JOURNAL OF
AVIAN BIOLOGY

Research article

Did you learn what to eat from your parents? A test of the early learning of the foraging niche hypothesis in great tits *Parus major*

Marta Olivé-Muñiz[1,2], Emilio Pagani-Núñez[3,4,5], Maria Kretzmann[1,6] and Juan Carlos Senar[1]

[1]Museu de Ciències Naturals de Barcelona, Barcelona, Spain
[2]Departament de Genètica, Microbiologia i Estadística, Universitat de Barcelona, Barcelona, Spain
[3]Department of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University, Suzhou, China
[4]School of Applied Sciences, Edinburgh Napier University, Edinburgh, UK
[5]Centre for Conservation and Restoration Science, Edinburgh Napier University, Edinburgh, UK
[6]Biology Division, Glendale Community College, Glendale, CA, USA

Correspondence: Juan Carlos Senar (jcsenar@bcn.cat)

Journal of Avian Biology
2024: e03335
doi: 10.1111/jav.03335

Subject Editor: Judith Morales
Editor-in-Chief: Jan-Åke Nilsson
Accepted 20 May 2024

A growing number of studies suggest that individuals can develop long-term foraging specializations independently of phenotypic or environmental variation, yet little is known about how the foraging niche is acquired. The early learning of the foraging niche hypothesis suggests a key role of vertical cultural transmission in shaping the foraging niche of vertebrates. In birds, direct evidence from natural conditions is limited to a single study that cross-fostered two related species. To date, no study has tested whether the diet received as an offspring determines the diet delivered as a parent within a single species. We tested the early learning of the foraging niche hypothesis using a Mediterranean population of great tits *Parus major*, which show great diet variability and moderate consistency in the diet they provide to their offspring across years. To do this, we recorded prey delivered to 9–14 day-old chicks over twelve years. Then we assessed vertical transmission of dietary specialization using data (percentage of caterpillars, spiders, and other prey types, as well as mean prey size) from individuals recorded as a chick and as an adult. We standardised the data to control for environmental factors and ran a Linear Model for each prey type to measure individuals' consistency within the group (relative consistency), correlating the diet they received as a chick and the one they provided to their own chicks at the adult stage. The correlations between the diet received as a chick and the diet provided as a parent were either not significant or negative. Hence, although individuals showed relatively consistent foraging niches across years regarding their parental provisioning behaviour, these diet preferences were not correlated to the diet they received in the nest. Further research is needed to determine whether the foraging niche is acquired during the post-fledgling stage.

Keywords: diet, early learning, foraging niche, great tit, offspring, vertical transmission

NORDIC SOCIETY OIKOS

www.avianbiology.org

Introduction

Traditionally it is assumed that individuals select different food types in line with the optimal foraging theory, which states that decisions will be made depending on the energetic content of prey and the particular traits of each individual (such as sex, age, morphology, and/or experience) (Cowie 1977, Stephens and Krebs 1986, Hughes 1990). However, a number of studies regarding this matter suggest that other factors can affect this choice (Sih and Christensen 2001). In fact, we are now realising that in many species, a population regarded as generalist is in fact composed of individuals that consistently consume a subset of all food resources exploited by the whole population, which is usually called individual diet specialization (Bolnick et al. 2002, Bolnick et al. 2003, Zango et al. 2019). Habitat heterogeneity and competition are considered its main drivers (Tinker et al. 2008, Newsome et al. 2015, Cachera et al. 2017).

Nevertheless, data from different studies seem to suggest that individuals can specialise in spite of the phenotypic or environmental variation, therefore exhibiting long-term inter-individual differences in diet (Estes et al. 2003, Costantini et al. 2005, Woo et al. 2008, Vander Zanden et al. 2010, van den Bosch et al. 2019, Balme et al. 2020). Evidence of life-long inter-individual variation in diet was demonstrated in sea otters (Estes et al. 2003), which individuals may learn from their mothers during the period of mother–young association. Nonetheless, despite its importance in species' life-history, we still have an incomplete understanding of how the foraging niche is acquired. Furthermore, other factors such as individual experience (Votier et al. 2017) or cultural transmission (learning from other individuals, more specifically called 'vertical cultural transmission' if it is transmitted from previous generations) (Estes et al. 2003, Slagsvold and Wiebe 2007, 2011, Araújo et al. 2011, Aplin 2019) may be relevant in the development and maintenance of long-term foraging specializations. The foraging culture has importance for fitness and population dynamics (Whitehead 1998) and may drive speciation events (Riesch et al. 2012). Yet, how this culture is acquired and maintained across generations and its role in shaping foraging specializations is unclear (Davis and Stamps 2004, Tonnis et al. 2005).

Previous research has investigated the role of cultural transmission in shaping the foraging niche of vertebrates (Galef and Giraldeau 2001). In addition to primates (van Schaik et al. 2003, Jaeggi et al. 2010), a foraging culture as a driver of inter-individual and inter-population differences in the foraging niche seems important in a relatively large number of marine mammal species (Connor 2001). In particular, dolphins (Krützen et al. 2005, Bender et al. 2009, Sargeant and Mann 2009), killer whales (Baird et al. 1992, Rendell and Whitehead 2001), and sea otters (Estes et al. 2003, Tinker et al. 2012) are well-known examples. Additionally, this process has been suggested to be relevant in other mammals such as bears (Mazur and Seher 2008), rats (Zohar and Terkel 1996), and mongooses (Sheppard et al. 2018). However, evidence from birds is scarce. New Caledonian crows have been suggested to display foraging cultures (Holzhaider et al. 2010), and Aplin et al. (2015) showed that wild great tits can indeed use social learning to acquire novel foraging behaviours. However, literature supporting our hypothesis in birds is still very scarce compared to other groups such as mammals.

If the foraging niche is acquired via cultural transmission the most favourable period to develop it would be when the individual still depends on its parents and thus can learn from them (Immelmann 1975). This is known as the early learning of the foraging niche hypothesis (hereafter the 'early learning hypothesis'), and suggests a fundamental role of learning at early life-stages to acquire the foraging niche, which is vertically transmitted from parents (Slagsvold and Wiebe 2007). Some studies have found results supporting this hypothesis in different animals such as bears (Mazur and Seher 2008), dolphins (Mann and Sargeant 2009), and hamsters (Lupfer et al. 2003), whereas in bats no evidence supporting this idea has been found (Rose et al. 2019). In birds, most evidence of an early learning of the foraging niche comes from studies carried out in captive conditions (Partridge 1979, Marchetti and Drent 2000) and from a single study in wild conditions that consisted in an experiment cross-fostering two related species (*P. major* and *Cyanistes caeruleus*). Interestingly, this last study found that both species shifted their diet in the direction of the foster species and that this change lasted for life (Slagsvold and Wiebe 2007, 2011). Nonetheless, no study has investigated this question within a single bird species. Mediterranean populations of great tits *P. major* represent a highly suitable model to study long-term consistency of diet and to test the early learning hypothesis because they exploit a great variety of prey (Banbura et al. 1994, Pagani-Núñez et al. 2011, 2015), show dietary specialization (Pagani-Núñez et al. 2015), and have a moderately consistent foraging niche when provisioning their chicks in the short term (Pagani-Núñez and Senar 2013) and across years (Olivé-Muñiz et al. 2021). Moreover, the results of another study (Slagsvold and Wiebe 2018) have found that great tit immigrants provided different prey items to their offspring than local recruits, a difference most evident in first-time breeders. A possible explanation proposed in the study was that immigrants needed time to learn which prey were more suitable in the new habitat, suggesting that great tits are likely to learn their foraging niche in their natal habitat, maybe during their early development.

In this study, we used wild great tits in their natural habitat to test the early learning of the foraging niche hypothesis, focusing on parental foraging behaviour during nestling provisioning. To do this, we compared the diet that the individuals received as a chick with the one they delivered to their offspring as breeding adults. The analyses were done from a relative point of view, wherein the consistency of individuals' positions within a group relative to others is assessed (Vaz et al. 2013). Following this reasoning, our study aims to determine whether individuals fed by parents specializing in specific prey types (e.g. caterpillars) will, as adults, rank among the primary providers of these prey types within the population when feeding their offspring. This relative approach avoids the confounding effect of uncontrolled variations in diet between years (Vaz et al. 2013). This rationale has been employed in previous studies (Senar and Quesada 2006, Pérez-Rodríguez 2008, Olivé-Muñiz et al. 2021). According to the early learning hypothesis, we predicted that the diet received in the nest as an offspring would be correlated to the diet delivered to offspring as a parent, in the first successfully recorded breeding season.

Material and methods

Species and study area

We collected information on foraging preferences of breeding great tits during twelve years (2011–2022) in the field station of Can Catà, within Collserola Natural Park (Cerdanyola, Barcelona, NE Iberian Peninsula, 45°27′N, 2°8′E). This area is characterized as a Mediterranean sclerophyllous mixed forest mainly composed of oaks *Quercus ilex* and *Q. cerrioides*, at the valley bottom, while the proportion of Aleppo pines *Pinus halepensis* increases with elevation, becoming progressively dominant (Pagani-Núñez et al. 2014). Our study site had 184 nest boxes evenly distributed throughout the area (80 ha). These nest boxes were located on the trunks of the trees at an approximate height of 1.30 m. Birds entered the nest boxes through a cylindrical tube of 10 cm length and 5 cm diameter designed to protect the nest from mammalian predators. The diameter of the hole was designed for titmice (30 mm); see Olivé-Muñiz et al. (2021) for more details.

Field procedures and diet recording

Each breeding season, we checked all nest boxes twice a week to determine nest building state, laying date, hatching date, and brood size. Each individual was marked with a numbered aluminium ring and a numbered PVC ring that could easily be read from a distance, or in video recordings without having to capture the individual. Additionally, all chicks were ringed at around 15 days of life. Thus, all individuals used in this study had known origins and were born in our nest boxes. Individuals were classified as yearlings (first year of life) or adults (second year or more) based on recording dates, and sexed according to their plumage characteristics (males have a large ventral black stripe, which is considerably smaller in females).

To obtain data about nestlings' diet, we attached infrared Micro-D cameras to the nest top inside the nest box and focused on the entrance, thus allowing us to identify delivered prey. Cameras were installed when chicks were around 9–14 days old, when provisioning rate is the highest (Pagani-Núñez and Senar 2013). To minimize the possible effects on parents' behaviour caused by the presence of the camera, the device was installed the afternoon before the day of the analysed recording. In the final analysis, we used data obtained during five full clock hours from 07:00 to 12:00, which is a reliable representation of the diet (Pagani-Núñez and Senar 2013).

Although previous research focused on the time period just after fledging or on the post-fledgling stage, we focused on the late nestling period to characterize parental niches. At this stage, nestlings are old enough to differentiate alarm calls (Toshitaka 2011). Consequently, they are probably aware of their environment and have adequately developed their cognitive capacities to be able to distinguish food type and size. Moreover, great tits show highly consistent feeding behaviour in the short term (Pagani-Núñez and Senar 2013), which suggests that this is an optimal period to characterize parental feeding preferences.

For each feeding event, prey type, prey size, and the exact time of delivery were determined using Micro D Player software. Prey were classified into three categories – caterpillars, spiders, and others – because caterpillars and spiders are the most important prey types for Mediterranean populations of great tits (Pagani-Núñez et al. 2011). The latter category consisted of Coleoptera, Orthoptera, Phasmidae, Diptera, unidentified prey, and fruits. The size of each prey item was determined according to a semi-quantitative scale in relation to beak size of the great tit, which has an average size of 9 mm. Size categories were: 1 = small (smaller than beak size), 2 = medium (similar to beak size), and 3 = large (larger than beak size) (Barba et al. 1996, García-Navas and Sanz 2010, Pagani-Núñez et al. 2015). As it was impossible to determine the assignment of each prey item to each nestling, all the information from each nest was pooled. Although some individuals were recorded breeding more than once, we decided to include two observations per individual (one as a nestling and one as an adult) to have the same quantity of data for all the individuals. There is more detailed information about the individuals' characteristics and prey data used in the Supporting information.

Statistical analyses

Vertical transmission of great tit foraging niches was analysed using data from individuals that had been recorded as a chick and as an adult feeding its offspring ($n = 47$ individuals). Initially, we attempted to analyse the data through a repeatability analysis (Stoffel et al. 2017), but unfortunately, the models failed to converge, in good part because we had too few individuals within a single year for the model to standardize for year effects and other collateral variables. Consequently, we opted to analyse the data from a relative point of view using linear models.

The diet of individuals may vary across years due to changing weather conditions and environmental factors affecting prey availability. Therefore, before comparing an individual's diet across different years, the data must be standardised for different variables. To do this, we ran a generalised linear mixed-effects model fitted by restricted maximum likelihood controlling for said environmental factors and extracted its residuals for further analysis (Supporting information). We characterised great tits' foraging niches studying relative prey frequency and size. We followed the procedure explained below for each dependent variable, selected based on previous results obtained studying the same population during some of the same years (2011–2016) (Olivé-Muñiz et al. 2021):

percentage of caterpillars, percentage of spiders, percentage of 'other prey', and mean prey size (of all prey categories). To perform the analyses the percentage of each type of prey (caterpillars, spiders, and 'other prey') were square-root transformed to approximate normality. We included the following variables as fixed factors: 'year', 'sex', 'age' (to distinguish if the breeding individual was yearling or adult), 'brood size', 'brood age', and 'date of recording' (taken as the number of days from 1 April to control for phenology (Pagani-Núñez and Senar 2014). To control for habitat variability we also included as fixed factor the proportion of oak trees in relation to Aleppo pines within 25 m of the nest box (Pagani-Núñez and Senar 2014). This procedure allowed us to obtain standardised residuals of the variables characterising the foraging niches of individual great tits and standardising for habitat and phenology effects, which could affect prey availability and, consequently, individuals' prey choices. Standardisation was carried out using all available data encompassing individuals from the entire population across all the years of monitoring (n = 718), which allowed for a better standardisation of collateral variables. This approach cannot be used when conducting a repeatability analyses, and it additionally reinforces our relative approach.

Using the previously obtained standardised residuals we performed multiple linear regression models using the *lm* function of the R software ver. 3.4 (www.r-project.org). For each model we used the prey data corresponding to the chick stage as dependent variable and the data from the adult stage as independent variable. As it is unknown if each parent influences chicks equally when it comes to vertical transmission of diet preferences, we performed the regression analysis using four different approaches. We used different variants of the diet data that individuals received as a chick: 1) using exclusively the father's data (referred to as Father Data), 2) using only the mother's data (referred to as Mother Data), 3) using the mean of both parents' prey data (referred to as Mean Data), and 4) using weighted parents' data depending on the number of provisioning trips (giving more importance to the prey delivered by the most actively feeding parent, referred to as Weighted Data). We considered all of these metrics for each of the standardised dependent variables (percentage of caterpillars, percentage of spiders, percentage of 'other prey', and mean prey size), thus performing 16 different analyses.

Results

For all dependent variables studied (percentage of caterpillars, percentage of spiders, percentage of 'other prey', and mean prey size), we found no significantly positive correlation

Table 1. Test of the individual relative foraging niche consistency between chick and adult stage.

Diet data used	β	−95% CI	+95% CI	pMCMC	β	−95% CI	+95% CI	pMCMC
	Caterpillars				**Other prey**			
Father data								
Intercept	0.90	0.64	1.14	< 0.01	0.62	0.44	0.80	< 0.01
Chick data	−0.05	−0.33	0.24	0.74	−0.13	−0.44	0.19	0.43
Mother data								
Intercept	1.17	0.90	1.45	< 0.01	0.77	0.61	0.93	< 0.01
Chick data	−0.37	−0.68	−0.06	**0.02**	−0.39	−0.66	−0.12	**< 0.01**
Mean data								
Intercept	1.03	0.78	1.28	< 0.01	0.75	0.55	0.95	< 0.01
Chick data	−0.36	−0.86	0.14	0.16	−0.62	−1.23	0.01	**0.048**
Weighted data								
Intercept	1.02	0.73	1.30	< 0.01	0.73	0.53	0.91	< 0.01
Chick data	−0.20	−0.53	0.13	0.23	−0.31	−0.63	0.03	0.07
	Spiders				**Mean prey size**			
Father data								
Intercept	0.32	0.18	0.47	< 0.01	3.08	2.44	3.74	< 0.01
Chick data	0.07	−0.31	0.43	0.72	−0.36	0.64	−0.08	**0.01**
Mother data								
Intercept	0.37	0.24	0.50	< 0.01	2.38	1.81	2.97	< 0.01
Chick data	−0.08	−0.44	0.26	0.66	−0.06	−0.31	0.20	0.65
Mean data								
Intercept	0.35	0.19	0.52	< 0.01	2.80	2.09	3.52	< 0.01
Chick data	−0.03	−0.84	0.73	0.93	−0.24	−0.56	0.06	0.12
Weighted data								
Intercept	0.35	0.20	0.50	<0.01	2.91	2.20	3.62	< 0.01
Chick data	−0.003	−0.42	0.39	0.99	−0.29	−0.59	0.03	0.07

Note: a MCMCglmm approach on the standardised values of each prey type (caterpillars, spiders, and 'other prey') and mean prey size was used. As dependent variable we used the values of the prey that the individuals delivered as adult. The data corresponding to the diet that the individual received as a chick were used as independent variable. The chick data were analysed using different approaches (Mother data: using only data delivered by the mother, Father data: using only data delivered by the father, Mean data: using the mean of the prey delivered both parents, Weighted data: using the weighted data of both parents depending on the number of delivering trips). Statistically significant models are marked in bold.

between the prey received by chicks and delivered to chicks by the same individuals once they were breeding. We found similar results when analysing consistency of all dependent variables in all variants (Father Data, Mother Data, Mean Data, and Weighted Data) (Table 1). Unexpectedly, we found a significantly negative correlation in four of the models ('Other prey' using the Mean Data, 'Caterpillars' and 'Other prey' using the Mother Data, and 'Mean prey size' using the Father Data) (Fig. 1).

Discussion

The early learning hypothesis suggests that individuals acquire their foraging niche from their parents during early life (Slagsvold and Wiebe 2007, 2011). The main advantage that cultural transmission offers (as opposed to genetic inheritance) is its high plasticity and adaptability (Immelmann 1975, Laland et al. 2000). Furthermore, learning through copying protects individuals from trial-and-error learning, which is more costly in terms of time and energy, and undoubtedly more risky than learning from parents (Boyd and Richerson 1988, Marchetti and Price 1989, Laland et al. 1993). Moreover, this process is likely related to the time-consistency of the foraging niche. If niches are consistent across time, the optimal strategy is, therefore, to acquire the niche through learning from experienced individuals (Laland et al. 1993, Galef and Laland 2005). However, despite the fact that in our population great tit individuals have moderately consistent foraging niches across years regarding parental provisioning behaviour (Olivé-Muñiz et al. 2021), we found that the diet that breeding great tits delivered to their offspring was distinct from the diet that they received from their parents. In some cases (Fig. 1), the relationship between the dietary preferences of individuals during their chick and adult stages was even negative, suggesting a rebellious response, where adult individuals selected their diet in direct contrast to what they received as chicks. However, we do not know the reason for this opposite change in diet selection.

Though our sample size could be larger and therefore our conclusions should be interpreted cautiously, we believe that our data is valuable as it is difficult to obtain in a wild population. Several factors may explain our general lack of correlation. First, we cannot eliminate the possibility that the foraging niche is acquired after the nesting stage by vertical transmission. This is because great tit families stay together for a relatively long time period (three weeks) after the breeding period (Matthysen et al. 2010, van Overveld et al. 2011, Slagsvold et al. 2014). Thus, vertical transmission of the foraging niche could still occur in a stage in which fledglings start to search for their own food and become progressively more independent (Matthysen et al. 2010, van Overveld et al. 2011). Another plausible scenario would be that post-fledgling individuals learn their foraging preferences from other

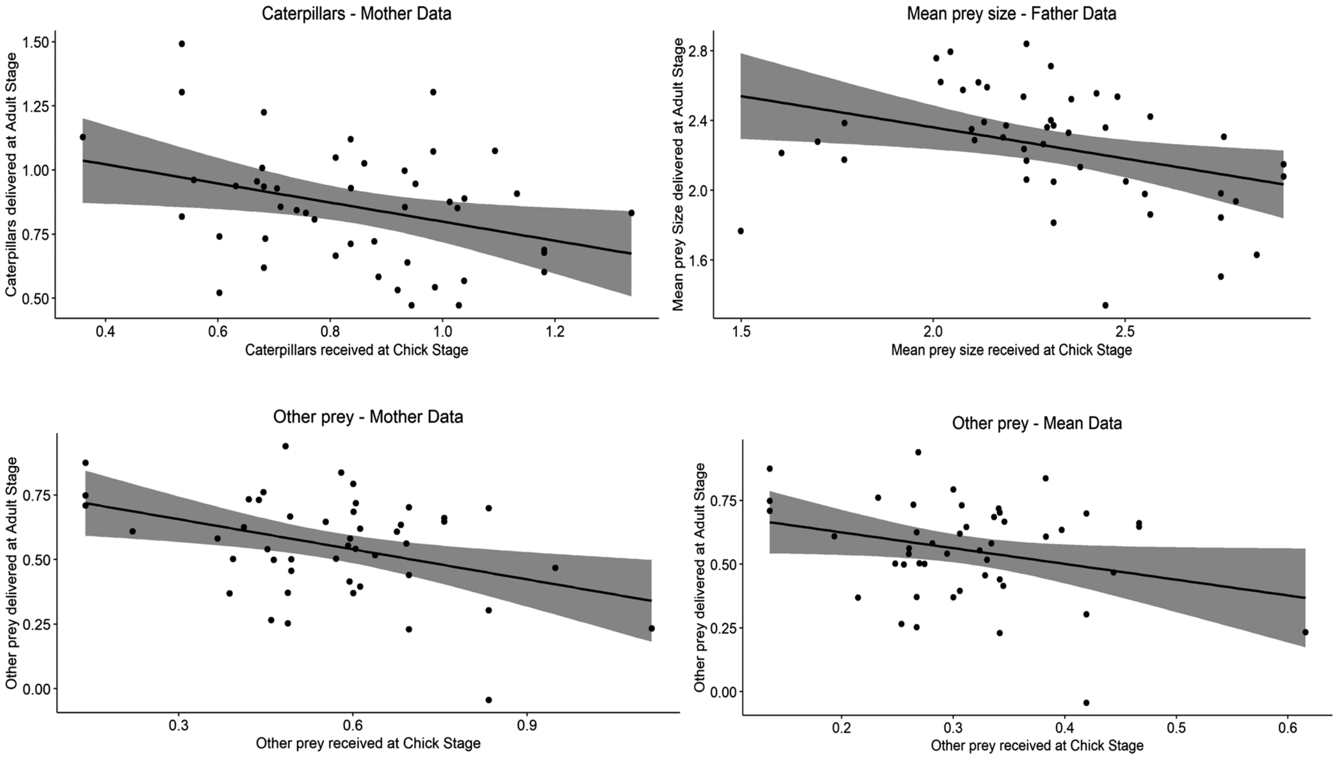

Figure 1. Regression models comparing the standardised percentage of prey type (caterpillars, or 'other prey') or mean prey size of the items received as a chick and the ones delivered as an adult (n = 47). Only the statistically significant models are shown, in which all of them a negative correlation is found. Regression lines and 95% confidence intervals are shown.

individuals in the population. This scenario would imply the use of cultural transmission instead of vertical transmission. Actually, evidence that new foraging behaviours can spread and be established via cultural transmission in a population of wild great tits (Wild et al. 2022) support this hypothesis.

Second, the foraging niche could be acquired by trial-and-error learning during the post-fledgling stage (Riotte-Lambert and Weimerskirch 2013), which is a learning strategy that might play a bigger role than vertical transmission in variable environments (Boyd and Richerson 1988). In relatively stable habitats, where diet shows little or no variability, cultural transmission would be less treacherous than trial-and-error learning and, therefore, favourable. Conversely, in highly variable habitats, where diet preferences vary among individuals and prey availability is highly variable across years, cultural transmission could be mal-adaptive as foraging strategies could easily become outdated. Although no study has compared foraging niches of passerine populations across large geographical gradients to date (Rytkönen and Krams 2003, van der Post and Hogeweg 2009), this disparity between previous research and our results could be explained by differences in habitat of studies conducted in a relatively stable mixed-forest in Norway (northern Europe) and a highly variable Mediterranean mixed-forest in Spain (southern Europe). Yet, the fact that foraging niches are relatively constant across years in our population (Olivé-Muñiz et al. 2021) contradicts this rationale.

It could also be argued that our sampled five hours of foraging is just a small snapshot of the foraging niche, but here we would like to stress that field experiments in which we manipulated parental effort by increasing or reducing the number of chicks, resulted in changes in the number of parental foraging trips, but not in diet composition (Pagani-Núñez et al. 2015). This stresses that birds are consistent in food selection within a breeding season. Our previous comparison of the diet of the same population in consecutive years (Olivé-Muñiz et al. 2021) also showed moderate but significant repeatability ($R = 0.24$) in the foraging preferences of birds, which again stresses that our sampling procedure was sufficient to describe the foraging niche of the birds.

Foraging behaviour is known to strongly vary at multiple time and spatial scales (Pettex et al. 2012). It is possible that environmental conditions were more variable when comparing long time spans, such as for an individual offspring until it becomes a parent itself, compared to assessing individual consistency in two consecutive years as we did in our previous study (Olivé-Muñiz et al. 2021). Regardless, we controlled for all relevant environmental factors in an attempt to reduce the noise introduced by them. Hence, our results also suggest that other aspects of learning such as individual experience or non-vertical cultural transmission may have shaped our results. Further research focusing on the post-fledgling stage and directly assessing adult diet rather than just parental foraging, which could be achieved using stable isotope analysis (Pagani-Núñez et al. 2017), is needed to provide convincing evidence of vertical transmission of the foraging niche.

Acknowledgements – We are most grateful to Ll. Arroyo, M. Valls, E. Plana, H. Navalpotro, S. Hernández, A. Garcia-Rico, José G. Carrillo-Ortiz and Daniele Mazzoni for their help in the field and in the lab. We also thank V. Morera-Pujol for the insights into the statistical analyses. We extend our thanks to the Gil family, owners of Can Catà, for allowing us to work on their property. The Catalan Institute of Ornithology (ICO) provided the rings.

Funding – This work was supported by funds from the Ministerio de Ciencia e Innovación, Spanish Research Council to JCS (CGL-2020 PID2020-114907GB-C21).

Permits – Birds were handled with the permission of the Departament de Medi Ambient, Generalitat de Catalunya (SF/542). Since the data are mostly observational, no ethics concerns are involved.

Author contributions

Marta Olivé-Muñiz: Data curation (equal); Formal analysis (equal); Investigation (equal); Writing – original draft (equal). **Emilio Pagani-Núñez**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Validation (equal); Writing – review and editing (equal). **Maria Kretzmann**: Data curation (equal); Writing – review and editing (equal). **Juan Carlos Senar**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/jav.03335.

Data availability statement

Data are available from the Zenodo Digital Repository: https://zenodo.org/records/12516536 (Olivé-Muñiz et al. 2024).

Supporting information

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

References

Aplin, L. M. 2019. Culture and cultural evolution in birds: a review of the evidence. – Anim. Behav. 147: 179–187.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A. and Sheldon, B. C. 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. – Nature 518: 538–541.

Araújo, M. S., Bolnick, D. I. and Layman, C. A. 2011. The ecological causes of individual specialisation. – Ecol. Lett. 14: 948–958.

Baird, R. W., Abrams, P. A. and Dill, L. M. 1992. Possible indirect interactions between transient and resident killer whales: implications for the evolution of foraging specializations in the genus *Orcinus*. – Oecologia 89: 125–132.

Balme, G. A., Le Roex, N., Rogan, M. S. and Hunter, L. T. B. 2020. Ecological opportunity drives individual dietary specialization in leopards. – J. Anim. Ecol. 89: 589–600.

Banbura, J., Blondel, J., de Wilde-Lambrechts, H., Galan, M. J. and Maistre, M. 1994. Nestling diet variation in an insular Mediterranean population of blue tits *Parus caeruleus*: effects of years, territories and individuals. – Oecologia 100: 413–420.

Barba, E., López, J. A. and Gil-Delgado, J. A. 1996. Prey preparation by adult great tits *Parus major* feeding nestlings. – Ibis 138: 532–538.

Bender, C. E., Herzing, D. L. and Bjorklund, D. F. 2009. Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. – Anim. Cogn. 12: 43–53.

Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M. and Svanbäck, R. 2002. Measuring individual-level resource specialization. – Ecology 83: 2936–2941.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. and Forister, M. L. 2003. The ecology of individuals: incidence and implications of individual specialization. – Am. Nat. 161: 1–28.

Boyd, R. and Richerson, P. J. 1988. An evolutionary model of social learning: the effects of spatial and temporal variation. – In: Zentall, T. R. and Galef Jr, B. G. (eds), Social learning: psychological and biological perspectives. Lawrence Erlbaum Associates, Inc., pp. 29–48.

Cachera, M., Ernande, B., Villanueva, M. C. and Lefebvre, S. 2017. Individual diet variation in a marine fish assemblage. Optimal foraging theory, niche variation hypothesis and functional identity. – J. Sea Res. 120: 60–71.

Connor, R. C. 2001. Individual foraging specializations in marine mammals. Culture and ecology. – Behav. Brain Sci. 24: 329–330.

Costantini, D., Casagrande, S., Di Lieto, G., Fanfani, A. and Dell'Omo, G. 2005. Consistent differences in feeding habits between neighbouring breeding kestrels. – Behaviour 142: 1403–1415.

Cowie, R. J. 1977. Optimal foraging in great tits (*Parus major*). – Nature 268: 137–139.

Davis, J. M. and Stamps, J. A. 2004. The effect of natal experience on habitat preferences. – Trends Ecol. Evol. 19: 411–416.

Dell'Omo, G., Costantini, D., Casagrande, S., Di Lieto, G. and Fanfani, A. 2005. Consistent differences in feeding habits between neighbouring breeding kestrels. – Behaviour 142: 1403–1415.

Estes, J. A., Riedman, M. L., Staedler, M. M., Tinker, M. T. and Lyon, B. E. 2003. Individual variation in prey selection by sea otters. Patterns, causes and implications. – J. Anim. Ecol. 72: 144–155.

Galef, B. G. and Giraldeau, L. A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. – Anim. Behav. 61: 3–15.

Galef, B. G. and Laland, K. N. 2005. Social learning in animals: empirical studies and theoretical models. – AIBS Bulletin 55: 489–499.

García-Navas, V. and Sanz, J. J. 2010. Flexibility in the foraging behavior of blue tits in response to short-term manipulations of brood size. – Ethology 274: 744–754.

Holzhaider, J. C., Hunt, G. R. and Gray, R. D. 2010. Social learning in New Caledonian crows. – Learn. Behav. 38: 206–219.

Hughes, R. N. (ed.) 1990. Behavioural mechanisms of food selection, Vol. 20. – Springer-Verlag (NATO ASI series. Series G, Ecological sciences).

Immelmann, K. 1975. Ecological significance of imprinting and early learning. – Annu. Rev. Ecol. Syst. 6: 15–37.

Jaeggi, A. V., Dunkel, L. P., van Noordwijk, M. A., Wich, S. A., Sura, A. A. L. and van Schaik, C. P. 2010. Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. – Am. J. Primatol. 72: 62–71.

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. and Sherwin, W. B. 2005. Cultural transmission of tool use in bottlenose dolphins. – Proc. Natl Acad. Sci. USA 102: 8939–8943.

Laland, K. N., Richerson, P. J. and Boyd, R. 1993. Animal social learning: toward a new theoretical approach. – In: Bateson, P. P. G., Klopfer, P. H. and Thompson, N. S. (eds), Perspectives in ethology, Vol. 10. Plenum Press, pp. 249–277.

Laland, K. N., Odling-Smee, J. and Feldman, M. W. 2000. Niche construction, biological evolution, and cultural change. – Behav. Brain Sci. 23: 131–146.

Lupfer, G., Frieman, J. and Coonfield, D. 2003. Social transmission of flavor preferences in two species of hamsters (*Mesocricetus auratus* and *Phodopus campbelli*). – J. Comp. Psychol. 117: 449–455.

Mann, J. and Sargeant, B. L. 2009. Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). – In: Fragaszy, D. M. and Perry, S. (eds), The biology of traditions, Vol. 13. Cambridge Univ. Press, pp. 236–266.

Marchetti, C. and Drent, P. J. 2000. Individual differences in the use of social information in foraging by captive great tits. – Anim. Behav. 60: 131–140.

Marchetti, K. and Price, T. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. – Biol. Rev. 64: 51–70.

Matthysen, E., van Overveld, T., van de Casteele, T. and Adriaensen, F. 2010. Family movements before independence influence natal dispersal in a territorial songbird. – Oecologia 162: 591–597.

Mazur, R. and Seher, V. 2008. Socially learned foraging behaviour in wild black bears, *Ursus americanus*. – Anim. Behav. 75: 1503–1508.

Newsome, S. D., Tinker, M. T., Gill, V. A., Hoyt, Z. N., Doroff, A., Nichol, L. and Bodkin, J. L. 2015. The interaction of intraspecific competition and habitat on individual diet specialization. A near range-wide examination of sea otters. – Oecologia 178: 45–59.

Olivé-Muñiz, M., Pagani-Núñez, E. and Senar, J. C. 2021. Breeding great tit *Parus major* individuals have moderately consistent foraging niches across years. – Ardeola 68: 409–422.

Olivé-Muñiz, M., Emilio Pagani-Núñez, E., Kretzmann, M. and Carlos Senar, J. 2024. Data from: Did you learn what to eat from your parents? A test of the early learning of the foraging niche hypothesis in great tits *Parus major*. – Zenodo Digital Repository, https://zenodo.org/records/12516536.

Pagani-Núñez, E. and Senar, J. C. 2013. One hour of sampling is enough. Great tit *Parus major* parents feed their nestlings consistently across time. – Acta Ornithol. 48: 194–200.

Pagani-Núñez, E. and Senar, J. C. 2014. Are colorful males of great tits *Parus major* better parents? Parental investment is a matter of quality. – Acta Oecol. 55: 23–28.

Pagani-Núñez, E., Ruiz, Í., Quesada, J., Negro, J. J. and Senar, J. C. 2011. The diet of great tit *Parus major* nestlings in a Mediterranean Iberian forest: the important role of spiders. – Anim. Biodivers. Conserv. 34: 355–361.

Pagani-Núñez, E., Uribe, F., Hernández-Gómez, S., Muñoz, G. and Senar, J. C. 2014. Habitat structure and prey composition generate contrasting effects on carotenoid-based coloration of great tit *Parus major* nestlings. – Biol. J. Linn. Soc. 113: 547–555.

Pagani-Núñez, E., Valls, M. and Senar, J. C. 2015. Diet specialization in a generalist population: the case of breeding great tits *Parus major* in the Mediterranean area. – Oecologia 179: 629–640.

Pagani-Núñez, E., Renom, M., Mateos-Gonzalez, F., Cotín, J. and Senar, J. C. 2017. The diet of great tit nestlings. Comparing observation records and stable isotope analyses. – Basic Appl. Ecol. 18: 57–66.

Partridge, L. 1979. Differences in behaviour between blue and coal tits reared under identical conditions. – Anim. Behav. 27: 120–125.

Pérez-Rodríguez, L. 2008. Carotenoid-based ornamentation as a dynamic but consistent individual trait. – Behav. Ecol. Sociobiol. 62: 995–1005.

Pettex, E., Lorentsen, S.-H., Grémillet, D., Gimenez, O., Barrett, R. T., Pons, J.-B., Bohec, C. and Bonadonna, F. 2012. Multiscale foraging variability in northern gannet (*Morus bassanus*) fuels potential foraging plasticity. – Mar. Biol. 159: 2743–2756.

Rendell, L. and Whitehead, H. 2001. Culture in whales and dolphins. – Behav. Brain Sci. 24: 309–324.

Riesch, R., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K. B. and Deecke, V. B. 2012. Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? – Biol. J. Linn. Soc. 106: 1–17.

Riotte-Lambert, L. and Weimerskirch, H. 2013. Do naive juvenile seabirds forage differently from adults? – Proc. R. Soc. B 280: 20131434.

Rose, A., Wöhl, S., Bechler, J., Tschapka, M. and Knörnschild, M. 2019. Maternal mouth-to-mouth feeding behaviour in flower-visiting bats, but no experimental evidence for transmitted dietary preferences. – Behav. Processes 165: 29–35.

Rytkönen, S. and Krams, I. 2003. Does foraging behaviour explain the poor breeding success of great tits Parus major in northern Europe? – J. Avian Biol. 34: 288–297.

Sargeant, B. L. and Mann, J. 2009. Developmental evidence for foraging traditions in wild bottlenose dolphins. – Anim. Behav. 78: 715–721.

Senar, J. C. and Quesada, J. 2006. Absolute and relative signals. A comparison between melanin- and carotenoid-based patches. – Behaviour 143: 589–595.

Sheppard, C. E., Marshall, H. H., Inger, R., Thompson, F. J., Vitikainen, E. I. K., Barker, S. Nichols, H. J., Wells, D. A., McDonald, R. A., and Cant, M. A. 2018. Decoupling of genetic and cultural inheritance in a wild mammal. – Curr. Biol. 28: 1846–1850.e2.

Sih, A. and Christensen, B. 2001. Optimal diet theory: when does it work, and when and why does it fail? – Anim. Behav. 61: 379–390.

Slagsvold, T. and Wiebe, K. L. 2007. Learning the ecological niche. – Proc. R. Soc. B. 274: 19–23.

Slagsvold, T. and Wiebe, K. L. 2011. Social learning in birds and its role in shaping a foraging niche. – Phil. Trans. R. Soc. B 366: 969–977.

Slagsvold, T. and Wiebe, K. L. 2018. Immigrants and locally recruited birds differ in prey delivered to their offspring in blue tits and great tits. – Anim. Behav. 139: 127–135.

Slagsvold, T., Hušek, J., Whittington, J. D. and Wiebe, K. L. 2014. Antipredator behavior: escape flights on a landscape slope. – Behav. Ecol. 25: 378–385.

Stephens, D. W. and Krebs, J. R. 1986. Foraging theory. Princeton Univ. Press (Monographs in behavior and ecology), http://press.princeton.edu/titles/2453.html.

Stoffel, M. A., Nakagawa, S. and Schielzeth, H. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. – Methods Ecol. Evol. 8: 1639–1644.

Tinker, M. T., Bentall, G. and Estes, J. A. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. – Proc. Natl Acad. Sci. USA 105: 560–565.

Tinker, M. T., Guimarães, P. R., Novak, M., Marquitti, F. M., Bodkin, J. L., Staedler, M., Bentall, G. and Estes, J. A. 2012. Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. – Ecol. Lett. 15 475–483.

Tonnis, B., Grant, P. R., Grant, B. R. and Petren, K. 2005. Habitat selection and ecological speciation in Galápagos warbler finches (*Certhidea olivacea* and *Certhidea fusca*). – Proc. R. Soc. B 272: 819–826.

Toshitaka, N. 2011. Parental alarm calls warn nestlings about different predatory threats. – Curr. Biol. 21: R15–R16.

van den Bosch, M., Baert, J. M., Müller, W., Lens, L. and Stienen, E. W. M. 2019. Specialization reduces foraging effort and improves breeding performance in a generalist bird. – Behav. Ecol. 30: 792–800.

van der Post, D. J. and Hogeweg, P. 2009. Cultural inheritance and diversification of diet in variable environments. – Anim. Behav. 78: 155–166.

van Overveld, T., Adriaensen, F. and Matthysen, E. 2011. Postfledging family space use in great tits in relation to environmental and parental characteristics. – Behav. Ecol. 22: 899–907.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. and Merrill, M. 2003. Orangutan cultures and the evolution of material culture. – Science 299: 102–105.

Vander Zanden, H. B., Bjorndal, K. A., Reich, K. J. and Bolten, A. B. 2010. Individual specialists in a generalist population: results from a long-term stable isotope series. – Biol. Lett. 6: 711–714.

Vaz, S., Falkmer, T., Passmore, A. E., Parsons, R. and Andreou, P. 2013. The case for using the repeatability coefficient when calculating test-retest reliability. – PLoS One. 8: e73990.

Votier, S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, J., Guilford, T., Hamer, K. C., Jeglinski, J. W. E., Morgan, G., Wakefield, E. and Patrick, S. C. 2017 (1859). Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. – Proc. R. Soc. B 284: 20171068.

Whitehead, H. 1998. Cultural selection and genetic diversity in matrilineal whales. – Science 282: 1708–1711.

Wild, S., Chimento, M., McMahon, K., Farine, D. R., Sheldon, B. C. and Aplin, L. M. 2022 (1843). Complex foraging behaviours in wild birds emerge from social learning and recombination of components. – Phil. Trans. R. Soc. B 377: 20200307.

Woo, K. J., Elliott, K. H., Davidson, M., Gaston, A. J. and Davoren, G. K. 2008. Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. – J. Anim. Ecol. 77: 1082–1091.

Zango, L., Reyes-González, J. M., Militão, T., Zajková, Z., Álvarez-Alonso, E., Ramos, R. and González-Solís, J. 2019. Year-round individual specialization in the feeding ecology of a long-lived seabird. – Sci. Rep. 9: 11812.

Zohar, O. and Terkel, J. 1996. Social and environmental factors modulate the learning of pine-cone stripping techniques by black rats, *Rattus rattus*. – Anim. Behav. 51: 611–618.