

1 *Running head: Learning dietary specialization*

2 **The ontogeny of individual specialization**

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34 **ABSTRACT**

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

52

53 **KEYWORDS**

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

## 56 1. INTRODUCTION

57 Among individuals of the same species, niche variation is common and may occur when  
58 availability of food resources or habitat structure change across the species' range. Ecological  
59 generalists, species with a wide niche, also seem to exhibit more individual specialization [1]  
60 and are hence particularly well adapted to persist under shifts in resource availability or  
61 composition enabling them to occupy larger distributional ranges than ecological specialists  
62 [2]. Individual variation is key for making species resilient towards changing resource  
63 availabilities in a rapidly changing world and may ultimately determine local persistence or  
64 extinction of species [3].

65 Inter- and intraspecific competition, predation and ecological opportunity, alter resource  
66 availability and have been identified as the main ecological drivers explaining variation in the  
67 degree of individual specialization between populations [4]. Yet, how individual variation  
68 emerges and is maintained within populations has been rarely quantified in the wild. In  
69 principle, four potential sources of variation exist: social and individual learning, genetic  
70 inheritance, the environment, and maternal effects. Individual differences in resource  
71 preference or competence to secure a resource may therefore be determined during early  
72 ontogeny through social (e.g., maternal) learning via imitation [5-9] leading to similarities  
73 between the offspring's and their mother's dietary phenotype. Effects of maternal learning  
74 can be lifelong or are modified through individual experiential learning [10]. Resource  
75 preferences have also been suggested to be genetically determined through genes inherited  
76 from both mother and father, where closely related individuals have more similar diets than  
77 distantly related individuals [11]. In addition, maternal effects account for lifelong  
78 similarities in dietary phenotype among offspring of the same mother [12]. Such similarities  
79 can arise from social interactions, maternal genotype, or maternal environment. Statistically,  
80 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,

106 therefore, differences in the environment. Brown bears maintain non-territorial home ranges  
107 but live a solitary lifestyle except for the period of offspring rearing with up to three years  
108 [22] of maternal care. In their first years of life, bear cubs accompany their mother and it is  
109 therefore reasonable to assume that brown bear offspring learn behaviors such as habitat, den  
110 site, or diet selection from their mothers and hence show similar behavior to their mother. If  
111 mothers differ in their dietary selection, these differences may hence be maintained in the  
112 population through learning by imitation of the mother (hereafter "maternal learning"), even  
113 after offspring gain independence, however such similarities may wane over time [23]. On  
114 the other hand, genetic heritability or maternal effects can have lifelong effects on offspring  
115 phenotype. Body size has been shown to be genetically heritable in the study population [24]  
116 suggesting greater similarity among closely related individuals also in other linked traits,  
117 such as trophic position. Alternatively, maternal effects (i.e., maternal genotype or maternal  
118 environment) alone can shape the phenotype of offspring. For example, milk quantity or  
119 quality [25] can vary among females either due to genetic differences or differences in the  
120 environments, leading to greater similarity among all offspring from the same mother (e.g.  
121 being smaller or larger in body size), which in turn could cause similarities in trophic position  
122 among siblings. To assess individual specialization along a continuum from a more plant-  
123 based to a more meat- or insect-based diet, we analyzed annual trophic positions from  
124 nitrogen stable isotopes ( $\delta^{15}\text{N}$ ) stored in bear hair keratin [26]. Stable isotopes reflect  
125 cumulative diet intake and are deposited into the hair during growth with, a delay of  
126 approximately one month (i.e. a growing hair in June reflects the diet intake in May, [27]).  
127 Bear hair is regularly renewed through molting in June, regrows over the summer and fall  
128 and stops growing during winter hibernation (**Fig 1A, [28, 29]**). Guard hair samples collected  
129 in spring and early summer (April - June) therefore reflect an individual's diet during the  
130 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.

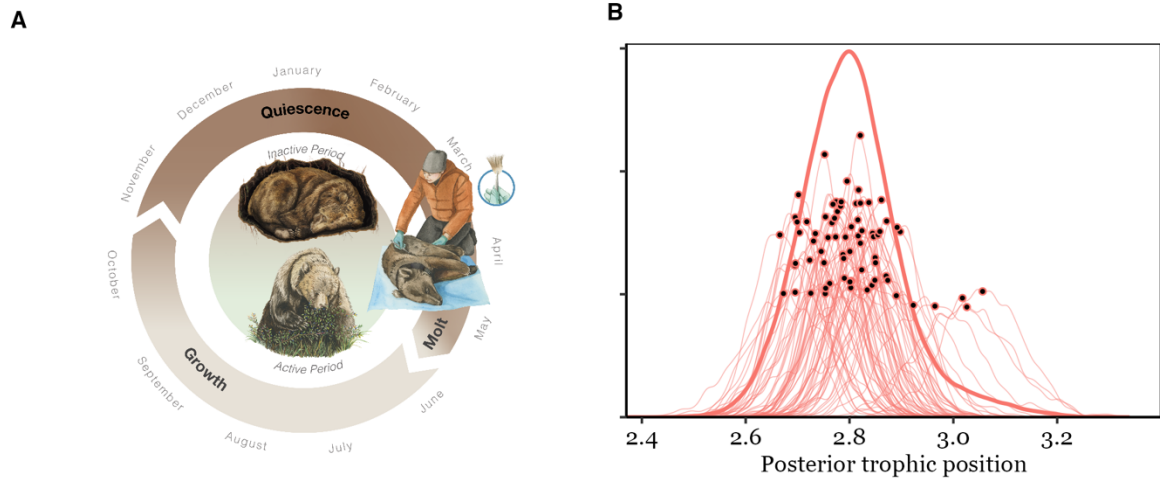
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## 157 2. RESULTS

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,



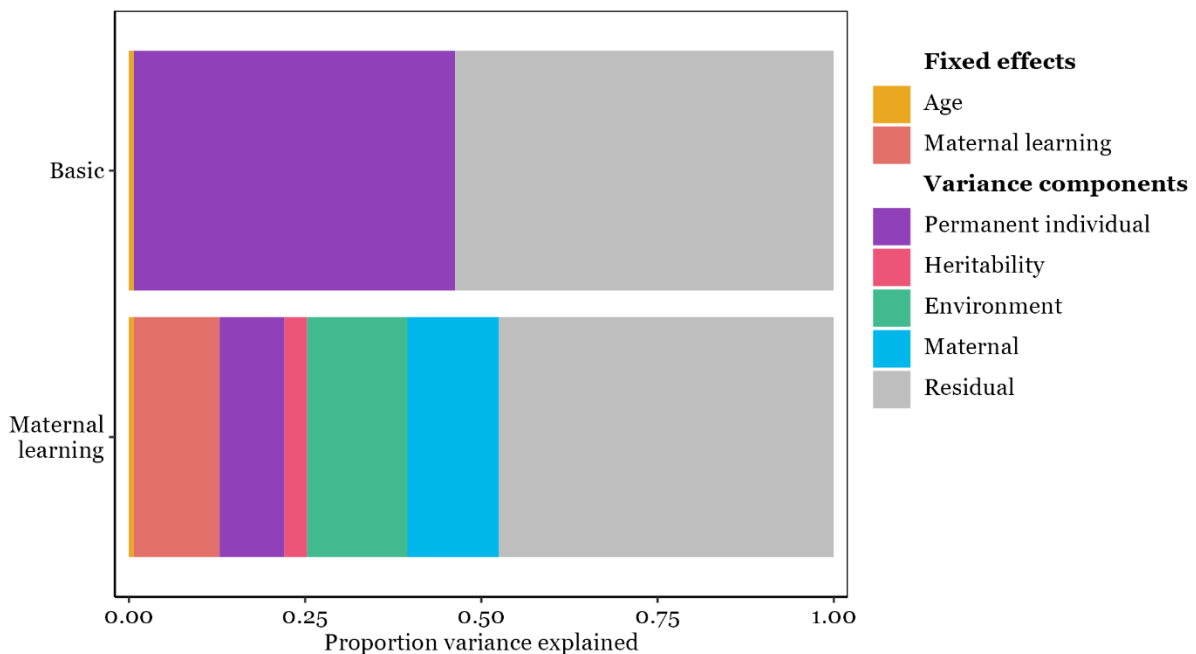
181 **Fig 3**). In the first years, offspring of more carnivorous mothers also had a high trophic  
182 position while offspring of less carnivorous mothers had a lower trophic position. About five  
183 years after the separation of the mother, this correlation ceased to exist. Bears inhabiting  
184 home ranges with a similar composition of mature and disturbed forest, as well as a similar  
185 habitat diversity in the home range, also had more similar trophic positions. The distance  
186 between pairwise home range centroids ranged from 0.7 to 172 km with a median pairwise  
187 distance of 48 km and individuals living in closer proximity had a more similar trophic  
188 position than individuals living farther apart (**Supplementary material S5**). Spatial distance  
189 and maternal effects seemed to be confounded in this female philopatric species (**Fig S5**):  
190 After excluding spatial distance, maternal learning and maternal effects but not heritability  
191 explained more variance in trophic position, corroborating that spatial proximity is  
192 confounded with philopatric females forming clusters of mothers and daughter in space, so  
193 called matriline (**Fig S6**). In a separate analysis (**Fig S7**) we could also show that the  
194 relationship between maternal and offspring trophic position in the first years after family  
195 breakup was not sex-specific. Both male ( $n = 31$ , Pearson correlation coefficient = 0.4) and  
196 female ( $n = 69$ , Pearson correlation coefficient = 0.45) offspring's trophic positions  
197 resembled their mother's trophic position in the first 4 years of independence, corroborating  
198 our findings that initial maternal learning determines foraging behavior in the early years  
199 after family breakup. Conversely, paternal trophic position had no effect on offspring trophic  
200 position in the first 4 years of independence (Pearson correlation coefficient = 0.13, **Fig S8**).  
201



202

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

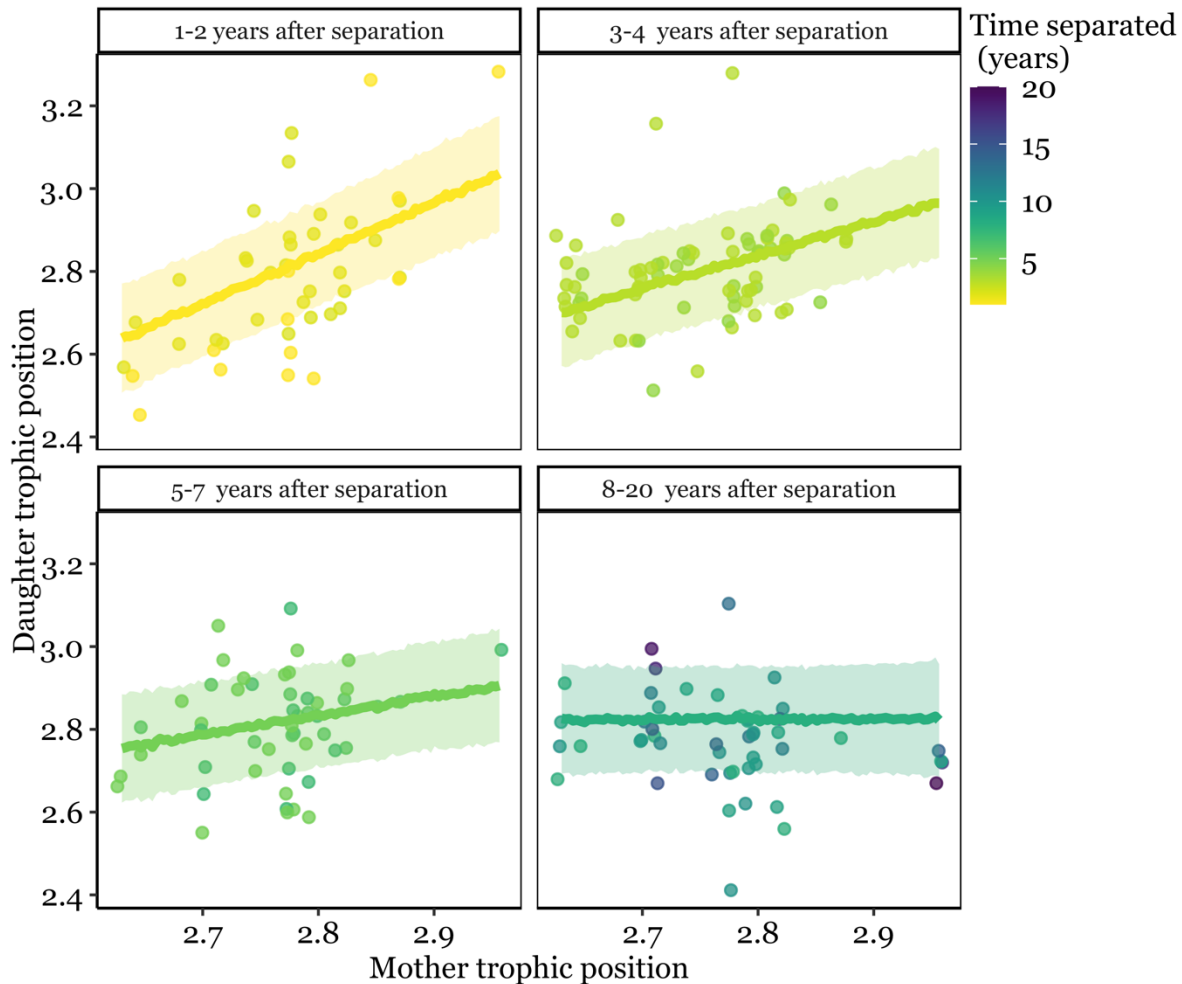
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211

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

214 environmental similarity, permanent maternal effects, genetic heritability, and residual  
215 components.  
216



217

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

222

### 223 3. DISCUSSION

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

228 independence. We interpret this relationship as evidence that maternal learning plays an  
229 important role in shaping an individual's dietary specialization. Five years into independence,  
230 the similarity between the mothers' and their daughters' trophic position slowly faded, likely  
231 due to individual learning and experience. In addition, siblings of the same mother also  
232 shared lifelong similarities in their trophic position, potentially mediated through maternal  
233 genetic or environmental effects on body size [24]. In general, previous ecological studies  
234 have mainly concentrated on resource availability as the main driver of resource selection  
235 [33] and individual specialization [4], however our results show that within populations, the  
236 environment is only one of several components shaping individual dietary variation. We  
237 conclude that early-life imitation of maternal dietary preferences and maternal effects (i.e.,  
238 maternal genotype and environment), which together explained about 24% of the variation in  
239 trophic position, play a pivotal role in spreading and maintaining feeding strategies within  
240 populations, even in species with otherwise solitary lifestyles. In addition, variation solely  
241 linked to individual variation (in our study 8 %) demonstrates potential for behavioral  
242 innovation and the potential to adapt to changing conditions.

243

244 Our findings are particularly relevant for species in which dietary specialization impacts  
245 individual fitness [7, 34, 35]. For example, protein-rich diets may promote greater offspring  
246 survival or mass gain [36]. Maternal and social learning in general therefore present an  
247 important, yet understudied pathway by which alternative behavioral strategies can establish  
248 and spread more rapidly within populations than by genetic evolution alone [37]. Species  
249 more adept in social learning of dietary strategies may therefore show greater behavioral  
250 variability on the population level, which could give them an advantage when adapting to  
251 changing environments due to landscape modification or urbanization, climatic variations or  
252 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].

278 Maternal learning of behavior [46], including dietary specialization and foraging on  
279 anthropogenic food resources is commonly observed in ursids [47-50]. However, none of  
280 these studies tracked offspring diet over their lifetimes or were able to simultaneously  
281 account for the mother's diet, genetics, the environment, and other maternal effects, that  
282 could explain similar patterns of dietary specialization. While some of the aforementioned  
283 studies suggest either the environment or maternal learning as primary drivers of individual  
284 specialization, we suggest using caution in assigning causality in dietary specialization, when  
285 potentially confounding alternative sources cannot be accounted for. Specifically, in female-  
286 biased philopatric species, spatial proximity does not only encode for spatial variation in  
287 resource abundance but is also conflated with relatedness and, in particular, with maternal  
288 effects. In brown bears, philopatric daughters settle close to their mother's home range [51]  
289 creating spatial clusters of closely related females, so called matrilinear assemblages [52].  
290 Due to spatial dependence of matrilinear assemblages, it can therefore be difficult to  
291 disentangle maternal learning from other maternal effects (i.e., maternal genotype or maternal  
292 environment) or the ambient environment. Our study population spanned over 170 km with  
293 spatial proximity explaining 59% of the total phenotypic variation in trophic position of  
294 female bears: individuals further apart tended to have more different diets. However, when  
295 replacing spatial proximity with environmental similarity among home ranges, the  
296 explanatory power was attributed to maternal learning and maternal effects along with the  
297 environment. Our results therefore demonstrate that individual dietary specialization is not  
298 caused by a single driver in isolation but the product of many factors, namely: maternal  
299 learning, maternal effects, and the environment.  
300  
301 Our finding that maternal learning has a similar impact on resource selection as the  
302 environment provides important insights for a range of studies on habitat selection, dispersal,

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

315

## 316 **Conclusion**

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

323

## 324 **4. METHODS**

### 325 **Bear sample collection**

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

328 Research Project; [www.bearproject.info](http://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<sub>2</sub> and CO<sub>2</sub> were separated chromatographically  
358 and introduced to an Elementar Isoprime isotope ratio mass spectrometer (Langensfeld,  
359 Germany). Two reference materials were used to normalize the results to VPDB and AIR:  
360 BWB III keratin ( $\delta^{13}\text{C} = -20.18\text{‰}$ ,  $\delta^{15}\text{N} = 14.31\text{‰}$ , respectively) and PRC gel ( $\delta^{13}\text{C} = -$   
361  $13.64\text{‰}$ ,  $\delta^{15}\text{N} = 5.07\text{‰}$ , respectively). Measurement precisions as determined from both  
362 reference and sample duplicate analyses were  $\pm 0.1\text{‰}$  for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

363

#### 364 **Bear trophic position**

365 We calculated the trophic position of each bear hair sample relative to the average  $\delta^{15}\text{N}$  value  
366 of moose (mean  $\pm$  sd =  $1.8 \pm 1.26\text{‰}$ , n = 21, **Fig S1**). Trophic position is calculated as the  
367 the discrepancy of  $\delta^{15}\text{N}$  in a secondary consumer and its food source divided by the  
368 enrichment of  $\delta^{15}\text{N}$  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.

$$372 \quad \text{Bear trophic position} = (\delta^{15}\text{N}_{\text{Ursus arctos}} - \text{average}(\delta^{15}\text{N}_{\text{Alces alces}})) / 3.4 + 2$$

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

### 378 **Genetic pedigree and parentage assignment**

379 A genetic pedigree based on 16 microsatellite loci was available for the population including  
380 1614 individual genotypes [61]. Genotyping followed the protocols of Waits, Taberlet [62],  
381 Taberlet, Camarra [63], and Andreassen, Schregel [64]. All female offspring in this study  
382 were genotyped and included in the population's genetic pedigree. All females included in  
383 this study had a known mother that was also captured and followed. We used Cervus 3.0 [65]  
384 for assignment of fathers and COLONY [66] for creating putative unknown mother or father  
385 genotypes and sibship reconstruction (see [61] for details).

386

### 387 **Maternal trophic position**

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

396

### 397 **Environmental similarity**

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

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

425

426 **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<sup>2</sup>-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 ( $\sigma^2_{\text{env}}$ ), additive genetic ( $\sigma^2_{\text{a}}$ ), permanent among-individual ( $\sigma^2_{\text{ind}}$ ),  
437 maternal ( $\sigma^2_{\text{mat}}$ ), and residual within-individual effects ( $\sigma^2_{\text{r}}$ ). 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]).

451 All models were fit using the R package “brms” [75] based on the Bayesian software  
452 Stan [76, 77]. We ran four chains to evaluate convergence which were run for 6,000  
453 iterations, with a warmup of 3,000 iterations and a thinning interval of 10. All estimated  
454 model coefficients and credible intervals were therefore based on 1200 posterior samples and  
455 had satisfactory convergence diagnostics with  $\hat{R} < 1.01$ , and effective sample sizes  $> 400$   
456 [78]. Posterior predictive checks recreated the underlying Gaussian distribution of trophic  
457 position well. For all parameters, we report the median and 89% credible intervals, calculated  
458 as equal tail intervals, as measure of centrality and uncertainty [79]. We deemed explained  
459 variance proportions as inconclusive when the lower credible interval limit was  $< 0.001$  (i.e.,  
460  $< 0.1\%$ ) [80]. All statistical analyses were performed in R 4.0.0 [81]. Primary data and code  
461 to reproduce all analyses are provided under (<https://doi.org/10.17605/OSF.IO/68B9U>, [74]).

462

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475

476 **AUTHOR'S CONTRIBUTIONS**

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

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