredient and nutrient PSi: feces versus bear individual

Ingredient PSi_{feces} values ranged from min. 0.0059 to max. 0.64 with an average of 0.24 (± 0.13) ($p_{MonteCarlo}$ = 0.001) (Fig. 2a). The ingredient PS$i_{individual}$ values ranged from min. 0.022 to
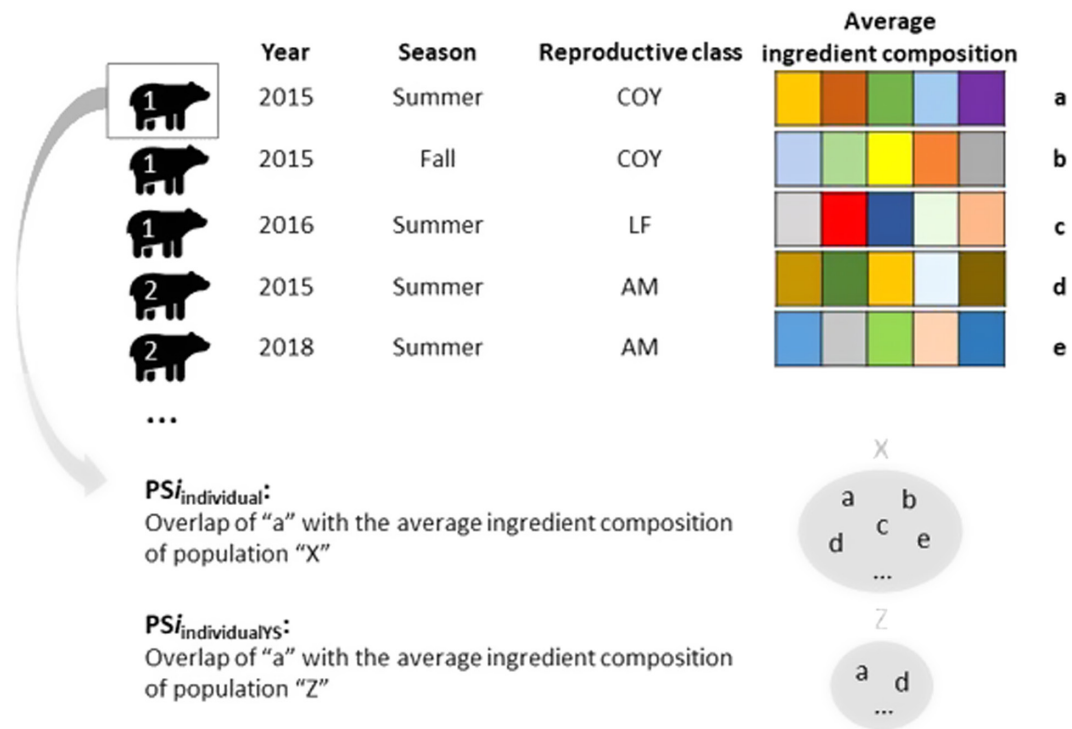
Figure 1. Fictional example of PS$i_{individual}$ calculations and within-year-season PSi calculations (PS$i_{individualYS}$) for the ingredient profiles of bears. Bear 1 in the summer of 2015 has a PS$i_{individual}$ value based on its own ingredient profile 'a' versus the average ingredient profile of the whole population (X) (incl. all years, seasons and reproductive classes). Bear 1 in the summer of 2015 also has a PS$i_{individualYS}$ value based on its own ingredient profile 'a' versus the average ingredient profile of the 2015-summer population (Z). AM = adult lone males; COY = females with cubs of the year; LF = adult lone females.

max. 0.76 with an average of 0.37 ($\pm$ 0.14) ($p_{MonteCarlo}$ = 0.001) (Fig. 2c), which is significantly higher than the average ingredient PSi_{feces} (p < 0.001). Nutrient PSi_{feces} values averaged at 0.73 ($\pm$ 0.10) ($p_{MonteCarlo}$ = 0.001) with a min. of 0.47 and max. 0.98 (Fig. 2b). The nutrient PS$i_{individual}$, with a min. of 0.50 and max. 0.98 (Fig. 2d), averaged at 0.79 ($\pm$ 0.10) ($p_{MonteCarlo}$ = 0.001) which is significantly higher than the average nutrient PSi_{feces} (p < 0.001). The ingredient PSi was lower than the average nutrient PSi, for both the fecal unit dataset (delta 0.49, p < 0.001), and the bear individual dataset (delta 0.42, p < 0.001).

The effects of year, season, and reproductive class on ingredient and nutrient PS$i_{individual}$

Ingredient PSi was not affected by season (p = 0.44). The year 2015 was characterized by the lowest ingredient PSi (0.32 $\pm$ 0.11) in comparison with all other years (p < 0.001) and the year 2016 with the highest PSi (0.49 $\pm$ 0.13) in comparison with all other years (p < 0.001). No distinct pattern emerged with respect to reproductive class. In the year 2015, females with cubs of the year were more specialized (PSi 0.24 $\pm$ 0.11) than adult lone males (0.37 $\pm$ 0.12) (p < 0.05) and females (0.36 $\pm$ 0.091) (p < 0.05); in 2016, females with yearlings were more specialized (0.39 $\pm$ 0.20) than females with cubs of the year (0.58 $\pm$ 0.11); in 2018, adult lone males (0.18 $\pm$ 0.077) and females with yearlings (0.30 $\pm$ 0.15) were more specialized than subadult males (0.52 $\pm$ 0.094) (p < 0.05) (Supporting information).

The year 2015 was also characterized by the lowest nutrient PSi (0.75 $\pm$ 0.088) in comparison with all other years (2016 0.83 $\pm$ 0.092; 2017 0.84 $\pm$ 0.073; 2018 0.81 $\pm$ 0.097) (p < 0.001). Nutrient PSi in summer (0.81 $\pm$ 0.11) was higher than in fall (0.79 $\pm$ 0.064) (p < 0.05) across years. In the year 2015, females with cubs of the year were more specialized (0.69 $\pm$ 0.080) than adult lone males (0.80 $\pm$ 0.11) and females (0.77 $\pm$ 0.063) (p < 0.05) (Supporting information).

Comparison of PS$i_{individual}$ with PS$i_{individualYS}$

Overall, the ingredient PS$i_{individualYS}$ values (Fig. 1) were higher (0.54 $\pm$ 0.17) than the (original) ingredient PS$i_{individual}$ values (0.37 $\pm$ 0.14) (p < 0.001). Similarly, for nutrient profiles, a shift towards higher values was observed when PS$i_{individualYS}$ was calculated (0.87 $\pm$ 0.10) in comparison to PS$i_{individual}$ (0.79 $\pm$ 0.10) (p < 0.001) (Fig. 3). In other words, when the basis for comparison was shifted from the total dataset to the data of the respective year and season, a lower degree of specialization was the result.

PS$i_{ndividualYS}$ versus the intake of specific ingredients and nutrients

PS$i_{individualYS}$-values were plotted against the corresponding EDC (%) of every ingredient and the % DM of every nutrient per year and season (Supporting information for all graphical representations). For certain ingredients and nutrients, with
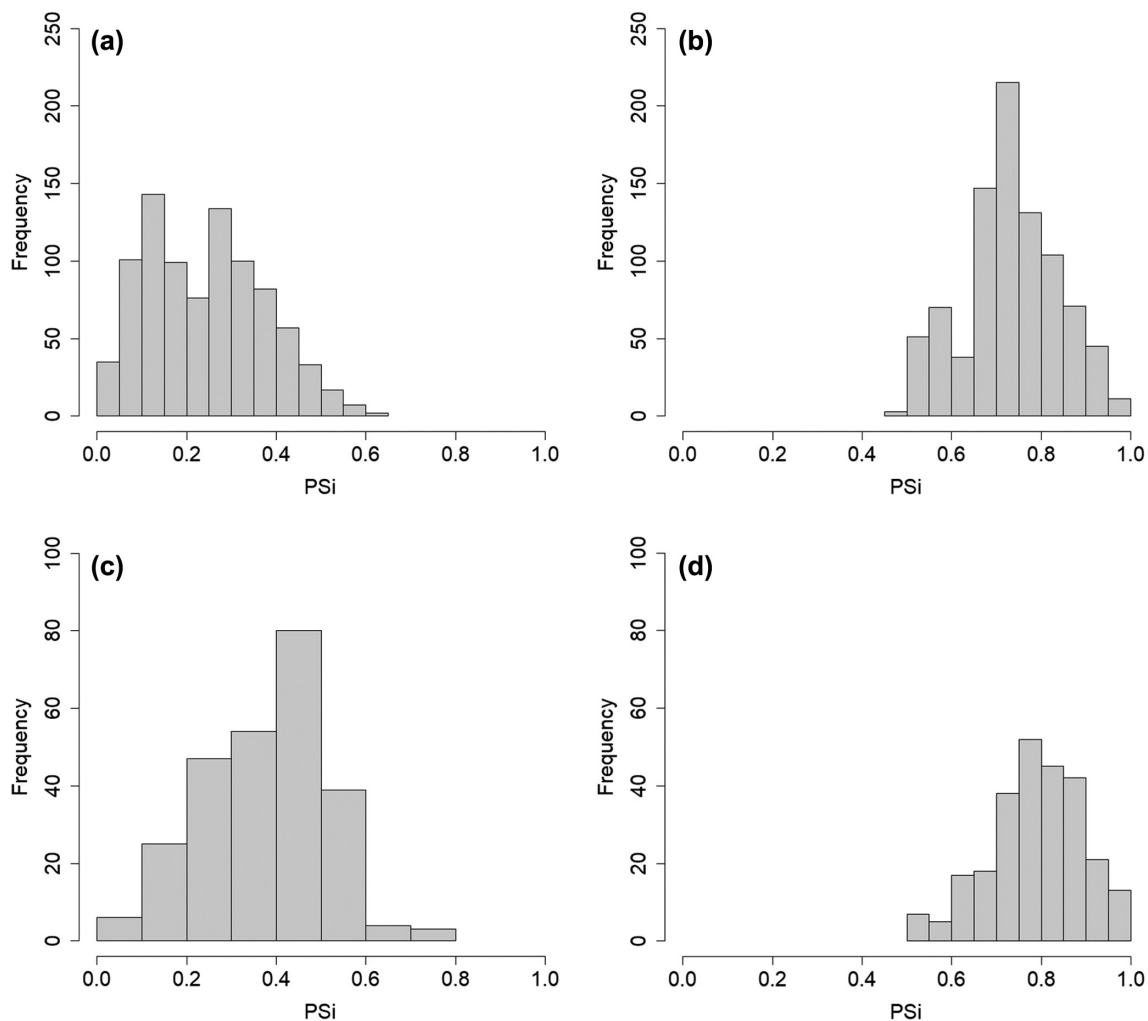
Figure 2. Frequency distributions of ingredient and nutrient PSi values. (a) Ingredient PSi with feces as the experimental unit (n = 886) (PSi_{feces}); (b) nutrient PSi with feces as the experimental unit (n = 886) (PSi_{feces}); (c) ingredient PSi with bear individual as experimental unit (individual-year-season-reproductive class combination; n = 258) (PS$i_{\text{individual}}$); (d) nutrient PSi with bear individual as experimental unit (individual-year-season-reproductive class combination; n = 258). Distributions include all years (2015–2018), all seasons (spring, summer, fall) and all reproductive classes (adult lone males, adult lone females, adult females with yearlings, adult females with cubs of the year, subadult lone females and subadult lone males).

increasing % EDC and % DM, the PS$i_{\text{individualYS}}$ increased (less specialization) but once a certain % EDC or % DM was exceeded (the PSi maximum), the PS$i_{\text{individualYS}}$ decreased. The most pronounced thresholds were those of bilberry in fall (ca 60% EDC), crowberry in fall (ca 20% EDC), moose (without age specification of moose) in summer (ca 25% EDC), graminoids in summer (ca 20% EDC) and oats in fall (ca 20% EDC) (Table 1). Whenever protein intake exceeded a threshold of approximately 40% DM in summer and 20% DM in fall, or fat intake exceeded a threshold of 10% DM in summer and 5% DM in fall, or carbohydrate intake exceeded a threshold of 35% DM in summer or 55% DM in fall, or fiber exceeded a threshold of 25% DM, then bear diets became more specialized (Table 2).

Repeatability of dietary specialization

Overall, the repeatability of PSi_{feces} values of bear individuals was low over the years for both ingredients and nutrients (the majority of R < 0.2 and p > 0.05) (Table 3). Only in spring were bear individuals moderately to highly repeatable in their degree of ingredient (R$_{\text{ALL}}$ 0.396; p = 0.06) and nutrient specialization (R$_{\text{ALL}}$ 0.732; p < 0.05) when no subdivision in reproductive classes was considered. When this subdivision was applied, only the class of females with yearlings was repeatable in PSi values over the years in spring (R$_{\text{YL}}$ 0.334, p = 0.28). In fall, only females with yearlings showed highly repeatable ingredient PSi values (R$_{\text{YL}}$ 0.761, p = 1). Summer PSi values were not repeatable (all R < 0.2).
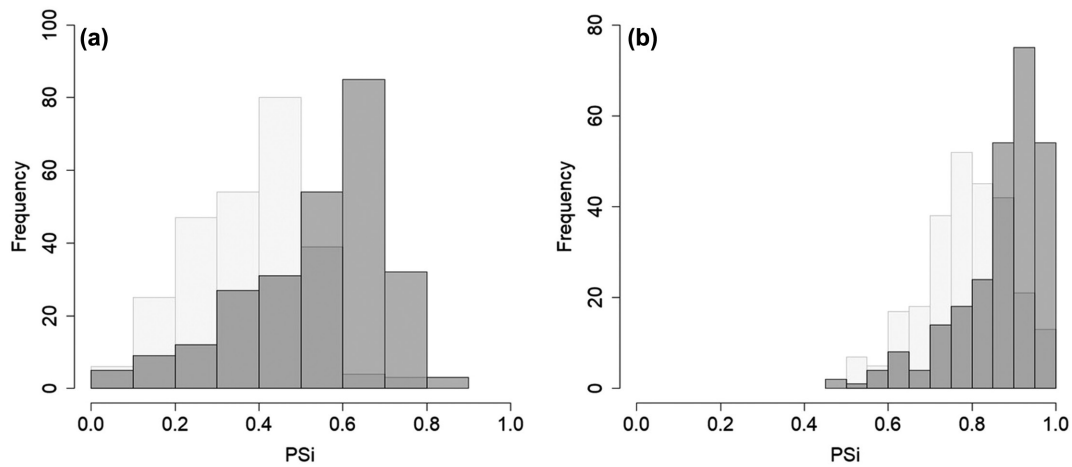
Figure 3. Frequency distributions of ingredient and nutrient $PSi_{individual}$ and $PSi_{individualYS}$. (a) ingredient values and (b) nutrient values. Light grey bars depict $PSi_{individual}$ and dark grey bars depict $PSi_{individualYS}$. Distributions include all years (2015–2018), all seasons (spring, summer, fall) and all reproductive classes (adult lone males, adult lone females, adult females with yearlings, adult females with cubs of the year, subadult lone females and subadult lone males).

Discussion

The general trend observed for foraging behavior of Swedish brown bears was a tendency towards specialization for ingredient consumption but no specialization in terms of nutrient intake (1). Factors such as year, season and/or reproductive class influenced bear diet specialization, both ingredient or nutrient-based, but effects were mild and mostly not affecting the magnitude of PSi (2). The degree of dietary specialization was mainly influenced by the dietary proportion of berries (bilberry and crowberry), moose, graminoids and oats. Only in very few cases was the degree of ingredient and nutrient specialization caused by individuals repeating their feeding behavior across years (4). Hence, dietary specialization did not appear to be a consistent individual trait in this population, which suggests that individuals should be followed across ontogeny in future research. The organization of raw data used for PSi calculations affected specialization outcomes: going from a 'fecal sample resolution' to 'individual resolution' led to higher or 'less specialized' PSi values for both ingredients and nutrients (1); calculating PSi with the comparative population restricted to the year and season of the bear datapoint ($PSi_{individualYS}$) almost always resulted in less specialization for both ingredients and nutrients (3).

PSi specialization based on ingredient and nutrient intake

Methodological implications

Using individual averages (year-season-reproductive class average of nutrient and ingredient compositions) for PSi calculations did not substantially influence the degree of nutrient specialization, which remained low (high PSi), whereas ingredient specialization became less pronounced (Fig. 2). We opted to work further with $PSi_{individual}$ (except for repeatability statistics) as PSi values calculated with individual diet averages provided more representative PSi values. Working with a 'single sample resolution' (here one feces) has the potential to overestimate specialization: it is only a 'snapshot' or representation of a foraging bout of an individual, and when foraging in a heterogenous environment (e.g. Swedish brown bears, Hertel et al. 2016), a generalist might appear as a specialist (Bolnick et al. 2002). A bear with high PSi_{feces} but a low $PSi_{individual}$ would then indicate an individual whose separate foraging bouts may strongly differ from the population average, but whose average intake is very similar to the population average. Our data confirm that when changing the PSi calculation to an individual resolution, less specialization was observed (Fig. 2c).

In the literature, both options are used. Mostly, when single measurements such as feces were used to calculate PSi and not individual averages, the effect of the individual was statistically accounted for in mixed effects regression models with PSi as a dependent variable, factors such as age or sex as fixed effects and individual as random factor (Araújo et al. 2011). Others first calculated averages of diet composition per individual (Martins et al. 2008, Jacquier et al. 2020b), per nest box of birds by using all regurgitated pellets in the next box (McDermot 2016) or per bird pair (Pagani-Núñez et al. 2015) before PSi calculations. Whenever there were no repeated measures per individual, e.g. only one feces per individual, or gastric content from killed individuals, the question of averaging did not pose itself.

We acknowledge that 26% of the $PSi_{individual}$ values (bear-year-season-reproductive class combination) were based on one feces (Supporting information). However, inflation of ingredient and nutrient $PSi_{individual}$ caused by low sample sizes was tested via a Monte Carlo replicate simulation with the R individual specialization 'RInSp' package (Zaccarelli et al. 2013) and allowed us to reject the null hypothesis that our data are similar to a random generalist population.

Table 1. PS$i_{\text{individualYS}}$ versus the ingredient intake (% EDC) per season and year.
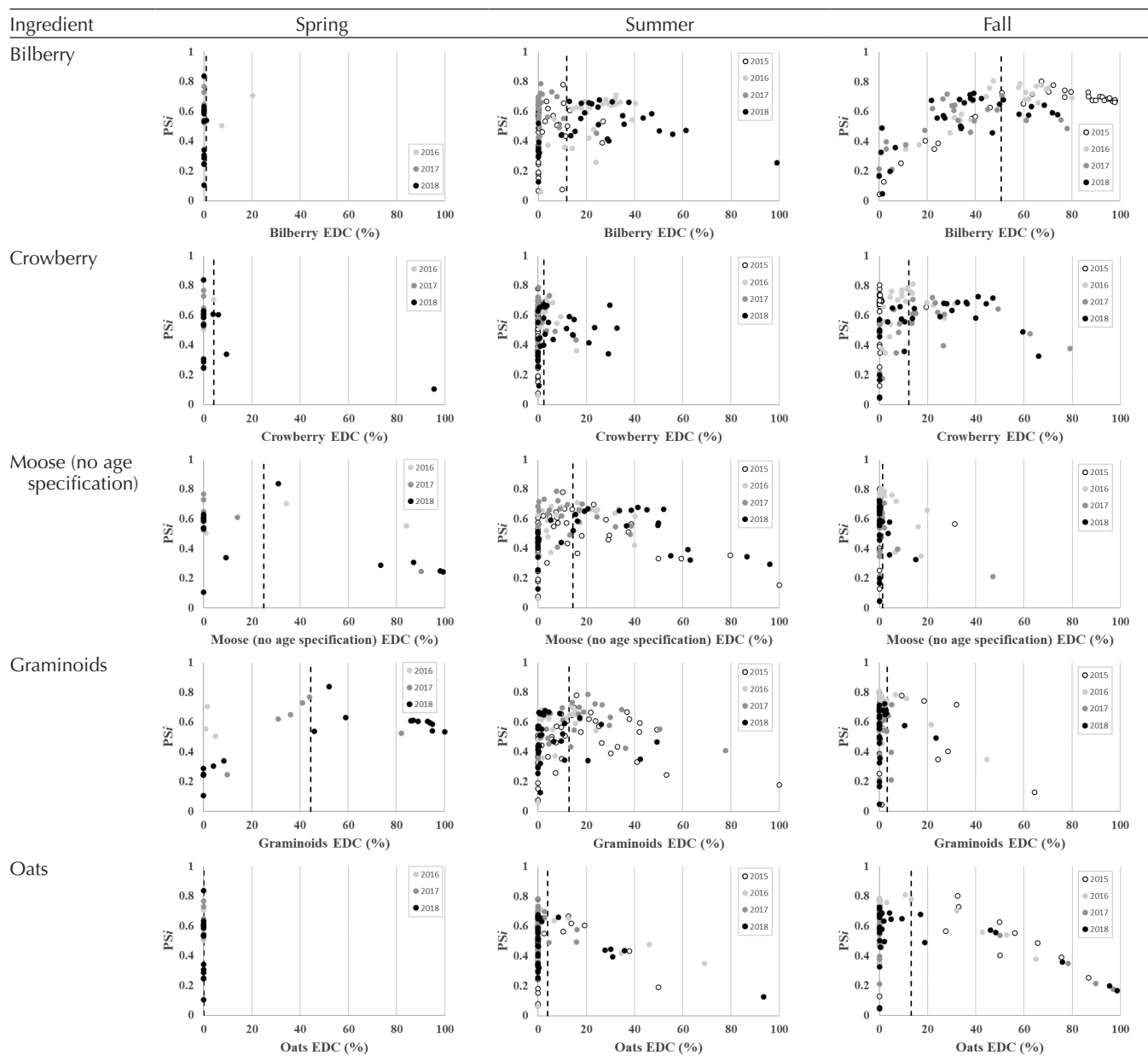
The vertical dashed lines represent the average ingredient proportion (% EDC) calculated for all years and reproductive classes taken from De Cuyper et al. (2023).

Ingredient specialization and nutrient non-specialization

Overall, frequency distributions of ingredient PS$i_{\text{individual}}$ showed that most values were below 0.5 and indicated a tendency towards specialization. Individual specialization has been investigated in several other generalist vertebrate and invertebrate species, including omnivores, and in some of which via indices that quantify the degree of specialization (such as the PSi) (reviewed by Bolnick et al. (2003) and Araújo et al. (2011)). Several studies reported specialization to some extent; however, this may have been caused by the fact that if no specialization was observed, results were not always published (Araújo et al. 2011). In ursids, only two studies used

a specialization index to our knowledge (Bolnick et al. 2002, Araújo et al. 2011): the Asian black bear in Mori et al. (2019) and the polar bear in Thiemann et al. (2011). For Asian black bears, the overall PSi ranged from 0.24 to 1, which indicated a certain degree of specialization with all bears following the same pattern of less specialization in times of high resource abundance and low diversity (spring and fall) and more specialization in summer when resources were less abundant. The average PSi of polar bears was high (averages ranging from 0.77 to 0.83 for different reproductive classes), although in some cases PSi decreased for adult males when the proportion of bearded seal increased in their diet.

Table 2. PS$i_\text{individualYS}$ versus the nutrient intake (%DM) per season and year.
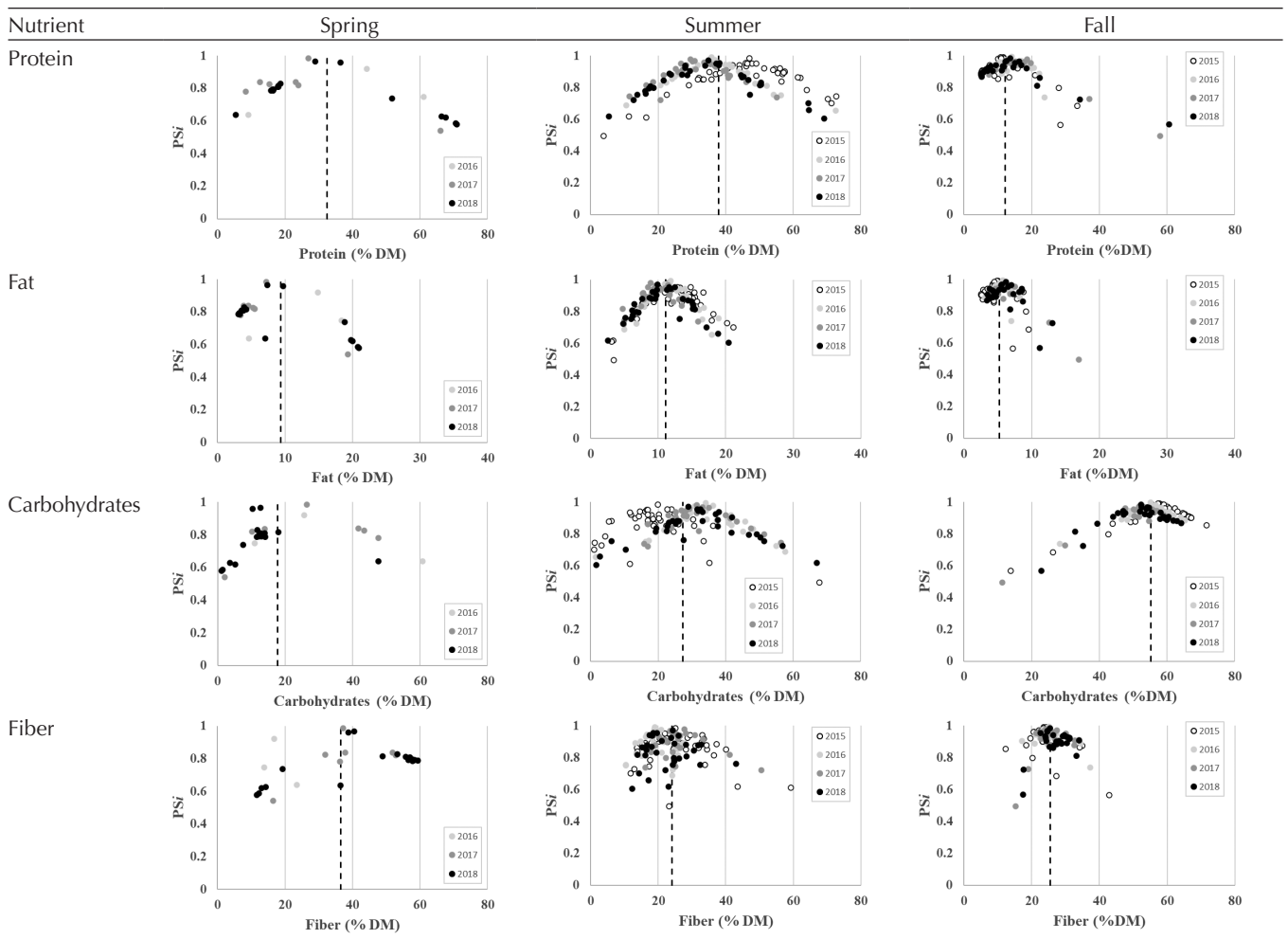
The vertical dashed lines represent the average nutrient concentration (% DM) calculated for all years and reproductive classes taken from De Cuyper et al. (2023).

In De Cuyper et al. (2023), the proportional ingredient composition of bear diets was evaluated and used in this study to compare it with ingredient PS$i_\text{individualYS}$ values (see below for the discussion of PS$i_\text{individualYS}$). Our data showed that certain ingredients (i.e., berries, graminoids, moose, oats) that are key ingredients in specific seasons (e.g. berry consumption in fall (Stenset et al. 2016, De Cuyper et al. 2023)) can strongly influence the degree of specialization of bear individuals (Table 1). The EDC – PS$i_\text{individualYS}$ plots of these ingredients all showed a PS$i_\text{individualYS}$ maximum (closer to 1, less specialization) at a certain EDC threshold. The latter indicated a scenario in which bears exhibit dietary patterns that closely match those of their population. Any deviation from this threshold, in either direction, resulted in a higher degree of dietary specialization (Table 1). Whether the 'population-state' (maximum) was more beneficial than the specialized state cannot be derived from our results and would require a link with fitness outcomes (e.g. reproductive success), although ingredient specialization did not coincide with nutrient specialization, indicating no superiority of

generalists or specialists in terms of the nutritional composition of their diet.

Nutrient specialization was indeed practically absent with the majority of PS$i_\text{individual}$ values staying above 0.5. The finding that with varying ingredient consumption, a similar dietary nutrient composition could be obtained was also reported by De Cuyper et al. (2023) for different brown bear reproductive classes. It is known that by eating different ingredients with similar nutrient profiles or by combining complementary foods, similar nutrient profiles can be obtained (Raubenheimer and Simpson 1997, Raubenheimer and Jones 2006, Mayntz et al. 2009). In predators this can be accomplished by eating selectively from the prey: e.g., spiders specializing on ants have been reported to eat different body parts to acquire a certain nutrient goal (Pekár et al. 2010). In the case of brown bears, probably a mixture of strategies is used as evidenced for example by bears eating selectively from salmon (*Oncorhynchu*s spp.) (Lincoln and Quinn 2019), or by adult males in our study population that sometimes had a high proportion of oats in their fall diet. Because oats are a

Table 3. The repeatability of individual ingredient and nutrient specialization calculated over 4 years (2015–2018) per reproductive class and season.

	Spring				Summer				Fall			
	R	p	CI	n	R	p	CI	n	R	p	CI	n
Ingredients												
All	0.396	0.062	[0, 0.976]	28	0	0.5	[0, 0.046]	519	0.046	0.115	[0, 0.125]	339
LF	–	–	–	–	0	0.5	[0, 0.089]	178	0.029	0.374	[0, 0.157]	144
SF	0	1	[0, 0.999]	6	0.046	0.452	[0, 0.251]	86	0.035	1	[0, 0.266]	68
COY	–	–	–	–	0.017	1	[0, 0.178]	93	0.043	1	[0, 0.371]	50
AM	–	–	–	–	0	1	[0, 0.211]	54	0.07	0.364	[0, 0.391]	41
SM	–	–	–	–	0	1	[0, 0.397]	33	0	0.5	[0, 0.568]	19
YL	0.429	0.11	[0, 0.999]	12	0.006	1	[0, 0.204]	75	0.761	1	[0, 0.952]	17
Nutrients												
All	0.732	0.021	[0, 0.994]	28	0.005	0.5	[0, 0.046]	519	0.051	0.122	[0, 0.139]	339
LF	–	–	–	–	0	1	[0, 0.096]	178	0.14	0.055	[0, 0.304]	144
SF	0	1	[0, 0.999]	6	0.06	0.436	[0, 0.257]	86	0.12	0.404	[0, 0.356]	68
COY	–	–	–	–	0	1	[0, 0.166]	93	0	1	[0, 0.277]	50
AM	–	–	–	–	0	0.5	[0, 0.235]	54	0.10	1	[0, 0.438]	41
SM	–	–	–	–	0	1	[0, 0.402]	33	0	0.5	[0, 0.544]	19
YL	0.334	0.28	[0, 0.999]	12	0.03	1	[0, 0.235]	75	0	1	[0, 0.682]	17

AM = adult lone males; COY = females with cubs of the year; LF = adult lone females; SF = subadult females; SM = subadult males; YL = females with yearlings. R = repeatability , p = significance level based on Likelihood ratio tests (LRT).

carbohydrate-rich food source, they were most likely a food item equivalent to carbohydrate-rich berries. Large carnivores have also been described as able to feed selectively on large prey (De Cuyper et al. 2019). A recent paper on white sharks looking into prey and nutrient specialization revealed that although specialization on specific prey was present in the population, this was not translated into specialization in nutrient intake (Grainger et al. 2023), again adding to the evidence that by complementing nutritionally different food items, a specific nutrient goal can be realized (Raubenheimer and Simpson 1997, Raubenheimer and Jones 2006).

The proportional nutrient composition (% DM) versus $PSi_{individualYS}$ plots (Table 2) revealed similar threshold patterns as with the ingredients, although all $PSi_{individualYS}$ values remained above 0.49. The protein $PSi_{individualYS}$ maximum in fall (the protein intake of individuals is very similar to the overall population) coincides with the low protein optimum in the diet of bears (typically around 20% DM) that was associated with beneficial physiological outcomes, i.e., efficient fattening before hibernation (Robbins et al. 2007, 2022, Erlenbach et al. 2014). In fall, this optimum was almost never surpassed. However, it was during summer.

Temporal and social effects on the degree of specialization

PSi fluctuations with year, season, and reproductive class

In De Cuyper et al. (2023), we showed that annual fluctuations, seasonal changes and social dynamics influenced the diet in this brown bear population. In summary, spring and early summer diets were dominated by vertebrates, insects and also natural vegetation (e.g. graminoids) and were protein-rich. In fall, bears relied heavily on fruits (mainly berries) which made their diets carbohydrate-rich in that period. The year 2015 had the most pronounced effect on

the diet composition with very low fruit and high insect shares in the summer diet, which also translated into low carbohydrate and high protein diets compared to all other years. Adult males could heavily rely on oats in fall instead of berries, and females with cubs of the year had a lower overall share of vertebrates in their diet compared to other adult female classes. However, differences in dietary ingredient composition between reproductive classes were not translated into differences in nutrient intake. Therefore, PSi frequency distributions (Fig. 2) should be evaluated for underlying temporal and social patterns. Our prediction that the dietary ingredient composition of bears in fall would be more specialized than in summer because of the heavy berry reliance in the former was not met. This result was also opposite to what Mori et al. (2019) found for Asian black bears, that had a less specialized diet during times with abundant resources (spring and fall) and more specialization in summer (less resource abundance). Our data showed no seasonal effect. The distinct situations between fall and summer might lead to similar specialization outcomes: the heavy berry reliance in fall compared to the population average all year round might lead to a $PSi_{individual}$ that is fairly similar to the $PSi_{individual}$ of summer diets. In summer, there was no high abundance of one specific food resource and individuals might have combined the food items they encounter, which in turn might have led to variation in ingredient intake between individuals that in turn then deviated from the all year round population mean. However, we did not quantify resource abundance. The year 2015 showed the most specialization compared to other years. This year was remarkable for the low fruit consumption and high insect consumption in summer (De Cuyper et al. 2023) which probably made it stand out from other years. Indeed, an index for annual bilberry and lingonberry production in the study region (Hertel et al. 2018) showed the year 2015 as a 'good' berry

year, which seems contradictory with the low berry intake in summer. However, this might have been caused by a late ripening of berries. Given the higher sampling frequency in 2015 (more feces were collected), it could be assumed that the higher specialization degree is a result of a larger sample size (Supporting information). However, annual effects were analyzed on PS$i_{individual}$ values with similar sample sizes across years. In 2015, females with cubs of the year were more specialized than adult lone males and adult lone females, which adds to the evidence that sexually selected infanticide can lead to spatiotemporal segregation of this reproductive class, which ultimately can affect their diet composition (Steyaert et al. 2013a, b). Other years, however, did not show this specific trend. Females with cubs and females with yearlings were fairly specialized compared to other groups in 2015 and 2016. These results were based on 7 females with cubs in 2015 and 5 females with yearlings in 2016 of which 4 had the same identity, which might imply that they showed similar ingredient specialization over reproductive class transitions. In 2018, adult males were more specialized in terms of ingredients than several other reproductive classes, which was most likely caused by the heavy oat reliance in the fall of that year. Overall, these mild ingredient PS$i_{individual}$ fluctuations almost always stayed under 0.5.

There was a significant difference in summer nutrient PS$i_{individual}$ (0.81 ± 0.11) versus fall nutrient PS$i_{individual}$ (0.79 ± 0.10) although this difference was minimal and both were very close to 1. Again, this outcome was opposite to our expectation: assuming that a fall diet is heavily carbohydrate dominated and a summer diet protein dominated, we would have expected these seasonal diets to be quite deviating from the all-year-round average (which we expected to even out all nutrients). Using data from De Cuyper et al. (2023), the all-year-round average of individuals (incl. the four years and all reproductive classes) was CP 28.0% DM, EE 8.8% DM, NfE 37.8% DM and TDF 25.0% DM. The overall fall nutrient composition (incl. all years and reproductive classes) was CP 12.2% DM, EE 5.3% DM, NfE 55.3% DM and TDF 25.5% DM and in summer was CP 38.0% DM, EE 11.1% DM, NfE 27.4% DM and TDF 24.0% DM. These nutrient profiles confirmed our predictions, but differences might have been too small to cause any substantial decrease in PS$i_{individual}$, or the deviation from the mean in one direction in summer and in the opposite direction in fall might have led to similar PS$i_{individual}$ for these two seasons. Nutrient intake fluctuations are also restricted and bound to metabolic limitations of the individual in contrast to ingredient intake. Additionally, the fiber proportion in bear diets was a steady component regardless of season or year. Similarly, as observed for ingredient PS$i_{individual}$, in the year 2015, bears were more specialized in terms of nutrients (although PS$i_{individual}$ values were all high) compared to other years and in the year 2015, a lower nutrient PS$i_{individual}$ was observed for females with cubs of the year compared to adult lone males and adult lone females. The difference in ingredient intake of females with cubs compared to adult lone males and adult lone females was reflected in the nutrient PS$i_{individual}$, which again adds to the evidence that

females with cubs can experience diet changes due to social dynamics (Ben-David et al. 2004, Steyaert et al. 2013a, b).

PSi recalculation within year-season datasets

Given the above mentioned annual and seasonal fluctuations in ingredient and nutrient PS$i_{individual}$, it might be more relevant to look at an individual as a specialist whenever it deviates from what the population is feeding on in a particular year and season. Similarly, in seabirds (Jaeger et al. 2010), marine predators (Carneiro et al. 2017) and the Brazilian gracile opossum *Gracilinanus microtarsus* (Martins et al. 2008), PSi values were calculated within seasons. Our recalculation of PS$i_{individual}$ to PS$i_{individualYS}$ (Fig. 1, 3) led to increased values for both ingredients and nutrients, with the ingredient average now exceeding 0.5. Without drawing any profound conclusions, this approach of comparing the average diet of a bear in a certain year and season to the average diet of the population in that year and season instead of the average diet of the whole population (incl. all datapoints from all years, seasons and reproductive classes), was more straightforward and rules out seasonal and annual confounding factors. The latter also made it a more appropriate measure to use in the seasonal PSi-EDC or PSi-DM plots (Table 1–2).

Is individual specialization repeatable?

Overall, individuals did not seem to repeat their level of specialization across years, which suggested that the actual ecological circumstances surrounding an individual were most important during the study period. Only in spring, bears showed moderate to high repeatability in their degree of specialization, which might be caused by the fact that resource availability and options are limited at this time of year. Hertel et al. (2023) reported on the ontogeny of individual specialization in brown bears and found strong links with social learning and maternal effects. The trophic position of offspring and mother (herbivorous to carnivorous) appeared similar but gradually decreased in the first four years of solitary life. Also trophic positions of siblings were closely related. We did not look at mother–offspring relations, i.e. we did not relate the diet habits of subadults to those of their mother. In this dataset, only a few mothers and their lone offspring were present. Claims about certain species being specialists should be corroborated by longer-term trends, not merely a cross-section in time. We therefore interpret the degree of ingredient specialization observed in this study as a result of individual flexibility that allows individuals to select (a combination of) specific ingredients to meet certain nutrient goals. This appears rather driven by fluctuating outer circumstances than individuals showing consistent foraging behavior over time.

Constraints

One criticism of our approach is that we based our conclusions only on the diet composition of brown bears. We did not additionally calculate the dietary niche breadth or

diversity per individual (via e.g. the Shannon–Wiener index) as did other authors (Thiemann et al. 2011, Mori et al. 2019). However, in future research this could add more detail to the (lack of) specialist behavior observed in this study population. We do, however, assume that ingredient and nutrient intake are ultimately what will affect the bear's metabolism. Additionally, the use of indices such as PSi has the advantage that one does not need the frequency distributions of resources in the environment. The latter is equated to the total diet of the population to which individuals are compared (Bolnick et al. 2002). Other factors have been considered to influence or be related to individual specialization and originate from intrinsic and/or extrinsic factors: inter- or intraspecific competition, size dimorphism, metabolism, food abundance, maternal learning (see below) (reviewed by Bolnick et al. 2003 and Araújo et al. 2011). Although we did not directly investigate any of these 'causal' factors, we likely have captured some (such as size dimorphism, metabolism and competition) by including potential effects related to reproductive class.

Conclusions

Data from this Swedish brown bear population revealed that, when ruling out temporal and social dynamics, foraging for specific food items can occur unnoticed in a supposedly generalist population. However, this does not necessarily mean that it concomitantly affects the nutrient intake. Rather, as seen in other species, nutrient profiles appear very similar among individuals, however, may be based on different dietary items. Specialization observed in this population appeared susceptible to actual environmental conditions rather than fixed individual preferences and was not stable over time, yielding the picture of a rather non-specialized but flexible population. The organization of raw data prior to PSi calculations can substantially impact results and warrants caution when interpreting results. Additionally, future studies should aim to have a higher number of feces per individual to fully characterize diet preference and specialization strategies.

Author contributions

Annelies De Cuyper: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Funding acquisition (equal); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead). **Diederik Strubbe**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Writing – review and editing (equal). **Marcus Clauss**: Supervision (equal); Visualization (equal); Writing – review and editing (equal). **Luc Lens**: Conceptualization (equal); Project administration (equal); Supervision (supporting); Writing – review and editing (equal). **Andreas Zedrosser**: Data curation (supporting); Resources (equal); Writing – review and editing (equal). **Sam M. J. G. Steyaert**: Resources (equal); Writing – review and editing (equal). **Alexander Kopatz**: Resources (equal); Writing – review and editing (equal). **Geert P. J. Janssens**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (lead); Validation (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.dbrv15f64 (De Cuyper 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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