Running head: Learning dietary specialization

The ontogeny of individual specialization

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ABSTRACT

Individual dietary specialization, where individuals occupy a subset of a population's wider dietary niche, is of key importance for species' resilience towards environmental change. However, the ontogeny of individual specialization, as well as the underlying social learning, genetic, and environmental drivers remain poorly understood. Using a multigenerational dataset of female European brown bears (*Ursus arctos*) followed since birth, we discerned the relative contributions of social learning, genetic predisposition, environment forcings, and maternal effects to individual dietary specialization. Individual specialization varied from omnivorous to carnivorous diets spanning half a trophic position. The main determinants of this dietary specialization were maternal learning during rearing (11%), environmental similarity (12%), and maternal effects (11%), whereas the contribution of genetic heritability was negligible. Importantly, the offspring's trophic position closely resembled the trophic position of their mother during the first 3-4 years after separation from the mother, but this relationship ceased with increasing time since separation. Our study reveals that social learning and maternal effects are as important for individual dietary specialization as environmental forcings. We propose a tighter integration of social effects into future studies of range expansion and habitat selection under global change, that to date are mostly explained by environmental drivers.

KEYWORDS

Dietary specialization, heritability, maternal effects, maternal learning, trophic position, trophic niche, omnivore, stable isotopes, carbon-13, nitrogen-15, *Ursus arctos*

1. INTRODUCTION

Among individuals of the same species, niche variation is common and may occur when availability of food resources or habitat structure change across the species' range. Ecological generalists, species with a wide niche, also seem to exhibit more individual specialization [1] and are hence particularly well adapted to persist under shifts in resource availability or composition enabling them to occupy larger distributional ranges than ecological specialists [2]. Individual variation is key for making species resilient towards changing resource availabilities in a rapidly changing world and may ultimately determine local persistence or extinction of species [3].

Inter- and intraspecific competition, predation and ecological opportunity, alter resource availability and have been identified as the main ecological drivers explaining variation in the degree of individual specialization between populations [4]. Yet, how individual variation emerges and is maintained within populations has been rarely quantified in the wild. In principle, four potential sources of variation exist: social and individual learning, genetic inheritance, the environment, and maternal effects. Individual differences in resource preference or competence to secure a resource may therefore be determined during early ontogeny through social (e.g., maternal) learning via imitation [5-9] leading to similarities between the offspring's and their mother's dietary phenotype. Effects of maternal learning can be lifelong or are modified through individual experiential learning [10]. Resource preferences have also been suggested to be genetically determined through genes inherited from both mother and father, where closely related individuals have more similar diets than distantly related individuals [11]. In addition, maternal effects account for lifelong similarities in dietary phenotype among offspring of the same mother [12]. Such similarities can arise from social interactions, maternal genotype, or maternal environment. Statistically, maternal effects are quantified as the similarity of repeated samples from siblings of the same

81 mother but not as the similarity of behavioral expression between mother and offspring (i.e.,
82 "maternal learning"). In range resident species, where individuals occupy a subset of a
83 population's range, the environment, in terms of habitat composition or availability of
84 particular food resources, may differ among home ranges and lead to individual
85 specialization [11]. Accounting for the environmental heterogeneity when studying the
86 drivers of individual specialization is therefore essential in range resident species [13, 14].
87 Attributing variation in diet to the individual level, to isolate its sources and to identify
88 developmental drivers of diet preferences requires multigenerational datasets of repeated
89 measures of the diet of individuals throughout their life. We harness a 30-year longitudinal
90 dataset of 72 female Scandinavian brown bears of known mothers with repeated measures of
91 annual diets to first assess whether individual specialization occurs. Using information about
92 their mother's diet, a genetic pedigree, and individual movement data we then aim to attribute
93 individual variation in diet to its sources: maternal learning, genetic heritability, environment,
94 and maternal effects.
95 Brown bears are ecological generalists with a species range spanning the northern
96 hemisphere from tundra to deserts, paralleled by extensive variation in diet: from populations
97 tracking food resource pulses, such as spawning fish [15], over ones scavenging on ungulate
98 carcasses or preying on ungulates neonates [16], feeding extensively on invertebrates, to
99 populations with primarily fruiting plant based diets [17, 18]. Given this extreme dietary
100 plasticity, it is not surprising that great dietary variation has been found within populations
101 [19, 20], however, the determinants and ontogeny of this variation at the individual level
102 remain largely unknown. In ecology, differences in diet are often primarily attributed to
103 differences in resource availability and abundance. Even within populations inhabiting a
104 continuous biome, home range scale variation in habitat composition [21] can lead to
105 variation in resource availability. The most parsimonious source of variation in diet are,

therefore, differences in the environment. Brown bears maintain non-territorial home ranges but live a solitary lifestyle except for the period of offspring rearing with up to three years [22] of maternal care. In their first years of life, bear cubs accompany their mother and it is therefore reasonable to assume that brown bear offspring learn behaviors such as habitat, den site, or diet selection from their mothers and hence show similar behavior to their mother. If mothers differ in their dietary selection, these differences may hence be maintained in the population through learning by imitation of the mother (hereafter "maternal learning”), even after offspring gain independence, however such similarities may wane over time [23]. On the other hand, genetic heritability or maternal effects can have lifelong effects on offspring phenotype. Body size has been shown to be genetically heritable in the study population [24] suggesting greater similarity among closely related individuals also in other linked traits, such as trophic position. Alternatively, maternal effects (i.e., maternal genotype or maternal environment) alone can shape the phenotype of offspring. For example, milk quantity or quality [25] can vary among females either due to genetic differences or differences in the environments, leading to greater similarity among all offspring from the same mother (e.g. being smaller or larger in body size), which in turn could cause similarities in trophic position among siblings. To assess individual specialization along a continuum from a more plant-based to a more meat- or insect-based diet, we analyzed annual trophic positions from nitrogen stable isotopes (δ^{15}N) stored in bear hair keratin [26]. Stable isotopes reflect cumulative diet intake and are deposited into the hair during growth with, a delay of approximately one month (i.e. a growing hair in June reflects the diet intake in May, [27]). Bear hair is regularly renewed through molting in June, regrows over the summer and fall and stops growing during winter hibernation (**Fig 1A, [28, 29]**). Guard hair samples collected in spring and early summer (April - June) therefore reflect an individual’s diet during the previous active season prior to hibernation [28]. Using repeated samples of known mother-

131 daughter pairs, we fit a spatially explicit Bayesian hierarchical model (i.e. ´animal model´)
132 [30-32] to disentangle the relative contributions of maternal learning, genetic relatedness, the
133 environment, and maternal effects as determinants of individual specialization. Specifically,
134 the model accounted for genetic relatedness with a pedigree and for environmental similarity
135 of bear home ranges with pairwise habitat similarity encompassing the proportion of mature
136 habitat such as old and mid-successional forests, disturbed habitat such as clearcuts and
137 regenerating young forest, and habitat diversity (measured as Simpson's diversity index) in a
138 bear's home range. The model also accounted for maternal effects by incorporating the
139 mother's ID as a random effect (i.e. if daughters from the same mother behaved in a similar
140 fashion throughout life), and for maternal learning as the fixed effect of a mother's trophic
141 positions on her daughter's trophic position. To this end, we determined maternal trophic
142 positions from a population-wide model accounting for sexual dimorphism, age, and
143 individual consistency in diet (**Supplement 3**). Because bears may alter diet selection over
144 time through individual learning, we allowed the effect of maternal learning to shift with time
145 since the offspring gained independence. Last, we also accounted for permanent individual
146 effects that could not be attributed to any of the aforementioned sources, by including a
147 random effect for bear ID. We focused on the effect of maternal trophic position on female
148 offspring trophic position, because male offspring were only monitored for a short period
149 after family breakup. In the supplementary material we provide an additional analysis of the
150 relationship between maternal and both female and male offspring trophic position in the first
151 4 years after family breakup and of the relationship between paternal trophic position and
152 offspring trophic position. We also provide an alternative analysis accounting for spatial
153 correlation via a spatial distance instead of the habitat similarity matrix. Last, we provide a
154 reduced model excluding the effect of environmental similarity to test whether spatial and
155 genetic effects are confounded in philopatric female bears.

156

157 ## 2. RESULTS

158 We analyzed annual trophic positions in 213 hair samples collected from 71 female brown
159 bears born to 33 unique mothers (1 – 7 daughters per mother; median 2 daughters). Repeated
160 sampling (median 3 years; range 1-11 years) revealed that female trophic position was
161 unaffected by age (explained variance = 1% [0 – 4%]) and that individuals showed long-term
162 individual specialization, accounting for 48% [31 – 61%] (median [89% equal tails credible
163 interval]) of the total variance in trophic position (**Fig 2,** *Basic model*). Individual
164 specialization spanned half a trophic position ranging from 2.7 to 3.1 for individual females
165 (**Fig 1B**), which is equivalent to the difference between an omnivore feeding on a mix of
166 plants and animal prey and a carnivore feeding predominantly on animal prey.
167 Individual specialization was primarily driven by initial maternal learning, the environment,
168 and maternal effects. Maternal trophic position dynamic over the time since separation
169 accounted for 13% [5% - 23%] of variation in trophic position, while environmental
170 similarity accounted for 9% [0.1 - 5%] of the total phenotypic variation in trophic position.
171 Additionally, maternal effects accounted for 11% [0.5% - 30%] of variation in trophic
172 position, indicating that siblings (full and half) of the same mother were more similar in
173 trophic position throughout life as compared to non-siblings. A remaining 8% [0.3 – 26%] of
174 variance in trophic position was attributed to permanent individual effects (**Fig 2**).Genetically
175 more closely related individuals did not share a more similar trophic position (3% [<0.1% –
176 17%] of variance explained) providing no evidence that dietary specialization could be
177 heritable in this population (**Fig 2**).
178 After separating from their mother, female offspring initially maintained a similar trophic
179 position as their mother (Pearson's r = 0.66 in the first two years after separation), which
180 gradually became more dissimilar over time (Pearson's r = 0.31 in year 3 - 4 after separation**,**

Fig 3). In the first years, offspring of more carnivorous mothers also had a high trophic position while offspring of less carnivorous mothers had a lower trophic position. About five years after the separation of the mother, this correlation ceased to exist. Bears inhabiting home ranges with a similar composition of mature and disturbed forest, as well as a similar habitat diversity in the home range, also had more similar trophic positions. The distance between pairwise home range centroids ranged from 0.7 to 172 km with a median pairwise distance of 48 km and individuals living in closer proximity had a more similar trophic position than individuals living farther apart (**Supplementary material S5**). Spatial distance and maternal effects seemed to be confounded in this female philopatric species (**Fig S5**): After excluding spatial distance, maternal learning and maternal effects but not heritability explained more variance in trophic position, corroborating that spatial proximity is confounded with philopatric females forming clusters of mothers and daughter in space, so called matrilines (**Fig S6**). In a separate analysis (**Fig S7**) we could also show that the relationship between maternal and offspring trophic position in the first years after family breakup was not sex-specific. Both male (n = 31, Pearson correlation coefficient = 0.4) and female (n = 69, Pearson correlation coefficient = 0.45) offspring's trophic positions resembled their mother's trophic position in the first 4 years of independence, corroborating our findings that initial maternal learning determines foraging behavior in the early years after family breakup. Conversely, paternal trophic position had no effect on offspring trophic position in the first 4 years of independence (Pearson correlation coefficient = 0.13, **Fig S8**).

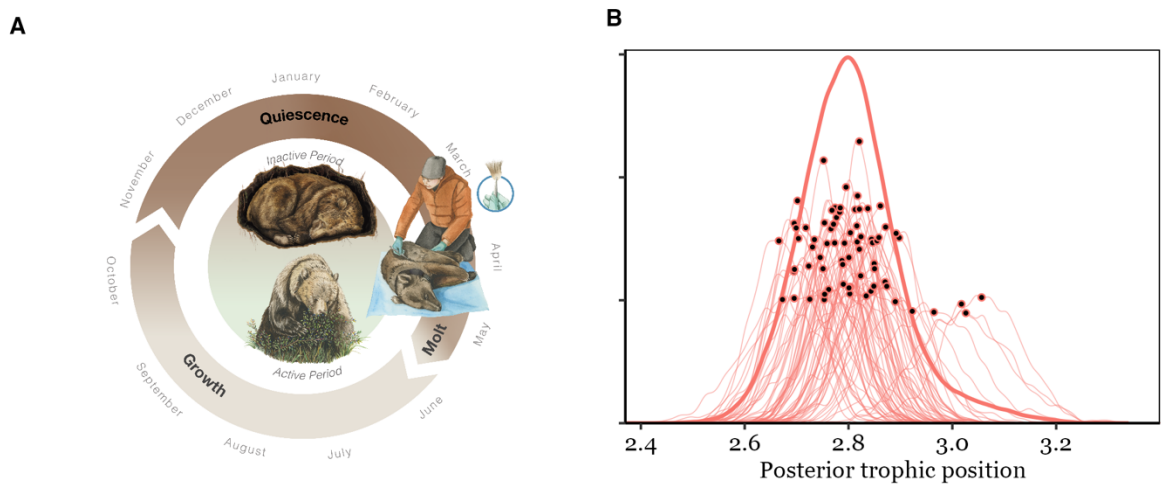

Figure 1. A) Bear hair generally grows from June until October. Stable isotopes are deposited into the growing hair with a delay of approximately one month. The quiescent phase, when hair ceases growing, lasts through hibernation, followed by emergence from the winter den and molting in late May-early June. Hair samples were taken in April - June and reflect the bears' diet in the previous year; **B**) Posterior distribution of the population trophic niche (bold line) and individual specialization indicated by each individual's posterior trophic position. Scientific illustration by Juliana D. Spahr, SciVisuals.com.

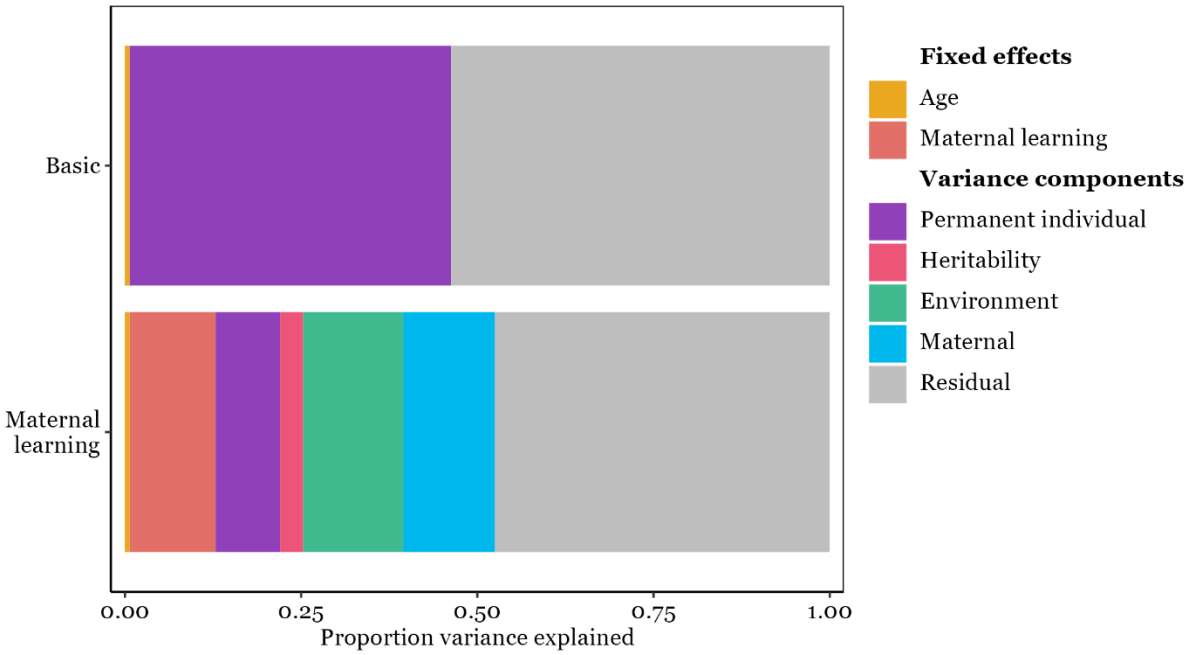

Figure 2. Proportion of variance (median of the posterior distribution) in brown bear trophic position explained by age, age sensitive maternal learning, permanent individual effects,

environmental similarity, permanent maternal effects, genetic heritability, and residual components.

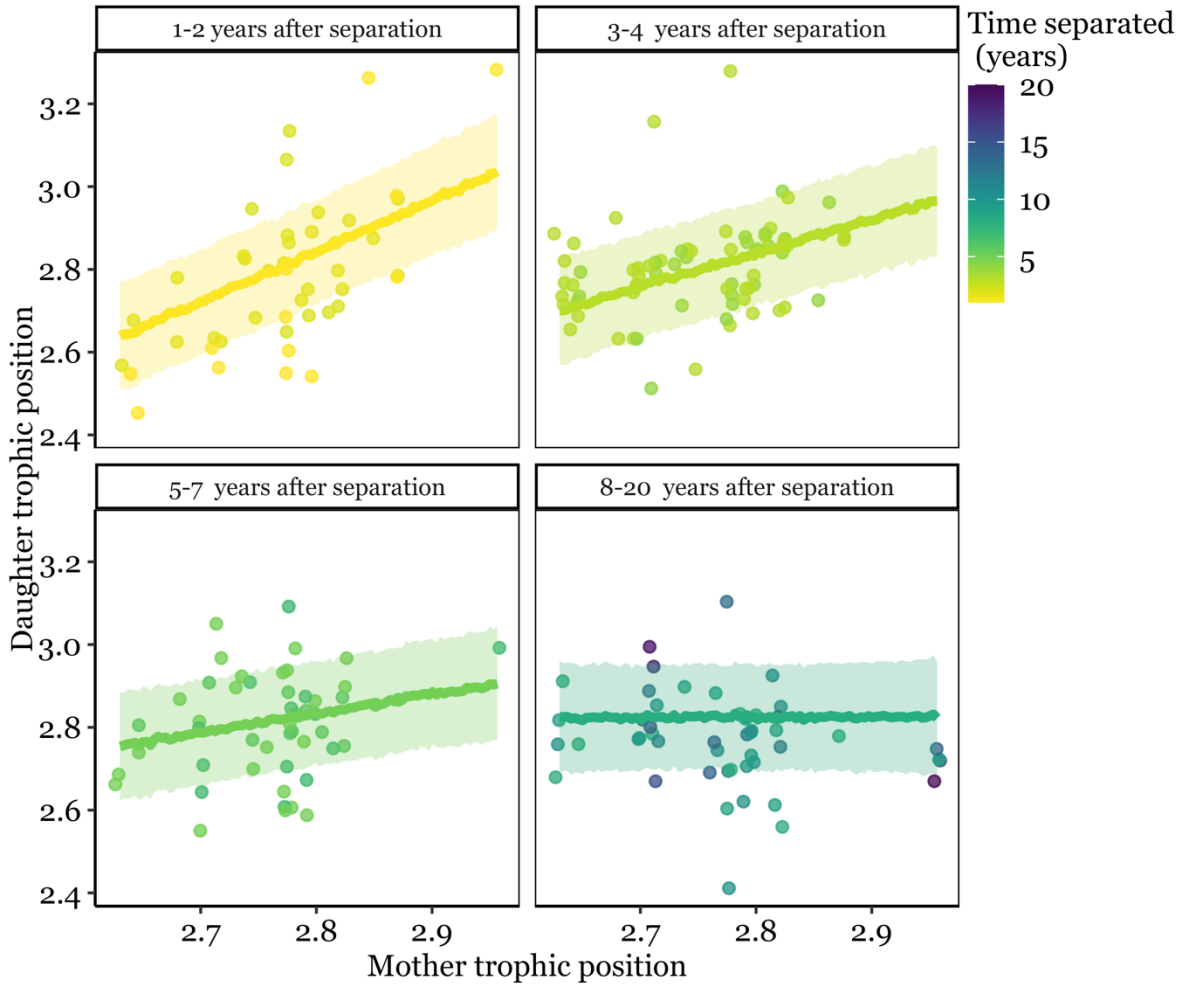

Figure 3. Relationship between female brown bear trophic position and their mother's trophic position over number of years since separation (i.e. since the female became independent, usually at 1.5 years of age). The females' trophic position resembled their mothers' in the first years after separation but this similarity ceased after 4 years.

3. DISCUSSION

Our multigenerational dataset reveals unique insights into the ontogeny of individual dietary specialization along a continuum from a more herbivorous to a more carnivorous diet in a long-lived omnivore. Specifically, the foraging strategy of sons and daughters was intimately tied to the foraging strategy of their mother, a relationship that lasted up to four years after

independence. We interpret this relationship as evidence that maternal learning plays an important role in shaping an individual's dietary specialization. Five years into independence, the similarity between the mothers' and their daughters' trophic position slowly faded, likely due to individual learning and experience. In addition, siblings of the same mother also shared lifelong similarities in their trophic position, potentially mediated through maternal genetic or environmental effects on body size [24]. In general, previous ecological studies have mainly concentrated on resource availability as the main driver of resource selection [33] and individual specialization [4], however our results show that within populations, the environment is only one of several components shaping individual dietary variation. We conclude that early-life imitation of maternal dietary preferences and maternal effects (i.e., maternal genotype and environment), which together explained about 24% of the variation in trophic position, play a pivotal role in spreading and maintaining feeding strategies within populations, even in species with otherwise solitary lifestyles. In addition, variation solely linked to individual variation (in our study 8 %) demonstrates potential for behavioral innovation and the potential to adapt to changing conditions.

Our findings are particularly relevant for species in which dietary specialization impacts individual fitness [7, 34, 35]. For example, protein-rich diets may promote greater offspring survival or mass gain [36]. Maternal and social learning in general therefore present an important, yet understudied pathway by which alternative behavioral strategies can establish and spread more rapidly within populations than by genetic evolution alone [37]. Species more adept in social learning of dietary strategies may therefore show greater behavioral variability on the population level, which could give them an advantage when adapting to changing environments due to landscape modification or urbanization, climatic variations or global change in general. Moreover, there is evidence that the strength of social learning in

253 shaping individual phenotypes is not only species-specific, but can also vary among
254 populations or individuals of the same species [38].
255
256 Our research also points to several aspects of maternal learning that warrant future research.
257 First, there is little information on whether maternal care and maternal learning tend to be
258 more prevalent in species or populations with greater dietary specialization. There is some
259 evidence that within populations, dietary generalists (i.e. those with a wider dietary niche)
260 seem to provide more intense parental care [39], than their conspecific dietary specialists (i.e.
261 ones with a narrower dietary niche), but the links to parental learning of foraging preferences
262 remains unclear. Second, while generalist species with a wide ecological niche have been
263 frequently shown to be more successful under changing environmental conditions, such as
264 urban environments or fragmented landscapes, than specialist species [40-42], it is currently
265 unknown whether this success could be partially mediated by social or maternal learning.
266 Last, social learning could alternatively limit behavioral innovation and adaptation due to
267 adherence to social traditions [43]. We therefore suggest that alternative hypotheses should
268 be evaluated that consider how social learning impacts individual specialization and in turn
269 the adaptability of species under global change.
270
271 Our findings that dietary specialization can be socially learned and transmitted are
272 particularly relevant for species where specialization is related to human-wildlife conflict
273 [44]. For example, the removal of single individuals which are known to cause conflict is an
274 effective strategy to halt the spread of problematic behavior, increase societal acceptance by
275 effectively mitigating the conflict, while minimizing the impact for species conservation
276 goals [44]. Foraging behavior that causes conflict has also been shown to change in ursids
277 across life time, remarking the crucial role of individuality and plasticity in behavior [45].

Maternal learning of behavior [46], including dietary specialization and foraging on anthropogenic food resources is commonly observed in ursids [47-50]. However, none of these studies tracked offspring diet over their lifetimes or were able to simultaneously account for the mother's diet, genetics, the environment, and other maternal effects, that could explain similar patterns of dietary specialization. While some of the aforementioned studies suggest either the environment or maternal learning as primary drivers of individual specialization, we suggest using caution in assigning causality in dietary specialization, when potentially confounding alternative sources cannot be accounted for. Specifically, in female-biased philopatric species, spatial proximity does not only encode for spatial variation in resource abundance but is also conflated with relatedness and, in particular, with maternal effects. In brown bears, philopatric daughters settle close to their mother's home range [51] creating spatial clusters of closely related females, so called matrilinear assemblages [52]. Due to spatial dependence of matrilinear assemblages, it can therefore be difficult to disentangle maternal learning from other maternal effects (i.e., maternal genotype or maternal environment) or the ambient environment. Our study population spanned over 170 km with spatial proximity explaining 59% of the total phenotypic variation in trophic position of female bears: individuals further apart tended to have more different diets. However, when replacing spatial proximity with environmental similarity among home ranges, the explanatory power was attributed to maternal learning and maternal effects along with the environment. Our results therefore demonstrate that individual dietary specialization is not caused by a single driver in isolation but the product of many factors, namely: maternal learning, maternal effects, and the environment.

Our finding that maternal learning has a similar impact on resource selection as the environment provides important insights for a range of studies on habitat selection, dispersal,

and range expansion. For example, a popular theory known as "natal habitat preference induction" suggests that dispersing animals select areas for settlement that resemble their natal habitat, even at fine habitat scales [21]. Our results challenge the notion that habitat similarity alone drives natal settlement strategies and rather suggest that maternally induced diet preferences, and hence the selection for food resources themselves, could play an important role in producing similar patterns of settlement selection like induced natal habitat preferences. Recent studies of migration and short stopover behavior in whooping cranes (*Grus americana*) have also observed that social learning rather than environmental conditions [53] or genetic inheritance [54] led to the emergence and establishment of alternative migratory behavior. Similar to what our study shows with respect to dietary specialization, social learning of migration strategies primarily determined behavior in early life whereas individual-experiential learning shaped behavior later in life [55].

Conclusion

Drivers of dietary specialization are well documented among populations of the same species, however, systematic studies delineating the sources of individual specialization within populations are lacking, likely because suitable datasets including multigenerational, genetic, environmental, and life-history information are rare. We show here that in addition to the environment, maternal learning and (other) maternal effects can be important sources of dietary specialization.

4. METHODS

Bear sample collection

We collected brown bear (*Ursus arctos*) hair samples in south-central Sweden (~N61°, E15°) as part of a long-term, individual-based monitoring project (Scandinavian Brown Bear

328 Research Project; www.bearproject.info). Hair samples were collected from known
329 individuals and their offspring during bear captures in spring (April - June) 1993 – 2015 after
330 bears emerged from hibernation. Bears were immobilized from a helicopter (Arnemo &
331 Fahlman, 2011). A vestigial premolar tooth was collected from all bears not captured as a
332 yearling to estimate age based on the cementum annuli in the root [56]. Bears were weighed
333 in a stretcher suspended beneath a spring scale. Tissue samples (stored in 95% alcohol) were
334 taken for DNA extraction to assign parentage and construct a genetic pedigree [52]. Guard
335 hairs and follicles were plucked with pliers from a standardized spot between the shoulder
336 blades and archived at the Swedish National Veterinary Institute. We used data of adult bears
337 (solitary or with offspring) and of offspring after separation from their mother. Bear cubs are
338 born in January or February during winter hibernation and are typically first captured
339 together with their mother as yearlings at the age of ~ 15 months. Cubs in this population
340 separate from their mother during the mating season in May or June after 1.5 or 2.5 years
341 [57]. Only hair samples of solitary, independent offspring taken in spring and early summer
342 at least 10 months after separation from the mother were included in this study. A hair sample
343 taken in spring reflects the summer-fall diet of the bear in the previous active season (**Fig**
344 **1A**).
345
346 **Food sample collection**
347 We collected samples of the natural foods most important for brown bear in the study area,
348 including 21 samples of moose hair (*Alces alces*), the most common meat source in the
349 brown bears' diet in our study area [58], in the spring-autumn field season of 2014 (**Fig S1**).
350 Samples were placed in a paper envelope and dried at ambient temperature for 48.
351
352 **Stable isotope analyses**

353 Hair samples were rinsed with a 2:1 mixture of chloroform:methanol or with pure methanol
354 to remove surface oils [59]. Dried samples were ground with a ball grinder (Retsch model
355 MM-301, Haan, Germany).
356 We weighed 1 mg of ground hair into pre-combusted tin capsules and combusted at 1030°C
357 in a Carlo Erba NA1500 elemental analyser. N_2 and CO_2 were separated chromatographically
358 and introduced to an Elementar Isoprime isotope ratio mass spectrometer (Langenselbold,
359 Germany). Two reference materials were used to normalize the results to VPDB and AIR:
360 BWB III keratin ($\delta^{13}C$ =- 20.18‰, $\delta^{15}N$ = 14.31‰, respectively) and PRC gel ($\delta^{13}C$ =-
361 13.64‰, $\delta^{15}N$ = 5.07‰, respectively). Measurement precisions as determined from both
362 reference and sample duplicate analyses were ± 0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$.
363
364 **Bear trophic position**
365 We calculated the trophic position of each bear hair sample relative to the average $\delta^{15}N$ value
366 of moose (mean ± sd = 1.8 ± 1.26 ‰, n = 21, **Fig S1**). Trophic position is calculated as the
367 the discrepancy of $\delta^{15}N$ in a secondary consumer and its food source divided by the
368 enrichment of $\delta^{15}N$ per trophic level, plus lambda, the trophic position of the food source
369 (e.g. 1 for primary producers, 2 for primary consumers, 3 for secondary consumer, 4 for
370 tertiary consumers) [60]. We used an average trophic enrichment factor of 3.4‰ [60] and
371 added a lambda of 2 given that the moose baseline trophic position as a strict herbivore.
372 $$\text{Bear trophic position} = (\delta^{15}N_{Ursus\ arctos} - \text{average}(\delta^{15}N_{Alces\ alces})) / 3.4 + 2$$
373 Under an omnivorous diet including the consumption of herbivores (in particular moose but
374 also herbivorous insects), bear trophic position values were expected to fall between 2 and 3.
375 Values approaching 4 indicate a trophic enrichment through consumption of other
376 omnivorous or carnivorous animals.
377

Genetic pedigree and parentage assignment

A genetic pedigree based on 16 microsatellite loci was available for the population including 1614 individual genotypes [61]. Genotyping followed the protocols of Waits, Taberlet [62], Taberlet, Camarra [63], and Andreassen, Schregel [64]. All female offspring in this study were genotyped and included in the population's genetic pedigree. All females included in this study had a known mother that was also captured and followed. We used Cervus 3.0 [65] for assignment of fathers and COLONY [66] for creating putative unknown mother or father genotypes and sibship reconstruction (see [61] for details).

Maternal trophic position

Based on repeated hair samples of 115 female (nfemale = 335) and 98 male (nmale = 219) bears, we fitted a *basic* linear mixed effects model for female and male bears respectively, to estimate sex-specific among individual variation in trophic position (**Supplementary analysis 3**). We modelled trophic position as a function of a quadratic relationship with age and we controlled for individual random intercepts. Female trophic position did not vary with age (**Fig S3A**) but was highly repeatable over multiple years (**Fig S3B**). For all daughters, we extracted their mother's (and father's) trophic position as the median of the posterior distribution of their respective random intercept.

Environmental similarity

Resources, i.e. access to moose and ants, may not be distributed evenly in space. For moose, population density and hunting quotas (which determine availability of slaughter remains) vary across the study area. For ants (*Formica* spp*., Camponotus herculeanus*), the availability of old forests and clearcuts determine their abundance [67]. Further, brown bear daughters are often philopatric with limited dispersal and settle close to their mother's home range [51].

Genetic, spatial, and maternal learning effects may therefore be confounded with related bears occupying adjacent ranges with similar environments and resource availability. Elsewhere, accounting for environmental similarity through spatial autocorrelation in animal models has revealed that a major portion of variance may be attributed to environmental similarity rather than genetic heritability [30, 31, 68, but see also 69]. Here, we accounted for environmental similarity by extracting habitat composition in each bear's lifetime home range. For individuals with sufficient locations (> 1000 GPS locations or VHF locations on at least 25 days) we constructed home ranges using a 95% kernel density estimator. We used a corine landcover map (25 m resolution) which we updated annually with polygons of newly emerged clearcuts (data obtained from the Swedish Forest Agency). We extracted home range composition in the year when diet was assessed. When individuals were monitored for multiple years, we extracted the home range composition for the median year. We calculated the proportion of mid-aged and old forest and proportion of disturbed forest (clearcuts and regenerating young forest) within the 95% utilization distribution. Additionally, we calculated habitat diversity using the Simpson diversity index from the R package landscapemetrics [70]. Following Thomson et al. [30] we calculated the Euclidean distance between scaled and centered habitat composition and habitat diversity in multivariate space, assuming equal importance of each component. Pairwise distances were scaled between 0 and 1, where increasing values indicated more similar habitat composition. In the supplementary material we provide an alternative analysis accounting for spatial autocorrelation in dietary specialization with a pairwise spatial distance matrix (S matrix; Supplementary analysis 5, **Fig S5**).

Statistical analysis

427 We applied a two-step modelling approach. First, we fitted a *basic* linear mixed effects model
428 to estimate individual specialization as among individual variation in annual trophic position.
429 We accounted for a nonlinear effect of age (second order polynomial) and for repeated
430 measures of the same individual with individual random intercepts. We extracted the variance
431 in fitted values (variance explained by fixed effects), among-individual, and residual variance
432 and estimated the proportional contribution of fixed and random effects on the total
433 phenotypic variance through variance standardization (i.e. repeatability [71], marginal and
434 conditional R^2-values [72]). Second, we used a spatially explicit Bayesian hierarchical model
435 (i.e. 'animal model') [30, 32] to partition among-individual variance in trophic position into
436 environmental similarity (σ^2_{env}), additive genetic (σ^2_a), permanent among-individual (σ^2_{ind}),
437 maternal ($\sigma 2_{mat}$), and residual within-individual effects (σ^2_r). Similar to the basic model, we
438 accounted for a nonlinear effect of age on trophic position (fitted as time since separation of
439 mother and daughter scaled by the standard deviation, true age and time since separation
440 were perfectly correlated: Pearson correlation coefficient > 0.99). We tested for maternal
441 effects on offspring trophic position by incorporating the mother's trophic position as a
442 covariate into the model. To account for a potential decrease of the maternal effect over time,
443 we let maternal trophic position interact with the time since separation of mother and
444 daughter (both scaled by their standard deviation and centered). We partitioned the variance
445 explained by the two components of the fixed effect, the effect of maternal learning over time
446 (i.e. maternal trophic position and the interaction between maternal trophic position and time
447 since separation) and age (i.e. the main effect of time since separation), respectively, by
448 calculating the independent contribution of each component to the total variance explained by
449 the fixed effects, following the approach by Stoffel, Nakagawa [73] adapted to a Bayesian
450 framework (see code under [74]).

All models were fit using the R package "brms" [75] based on the Bayesian software Stan [76, 77]. We ran four chains to evaluate convergence which were run for 6,000 iterations, with a warmup of 3,000 iterations and a thinning interval of 10. All estimated model coefficients and credible intervals were therefore based on 1200 posterior samples and had satisfactory convergence diagnostics with $\hat{R} < 1.01$, and effective sample sizes > 400 [78]. Posterior predictive checks recreated the underlying Gaussian distribution of trophic position well. For all parameters, we report the median and 89% credible intervals, calculated as equal tail intervals, as measure of centrality and uncertainty [79]. We deemed explained variance proportions as inconclusive when the lower credible interval limit was < 0.001 (i.e., < 0.1%) [80]. All statistical analyses were performed in R 4.0.0 [81]. Primary data and code to reproduce all analyses are provided under (https://doi.org/10.17605/OSF.IO/68B9U, [74]).

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AUTHOR'S CONTRIUTIONS

AH, JA, and TM developed the work. AZ, JK, KAH, NS and AS provided the data. AZ managed the sample collection. AS managed the hair samples database and prepared samples for stable isotope analyses by KAH. DMJ provided laboratory space and resources and supervised preparatory procedures. SF constructed and provided the genetic pedigree. JH provided home range centroids. AM and JA advised to the analysis and interpretation of stable isotope data. TM, NS and AZ secure project funding. AH performed the statistical analyses with input from JA. AH wrote the manuscript with help from TM, JA, and input from all authors.

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