Research article

Long-lasting negative effects of poor early life conditions on cognitive performance in adulthood in a wild bird

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Abstract

Adverse conditions encountered during growth, such as stress or malnutrition, are known to affect cognitive development and functions in adulthood in humans and laboratory animals. However, how early life conditions can influence adult cognition in wild animals remains unclear. Yet cognitive abilities such as innovation can be crucial for animals to cope with rapidly changing environments. We examined whether growing conditions (measured by hatching date, brood size, fledging body condition, parents' age and condition) predict problem-solving, neophobia, accuracy, activity and exploration in adulthood in a natural population of great tits (*Parus major*). Over 10 years, 348 nestlings recruited locally were tested as adults on a problem-solving task. The results show that nestlings in poorer condition were less likely to become solvers and more prone to making errors when solving problems. Our results provide rare evidence from a natural population that adverse conditions experienced during development can have negative, long-lasting effects on cognitive traits in adulthood, particularly the ability to solve problem, which has previously been shown to rely on associative learning and affect breeding performance in this population.

Keywords: associative learning, body condition, cognition, developmental stress, great tit, innovation, parental care, *Parus major*, personality, string-pulling task

Introduction

Environmental conditions experienced early in life are increasingly recognised as key drivers of adult phenotypic variation in animals. While research on this theme has mostly focused on morphological and physiological traits so far (Lindström, 1999; Metcalfe et Monaghan, 2001; Lemaître *et al.*, 2015), there is growing interest in how early-life environments can shape behavioural phenotypes. Several studies have shown that the conditions experienced by juveniles can modulate adult personality traits such as boldness, exploration, aggressivity, and sociability in various animal taxa (Braithwaite & Salvanes, 2005; Haller et al., 2014; Le Galliard et al., 2015; Stamps & Groothuis, 2010). For example, in laboratory rats (*Rattus norvegicus*), exploration propensity at adulthood increased with pup body mass (Rödel & Meyer, 2011). In laying hens, increasing group size during growth lead to high propension of adult anxiety and aggressive behaviour such as feather pecking or cannibalism (Rodenburg et al., 2008). These links between conditions during development and variations in adult behavioural traits may arise through changes in neuronal development and neuroendocrine systems, or genetic and epigenetic modifications (Veenema, 2009).

Given that cognition often shapes behavioural responses, early-life conditions may also affect adult behaviour through changes in cognitive functions, such as attention, learning or memory (e.g., Kotrschal and Taborsky, 2010; Foraita, Howell and Bennett, 2021). Interestingly, studies to date have proposed two opposite ways by which early-life conditions could affect cognitive functions. First, early-life conditions could negatively affect future cognitive performance if the resources needed for cognitive development are limited (i.e., constrained or non-adaptive hypothesis). For example, poor early nutritional conditions have clearly been shown to negatively affect cognitive performance. In humans, people who suffered from childhood malnutrition have lower IQ scores, poorer cognitive function and lower academic achievement (Johnson et al., 2021; Kirolos et al., 2022; Prado & Dewey, 2014). In rats, food deprivation during neonatal period can impair visuo-spatial memory and decrease neurogenesis (Akman et al., 2004). In singing birds, song complexity, controlled by the song control nucleus High Vocal Centre (HVC), is negatively affected by stress level during early life (Buchanan et al., 2004). These results from human and laboratory animals suggest that constraints in the early life nutritional conditions prevent the full development of cognitive functions with lifelong consequences on cognitive performance. Second, perturbations of environmental quality early in life could on the contrary signal to the developing individual the future conditions that it can expect to be exposed to as an adult and therefore stimulate cognitive development (i.e., informed or adaptive hypothesis). For example, food resource unpredictability during rearing may require increased learning abilities to optimally adjust behavioural responses (Braithwaite & Salvanes, 2005). In a cichlid fish (*Simochromis pleurospilus*), early environmental stress experienced as unpredictability in food availability increased learning ability (Kotrschal & Taborsky, 2010). Thus, early-life conditions could be used as a source of information during the developmental period in order to plastically adjust cognitive functions and consequently adult behaviour.

Despite increasing evidence showing effects of early life conditions on cognitive performance in adulthood from laboratory and semi-natural studies (Hedges & Woon, 2011; Holubová et al., 2018; Menezes et al., 2020; Pravosudov et al., 2005), the ecological relevance and long-term consequences of such effects remain little investigated in wild populations. Because individuals in the wild are exposed to multiple sources of stress, the resulting effect of early growing conditions on adult cognition depending on these many factors may be difficult to predict. In food caching chickadees (*Poecile gambeli*), early developmental stress, measured using corticosterone in feathers, was negatively related to young adult memory performance, but only in one out of three study years (Sonnenberg et al., 2022). Many other cognitive traits apart from memory are relevant for making fitness-related decisions in natural settings, for example to navigate, track resources, choose a mate or avoid predators (Szabo et al., 2022). In the current context of rapid and broad environmental changes, cognitive abilities such as innovation (i.e., the emergence of a new behaviour or the modification of an old one in response to a novel situation; Reader et Laland, 2003), might in particular play a most important role in allowing individuals to adjust their behaviour rapidly and adaptatively in response to changing environments (Cantalapiedra et al., 2014; Reader & MacDonald, 2003; Sol et al., 2002). Yet, we currently lack empirical information about the effect of early life conditions on innovation ability in adulthood.

Here, we examined how early-life conditions influence innovation ability in adulthood, assessed via problem-solving performance (Cauchoix et al., 2018; Griffin & Guez, 2014), together with a suite of behavioural traits, measured in a natural ecological context during breeding in wild great tits. The problem-solving performance of great tits has been widely studied in both captive and natural conditions due to their acknowledged innovative abilities (Aplin et al., 2015; Cauchard et al., 2024; Isaksson et al., 2024; Preiszner et al., 2017; Urhan et al., 2023). Over a decade, we measured the problem-solving performance of breeding great tits on a string-pulling task presented at their nest during the nestling provisioning period, as well as their accuracy, neophobia, activity and exploration traits while interacting with the task. Among these great tits, some were local recruits in the population, for which we thus had information about their natal environment. We then explored the links between their behavioural traits measured as adults and integrative variables known to reflect their overall conditions experienced as nestlings: hatching date, body condition at fledging, brood size, parental age and body condition (Linden et al., 1992; Naef-Daenzer et al., 2001; Tilgar et al., 2010; Tinbergen & Boerlijst, 1990; Visser & Verboven, 1999). If early-life conditions act as a constraint, with poor conditions restraining the resources needed for cognitive development and developmental plasticity, nestlings reared in less favourable conditions (e.g., hatching date out of sync from the peak of food availability, poorer body condition, high siblings competition, young parents, and/or parents in poor condition) should be less likely to solve the task once adults, and show reduced accuracy, greater neophobia, lower exploration and activity while interacting with it. Conversely, if early-life conditions act as a source of information for developing individuals to plastically adjust their cognitive and behavioural functions, we expect the opposite pattern.

Material and methods

Study site and population monitoring

This study was conducted in a wild population of great tits monitored on the island of Gotland, Sweden (57◦10'N, 18◦20'E). Great tits are monogamous cavity-nesting passerine birds that readily accept to breed in the nest boxes provided in the study area (N = ~1500 nest boxes distributed across 8 geographical areas). To monitor breeding events, nest boxes were visited regularly every year from mid-April to the end of June to collect main breeding data, in particular laying and hatching date, clutch and brood size. When nestlings were 9 days old, they were ringed and when they were 14 days old, they were weighed (to the nearest 0.1g) and their tarsus length was measured (to the nearest 0.1mm). Nestling body condition at day 14 was computed as the ratio of body mass divided by tarsus length (Haas, 2021). From 10 days after hatching, parents were caught using nest box traps or mist nets to identify them (and ring them if not ringed already). Caught adults were sexed (male vs. female) and aged (yearling vs. older adult) using plumage characteristics (Svensson, 1992), and their body mass and tarsus length were measured to calculate body condition as for nestlings.

Problem-solving and behavioural measurements

From 2010 until 2016, and 2021 until 2024, we measured problem-solving performance of breeding adults using a problem-solving task attached to their nest box during the rearing period (Cauchard et al., 2013, 2024). The task featured a door placed temporarily over the nest box entrance hole, closed by default. To enter, parents had to pull with the leg a string hanging under the door, which opened it, and simultaneously slide their body under the door. The door then closed behind them, but they could push it from inside the nest box to exit (see figure 1 in Cauchard et al., 2024). This task simulates a natural obstacle that birds could remove on each entrance using a new behaviour involving pulling with their legs predominantly, as opposed to the classical use of their beak to pull material. Previous studies using this task have shown that inter-individual variation in problem-solving performance was primarily explained by a cognitive mechanism involving associative learning: solvers make fewer errors after the first cue to the solution (i.e., the first contact with the string that opened the door), and along successive attempts, compared to non-solvers (Cauchard et al., 2024). Furthermore, inter-individual variation in problem-solving performance was not related to neophobia (measured as the latency to first touch the task) or motivation (measured either by the time spent interacting with the task or by brood size) (Cauchard et al., 2017, 2024).

Problem-solving tests were conducted before adult capture to avoid any impact of disturbance and/or handling on behavioural measures. When nestlings were 6 days old, we attached the task to the nest box during 1 hour, between 07:00 AM and 04:00 PM. Tests were launched only if nestlings were satiated (i.e., not begging intensely at the beginning of the test) so that they would be able to endure not being fed for 1 hour should both parents be non-solvers. If nestlings were begging intensively, we cancelled the test and tried again later on the same day or the day after. A second test was conducted following the same protocol on the subsequent day, resulting in a total of 2 hours of test, to let parents enough time to explore the task while reducing the time per day during which nestlings potentially remained unfed. Tests were recorded by a video recorder hidden in the vegetation approx. 6 to 10 meters from the nest box, facing the entrance of the nest box.

Video recordings were analysed blindly with respect to the hypotheses tested. Using the two 1-hour tests merged as a single test, we scored:

- problem-solving performance, as whether or not the birds succeeded in pulling the string and entering the nest box (problem-solving status: 1 = solver, 0 = non-solver);
- accuracy, as the proportion of task-relevant contacts (i.e., contacts with the door and the string) over all contacts (8 areas in total, see below) until the first entrance, or until the end of the test for non-solvers (accuracy thus varies from 0 when a bird never contacted the door or the string, to 1 when a bird only contacted those areas of the task).
- neophobia, i.e., the fear of novelty, as the total time (in seconds) elapsed between the first contact with the nest box and the first contact with the task. A score of 7200 seconds (i.e., maximum duration of the two tests performed) is attributed to birds that were observed on the nest box but never touched the task (N = 4, 1.1%);
- activity, as the total number of movements between areas defined on the nest box (6 nest box areas: roof, front, left and right sides, left and right corners, and two task areas: door and string; Cauchard, Bize et Doligez, 2024) until the first entrance for solvers, or until the end of the test for non-solvers;
- exploration, as the total number of different areas on the nest box contacted (varies from 1 to 8) until the first entrance for solvers, or until the end of the test for non-solvers.

Birds were caught, handled and ringed under a licence from the Stockholm Museum Ringing Centre (license number 644:M03 to BD) and behavioural tests are conducted under a licence from the Swedish Committee for Experiments on Animals for all experiments on the site (license number C 108/7).

Statistical analyses

We ran separate models for the five behavioural traits measured during the problem-solving test ($-0.41 < r < 0.52$), using linear mixed models (LMMs) for continuous response variables (i.e., accuracy, neophobia, activity) and generalised linear mixed models (GLMMs) for binary or count response variables (i.e., problem-solving status, exploration). Initial models included as fixed factors (i) sex, (ii) body condition at fledging, (iii) brood size, (iv) hatching date, (v) age of each parent, and (vi) body condition of each parent. We also added (vii) adult body mass (i.e., in the year of the test) as a fixed effect to account for its effect on problem-solving status (i.e., lighter individual are more prone to solve), as previously found in this population (Cauchard et al., 2024). We initially included (viii) the square value of hatching date to account for the potential quadratic effect of the timing of the season (e.g., both early and late hatching dates could represent harsher environmental conditions) but removed it was never significant. We added as random factors: (i) the year and (ii) the area of birth to account for environmental variation. We initially included (iii) nest rearing identity as a random factor to account for the potential non-independence of siblings, but removed it as it explained a negligible amount of variance and models converged with difficulty when included. If an individual was tested multiple times in adulthood (i.e., there is at maximum of one test per year, but the same individual can be tested over multiple years), we restricted the analyses to behavioural measures collected in the first year of testing in order to make the data comparable across all individuals.

All statistical analyses were conducted using R version 4.2.1 (R. C. Team, 2020) and RStudio version 2022.07.2 (Rs. Team, 2019). Explanatory continuous variables were scaled to improve the interpretability of model estimates. Neophobia and activity were log-transformed to reach normality. All tests were two-tailed, and we removed non-significant factors ($p > 0.05$) from final models using a stepwise backward selection procedure. We checked for multicollinearity between explanatory variables using variance inflation factors (VIF) and for homogeneity and normality of the residuals using the package *DHARMa* (Hartig, 2024). Sample size can vary between models because of missing data.

Results

A total of 348 local recruits were tested at least once with the problem-solving task over 9 years. Of these 348 recruits, 143 (i.e., 41%) were solvers, including 68 males (out of 200 males, i.e., 34%) and 75 females (out of 148 females, i.e., 51%). Recruit hatching dates varied from May 11 to June 26, in broods varying from 1 to 12 nestlings with a mean (± SD) of 7.4 ± 1.9 nestlings. Nestling body condition varies from 0.58 to 0.88, with a mean (± SD) of 0.77 ± 0.05.

The probability to solve the task in adulthood increased with nestling body condition at day 14 (Figure 1a), was lower in males (Figure 1a), and decreased with increasing adult body mass (Table 1). The probability to solve the task also tended to increase with hatching date (Table 1). Accuracy (i.e., the proportion of relevant contacts during problem-solving) increased with increasing body condition at fledging (Figure 1b; Table 1) and was lower in males (Table 1). No other variable reflecting early life conditions affected solving probability or accuracy in adulthood (Table 1).

Neophobia (i.e., time to first contact the task) tended to decrease with nestling body condition at day 14 (Figure 1c, Table 1). Activity differed only between sexes, with females being more active than males (Table 1). No other variable reflecting early life conditions affected neophobia, activity and exploration (Table 1).

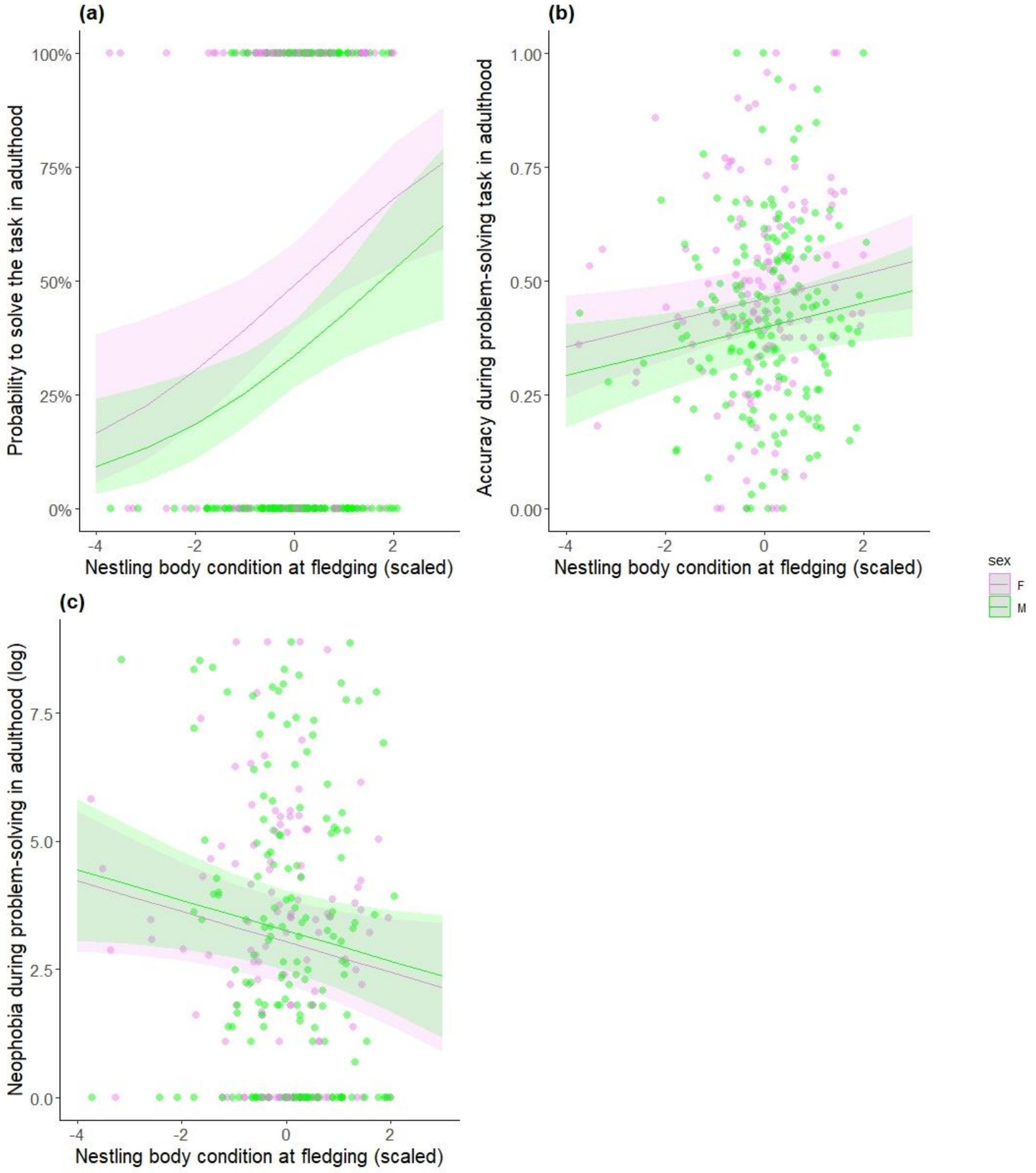

Figure 1. Variation in behavioural traits measured in adulthood in relation to body condition of the individual at fledging in wild great tits exposed to a new problem-solving task. Nestling body condition at fledging (14 days old) is related to: (a) problem-solving status (0 = non-solver, 1 = solver), (b) accuracy during solving, and (c) neophobia when approaching the task. Females are presented in purple and males in green. Dots are raw data and lines and shaded areas represent predicted estimates and 95% CI from models presented in the Table 1.

	Problem-solving status			Accuracy			Neophobia			Activity			Exploration		
Predictors	*Log-Odds*	*CI*	*p*	*Est.*	*CI*	*p*	*Est.*	*CI*	*p*	*Est.*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	-0.02	-0.39 – 0.36	0.934	0.46	0.39 – 0.53	<0.001	3.17	2.43 – 3.91	<0.001	3.54	3.24 – 3.84	<0.001	5.08	4.84 – 5.33	<0.001
Sex [Males]	**-0.65**	**-1.16 – -0.14**	**0.013**	**-0.06**	**-0.11 – -0.02**	**0.007**	0.22	-0.36 – 0.80	0.452	**-0.22**	**-0.42 – -0.02**	**0.034**	0.97	0.88 – 1.07	0.549
Body condition at fledging	**0.40**	**0.13 – 0.66**	**0.003**	**0.03**	**0.00 – 0.05**	**0.023**	*-0.29*	*-0.58 – 0.01*	*0.054*	0.06	-0.05 – 0.16	0.292	1.00	0.95 – 1.05	0.941
Brood size	0.08	-0.16 – 0.32	0.506	0.01	-0.01 – 0.03	0.398	-0.16	-0.47 – 0.16	0.326	0.02	-0.09 – 0.12	0.712	1.02	0.97 – 1.07	0.417
Hatching date	*0.26*	*-0.01 – 0.52*	*0.055*	0.01	-0.02 – 0.04	0.529	0.14	-0.22 – 0.50	0.449	-0.04	-0.16 – 0.07	0.445	1.02	0.97 – 1.07	0.471
Mother age [Yearlings]	0.36	-0.17 – 0.90	0.185	-0.01	-0.06 – 0.04	0.575	0.48	-0.15 – 1.12	0.136	0.09	-0.14 – 0.32	0.456	0.96	0.86 – 1.08	0.523
Father age [Yearlings]	0.03	-0.66 – 0.71	0.940	-0.02	-0.09 – 0.05	0.589	0.30	-0.54 – 1.15	0.477	-0.11	-0.42 – 0.19	0.466	0.97	0.84 – 1.11	0.631
Mother body condition	-0.17	-0.43 – 0.10	0.218	-0.01	-0.04 – 0.01	0.267	-0.01	-0.36 – 0.34	0.963	0.03	-0.09 – 0.16	0.568	1.02	0.96 – 1.07	0.573
Father body condition	-0.06	-0.33 – 0.21	0.652	0.00	-0.02 – 0.03	0.798	-0.07	-0.43 – 0.29	0.692	0.09	-0.04 – 0.21	0.163	1.02	0.96 – 1.07	0.581
Adult mass	**-0.32**	**-0.60 – -0.04**	**0.023**												
Random Effects															
σ^2	3.29			0.04			6.11			0.81			--		
τ_{00} year.hatch	0.00			0.01			0.78			0.14			0.00		
τ_{00} area.hatch	0.00			0.00			0.28			0.02			0.00		
ICC	--			0.22			0.15			0.17			--		
N area.hatch	8			8			8			8			8		
N year.hatch	12			12			12			12			12		
Observations	313			305			301			328			328		
Marginal R^2 / Conditional R^2	0.111 / NA			0.031 / 0.245			0.012 / 0.157			0.012 / 0.177			NA		

Table 1: Results of mixed models testing the effects of variables reflecting early life conditions on behavioural traits in adulthood in wild great tits exposed to a new problem-solving task (see text for the definition of trait measured)**.** The effect of sex is expressed as the estimate for males compared to females, and the effect of parental age as yearlings compared to two years old or older adults. Final models, retaining significant or marginally significant effects, and intercepts, are reported in black font and significant effects are reported in bold. Non-significant effects removed from the models following a stepwise backward selection procedure are shown in dark grey font.

Discussion

In this study, we investigated whether environmental conditions encountered during growth influenced cognitive and behavioural traits in adulthood in the great tit, a wild passerine bird known for its behavioural plasticity (e.g., Aplin *et al.*, 2015; Isaksson, Utku Urhan et Brodin, 2018; Cauchard, Bize et Doligez, 2024). We found that, regardless of sex, nestlings in better condition just before fledging (measured as a higher ratio of body mass on tarsus length), were more likely to solve a new problem-solving task as adults, made fewer mistakes when solving the problem (i.e., were more accurate), and were less neophobic (i.e., interacted faster with the new task) than nestlings in poorer condition (Figure 1). There is now strong evidence for the importance of early growth conditions on adult physiological, morphological and behavioural traits, such as dispersal or personality, in wild animals (Benard & McCauley, 2008; Lemaître et al., 2015), but the effects on cognitive traits remain poorly studied (Sonnenberg et al., 2022; Soravia et al., 2024), even though they play a decisive role in all decision-making processes, such as habitat selection, mate choice or foraging strategies. Hence, by pinpointing a link between body condition early in life and problem-solving performance and accuracy in adulthood, this 10-year-long study, based on over 300 recruits, helps to consolidate our knowledge on the long-term effects of early growth on cognitive traits and, in turn, on the many fitness-related traits that may be affected by individual decisions through cognition.

In this correlative study, we investigated a broad set of integrative variables known to reflect early conditions in wild birds: namely, laying date, brood size, nestling body condition, parental age and body condition. Of these, only nestling body condition close to fledging predicted adult problem-solving performance. In great tits and other birds, fledging body condition is a widely used proxy for overall nestling physiological condition. It integrates early-life environmental and parental effects and strongly predicts post-fledging survival and recruitment (Ronget et al., 2018). Indeed, fledgling condition directly reflects physiological condition (e.g., Hõrak *et al.*

1999; Kaliński *et al.* 2019; Landys *et al.* 2011), indicating the nutritional status and energy reserves of an individual (Bańbura et al., 2011) just before the post-fledging phase, a critical period of life (Naef-Daenzer et al. 2001). Because cognitive traits rely on costly neuronal processes (e.g., electrical signalling processes located in the brain can account for over 50% of total energy intake in humans during development; Heldstab *et al.*, 2022), poor conditions during development can drive redirection of energy towards short-term survival rather than neural development and function (Bick & Nelson, 2016; Heldstab et al., 2022; Isler & van Schaik, 2009; Kotrschal et al., 2019). Accordingly, food availability and quality are well known to affect cognitive performance in humans and laboratory animals (Akman et al., 2004; Kriengwatana et al., 2015; Nowicki et al., 2002), and our results add to this body of research by showing links between body condition early in life, caused by nutritional restrictions during development, and problem-solving performance as adults in wild birds. The impacts of early life stressors on cognition are, however, not due to nutrition only as recently demonstrated wild southern pied babblers (*Turdoides bicolor*) where higher temperatures during the nestling stage led to long-term impairments in associative learning performance but not in reversal learning performance (Soravia et al., 2024).

Environmental stressors, including nutritional stress, are known to increase levels of corticosteroid stress hormones in animals, and these hormones play a central role in redirecting energy towards short-term survival (Buchanan, 2000). The links between adverse early environmental conditions and adult cognitive performance may therefore be mediated by changes in corticosteroid stress hormone, which have an adverse effects on neural development (Buchanan et al., 2004; Schoech et al., 2011). In wild food-caching mountain chickadees, feather corticosterone levels before fledging in individuals living at high elevation were negatively related to short-term memory in adulthood in one out of the three years of the study (Sonnenberg et al., 2022). In birds, species with larger brains (relative to their body size) show lower baseline and peak of corticosterone levels than those with smaller brains, supporting the hypothesis that enhanced cognition allows animals to better cope with stressful situations (Lendvai et al., 2013). Unfortunately, we have no measures of corticosteroid levels during nestling development in our study system with which to explore these mechanistic pathways further.

In birds and other animals, individuals in better body condition near fledging or independence have higher survival to adulthood and recruitment probabilities as breeders (e.g., Tinbergen et Boerlijst, 1990; Garant *et al.*, 2004; Ronget *et al.*, 2018). In other words, individuals in poor condition are more likely to die before recruitment; this likely obscures long-term negative effects of suboptimal early conditions on cognitive performance through selective disappearance of the most affected individuals (i.e., those with the strongest reduction in adult cognition). Detecting long-term effects of poor early growth conditions therefore typically requires large sample sizes and multi-year studies, as in our study. It is also important to note that higher mortality in harsh years may also filter out the poorest individuals (Hadfield, 2008), potentially generating positive correlations between annual environmental conditions and cognition that may further mask links between early growth conditions and adult cognitive performance.

Hatching date is another important measure of early growth conditions in animals under strong seasonality (de Villemereuil et al., 2020). Indeed, in these species, hatching date plays a particularly important role in determining the optimal synchronization of growth with temperature and food abondance (e.g., in great tits, Verboven et Visser, 1998; Greño, Belda et Barba, 2008; Rodríguez *et al.*, 2016). Thus, the timing of breeding, by determining access to food resources, might influence nestling brain development and cognitive abilities at adulthood (Bertin et al., 2018; DuRant et al., 2013; Hope et al., 2018). In our study, nestlings that hatched later during the breeding season tended to be more prone to solve the task than those hatched earlier. This is opposite to our expectation since in great tits, a late hatching date is usually associated with poor early life conditions either because breeding parents are less competitive (i.e., secured a territory later, thus of lower quality) or they missed the peak of food resources (Monrós et al., 2002). Importantly, in our study, even though recruit hatching dates spanned from May 11 to June 26, 89.1% of our measured recruits hatched between May 15 and June 4, i.e., over a very short period, and this may have limited our ability to detect a clear effect of hatching date on behavioural performances. This high synchrony of hatching might indeed have hidden the relationship with food abondance, resulting in no correlation between hatching date and nestling condition in our sample of measured recruits (N = 315, r = 0.03).

Brood size could also act as a constraint on the development of cognitive performance when parents have to share limited food resources between more nestlings (Hõrak, 2003), limiting the energy available for brain development in each nestling. Here, we found no effect of brood size on the behavioural traits measured at adulthood. A recent study found that in great tits, manipulated brood size affected nestling mass but not physiological traits related to energetical production such as mitochondrial metabolism and reactive oxygen species production (Cossin-Sevrin et al., 2023). In our study, brood size was poorly correlated to nestling body condition (N = 322, r = -0.05), it is thus possible that brood size did not affect the allocation of energy for brain development in our growing great tits. Parental age has also been found to influence breeding success in great tits, even though in this species, reproductive success can either decrease (with decreasing parental effort), increase (with increasing parental experience) or remain unchanged with increasing age (e.g., Perrins et McCleery, 1985; Pigeault *et al.*, 2020; Verhulst, 2026). Here, we found no effect of parental age on nestling behavioural traits in adulthood, nor on nestling body condition ($t_{(255.8)} = -1.09$, $p = 0.27$ and $t_{(71.5)} = 0.15$, $p = 0.88$ for females and males, respectively), supporting that age either did not affect growing conditions in our great tit population, or that our binary age measure (yearling vs. older adults) did not capture age variation relevantly enough. Finally, great tit parents in better condition were also found to raise offspring more successfully, which likely relates to their higher efficiency to find food and/or higher genetic quality (Gebhardt-Henrich & Van Noordwijk, 1991; Norte et al., 2010; Pickett et al., 2013). In our study, we found no direct effect of parental condition on nestling behavioural performances at adulthood, and weak correlations between parental condition and nestling body condition (N = 280, r = 0.12 and N = 268, r = 0.22 for females and males, respectively). It is possible that the effect of nestling condition at fledging on behavioural performances masked a potential role of parental condition.

In conclusion, our results clearly suggest that early environment has strong developmental effects on problem-solving ability and accuracy, as well as potential effects on neophobia (only marginally significant here), which are three cognitive and behavioural traits known to help species to adjust to new conditions. Indeed, the ability to solve new problems and to flexibly adjust behaviour based on cues to solution (i.e., accuracy here), as well as a low neophobia level, are behavioural traits that are most likely under natural selection by enabling fast and flexible construction of new behavioural responses (Ducatez et al., 2020; Sol et al., 2016). Yet, we cannot rule out the possibility that some other, unmeasured factor could have a role in driving the relationship observed between nestling condition and cognitive performance in adulthood by simultaneously but independently influencing both variables. Therefore, directly manipulating growth conditions, through for example the supplementation of nestlings, in particular with nutrients known to be important for brain development, is now needed to experimentally demonstrate the role of early life conditions (here nutritional stress) in shaping innovative performance in adulthood.

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References

Akman, C., Zhao, Q., Liu, X., & Holmes, G. L. (2004). Effect of food deprivation during early development on cognition and neurogenesis in the rat. *Epilepsy & Behavior*, *5*(4), 446–454. https://doi.org/10.1016/j.yebeh.2004.03.008

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, *518*, 538–541. https://doi.org/10.1038/nature13998

Bańbura, J., Bańbura, M., Glądalski, M., Kaliński, A., Markowski, M., Michalski, M., Nadolski, J., Skwarska, J., & Zieliński, P. (2011). Body condition parameters of nestling great tits Parus major in relation to experimental food supplementation. *Acta Ornithologica*, *46*(2), 207–212. https://doi.org/10.3161/000164511X625991

Benard, M. F., & McCauley, S. J. (2008). Integrating across life-history stages: Consequences of natal habitat effects on dispersal. *The American Naturalist*, *171*(5), 553–567. https://doi.org/10.1086/587072

Bertin, A., Calandreau, L., Meurisse, M., Georgelin, M., Palme, R., Lumineau, S., Houdelier, C., Darmaillacq, A.-S., Dickel, L., Colson, V., Cornilleau, F., Rat, C., Delaveau, J., & Arnould, C. (2018). Incubation temperature affects the expression of young precocial birds' fear-related behaviours and neuroendocrine correlates. *Scientific Reports*, *8*(1), 1857. https://doi.org/10.1038/s41598-018-20319-y

Bick, J., & Nelson, C. A. (2016). Early adverse experiences and the developing brain. *Neuropsychopharmacology*, *41*(1), 177–196. https://doi.org/10.1038/npp.2015.252

Braithwaite, V. A., & Salvanes, A. G. V. (2005). Environmental variability in the early rearing environment generates behaviourally flexible cod: Implications for rehabilitating wild populations. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1568), 1107–1113. https://doi.org/10.1098/rspb.2005.3062

Buchanan, K. L. (2000). Stress and the evolution of condition-dependent signals. *Trends in Ecology & Evolution*, *15*(4), 156–160. https://doi.org/10.1016/s0169-5347(99)01812-1

Buchanan, K. L., Leitner, S., Spencer, K. A., Goldsmith, A. R., & Catchpole, C. K. (2004). Developmental stress selectively affects the song control nucleus HVC in the zebra finch. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1555), 2381–2386. https://doi.org/10.1098/rspb.2004.2874

Cantalapiedra, J. L., FitzJohn, R. G., Kuhn, T. S., Fernández, M. H., DeMiguel, D., Azanza, B., Morales, J., & Mooers, A. Ø. (2014). Dietary innovations spurred the diversification of ruminants during the Caenozoic. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1776), 20132746. https://doi.org/10.1098/rspb.2013.2746

Cauchard, L., Angers, B., Boogert, N. J., Lenarth, M., Bize, P., & Doligez, B. (2017). An experimental test of a causal link between problem-solving performance and reproductive success in wild great tits. *Frontiers in Ecology and Evolution*, *5*, 107. https://doi.org/10.3389/fevo.2017.00107

Cauchard, L., Bize, P., & Doligez, B. (2024). How to solve novel problems: The role of associative learning in problem-solving performance in wild great tits Parus major. *Animal Cognition*, *27*(1), 32. https://doi.org/10.1007/s10071-024-01872-8

Cauchard, L., Boogert, N. J., Lefebvre, L., Dubois, F., & Doligez, B. (2013). Problem-solving performance is correlated with reproductive success in a wild bird population. *Animal Behaviour*, *85*(1), 19–26. https://doi.org/10.1016/j.anbehav.2012.10.005

Cauchoix, M., Chow, P. K. Y., van Horik, J. O., Atance, C. M., Barbeau, E. J., Barragan-Jason, G., Bize, P., Boussard, A., Buechel, S. D., Cabirol, A., Cauchard, L., Claidière, N., Dalesman, S., Devaud, J. M., Didic, M., Doligez, B., Fagot, J., Fichtel, C., Henke-von der Malsburg, J., … Morand-Ferron, J. (2018). The repeatability of cognitive performance: A meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170281. https://doi.org/10.1098/rstb.2017.0281

Cossin-Sevrin, N., Stier, A., Hukkanen, M., Zahn, S., Viblanc, V. A., Anttila, K., & Ruuskanen, S. (2023). Early-life environmental effects on mitochondrial aerobic metabolism: A brood size manipulation in wild great tits. *Journal of Experimental Biology*, *226*(21), jeb245932. https://doi.org/10.1242/jeb.245932

de Villemereuil, P., Charmantier, A., Arlt, D., Bize, P., Brekke, P., Brouwer, L., Cockburn, A., Côté, S. D., Dobson, F. S., Evans, S. R., Festa-Bianchet, M., Gamelon, M., Hamel, S., Hegelbach, J., Jerstad, K., Kempenaers, B., Kruuk, L. E. B., Kumpula, J., Kvalnes, T., … Chevin, L.-M. (2020). Fluctuating optimum and temporally variable selection on breeding date in birds and mammals. *Proceedings of the National Academy of Sciences*, *117*(50), 31969–31978. https://doi.org/10.1073/pnas.2009003117

Ducatez, S., Sol, D., Sayol, F., & Lefebvre, L. (2020). Behavioural plasticity is associated with reduced extinction risk in birds. *Nature Ecology & Evolution*, *4*(6), 788–793. https://doi.org/10.1038/s41559-020-1168-8

DuRant, S. E., Hopkins, W. A., Hepp, G. R., & Walters, J. R. (2013). Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biological Reviews*, *88*(2), 499–509. https://doi.org/10.1111/brv.12015

Foraita, M., Howell, T., & Bennett, P. (2021). Environmental influences on development of executive functions in dogs. *Animal Cognition*, *24*(4), 655–675. https://doi.org/10.1007/s10071-021-01489-1

Garant, D., Kruuk, L. E. B., McCleery, R. H., & Sheldon, B. C. (2004). Evolution in a changing environment: A case study with great tit fledging mass. *The American Naturalist*, *164*(5), E115-129. https://doi.org/10.1086/424764

Gebhardt-Henrich, S. G., & Van Noordwijk, A. J. (1991). Nestling growth in the Great Tit I. Heritability estimates under different environmental conditions. *Journal of Evolutionary Biology*, *4*(3), 341–362. https://doi.org/10.1046/j.1420-9101.1991.4030341.x

Greño, J. L., Belda, E. J., & Barba, E. (2008). Influence of temperatures during the nestling period on post-fledging survival of great tit Parus major in a Mediterranean habitat. *Journal of Avian Biology, 39*(1), 41–49. https://doi.org/10.1111/j.0908-8857.2008.04120.x

Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common mechanisms. *Behavioural Processes*, *109, Part B*(0), 121–134. https://doi.org/10.1016/j.beproc.2014.08.027

Haas, M. (2021). The influence of the environment on growth parameters of great tits (Parus major). *Oecologia Montana*, *30*(2), 59–65.

Hadfield, J. D. (2008). Estimating evolutionary parameters when viability selection is operating. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1635), 723–734. https://doi.org/10.1098/rspb.2007.1013

Haller, J., Harold, G., Sandi, C., & Neumann, I. D. (2014). Effects of adverse early-life events on aggression and anti-social behaviours in animals and humans. *Journal of Neuroendocrinology*, *26*(10), 724–738. https://doi.org/10.1111/jne.12182

Hartig, F. (2024). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models* (Version R package version 0.4.7) [Computer software]. http://florianhartig.github.io/DHARMa/

Hedges, D. W., & Woon, F. L. (2011). Early-life stress and cognitive outcome. *Psychopharmacology*, *214*(1), 121–130. https://doi.org/10.1007/s00213-010-2090-6

Heldstab, S. A., Isler, K., Graber, S. M., Schuppli, C., & Schaik, C. P. van. (2022). The economics of brain size evolution in vertebrates. *Current Biology*, *32*(12), R697–R708. https://doi.org/10.1016/j.cub.2022.04.096

Holubová, A., Lukášková, I., Tomášová, N., Šuhajdová, M., & Šlamberová, R. (2018). Early postnatal stress impairs cognitive functions of male rats persisting until adulthood. *Frontiers in Behavioral Neuroscience*, *12*. https://doi.org/10.3389/fnbeh.2018.00176

Hope, S. F., Kennamer, R. A., Moore, I. T., & Hopkins, W. A. (2018). Incubation temperature influences the behavioral traits of a young precocial bird. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, *329*(4–5), 191–202. https://doi.org/10.1002/jez.2176

Hõrak, P. (2003). When to pay the cost of reproduction? A brood size manipulation experiment in great tits (Parus major). *Behavioral Ecology and Sociobiology*, *54*(2), 105–112. https://doi.org/10.1007/s00265-003-0608-1

Hõrak, P., Tegelmann, L., Ots, I., & Møller, A. P. (1999). Immune function and survival of great tit nestlings in relation to growth conditions. *Oecologia*, *121*(3), 316–322. https://doi.org/10.1007/s004420050934

Isaksson, E., Morand-Ferron, J., & Chaine, A. (2024). Environmental harshness does not affect the propensity for social learning in great tits, Parus major. *Animal Cognition*, *27*(1), 25. https://doi.org/10.1007/s10071-024-01862-w

Isaksson, E., Utku Urhan, A., & Brodin, A. (2018). High level of self-control ability in a small passerine bird. *Behavioral Ecology and Sociobiology*, *72*(7), 118. https://doi.org/10.1007/s00265-018-2529-z

Isler, K., & van Schaik, C. P. (2009). The Expensive Brain: A framework for explaining evolutionary changes in brain size. *Journal of Human Evolution, Paleoanthropology Meets Primatology*, *57*(4), 392–400. https://doi.org/10.1016/j.jhevol.2009.04.009

Johnson, D., Policelli, J., Li, M., Dharamsi, A., Hu, Q., Sheridan, M. A., McLaughlin, K. A., & Wade, M. (2021). Associations of early-life threat and deprivation with executive functioning in childhood and adolescence: A systematic review and meta-analysis. *JAMA Pediatrics*, *175*(11), e212511. https://doi.org/10.1001/jamapediatrics.2021.2511

Kaliński, A., Bańbura, M., Glądalski, M., Markowski, M., Skwarska, J., Wawrzyniak, J., Zieliński, P., & Bańbura, J. (2019). Physiological condition of nestling great tits (Parus major) declines with the date of brood initiation: A long term study of first clutches. *Scientific Reports*, *9*(1), 9843. https://doi.org/10.1038/s41598-019-46263-z

Kirolos, A., Goyheneix, M., Eliasz, M. K., Chisala, M., Lissauer, S., Gladstone, M., & Kerac, M. (2022). Neurodevelopmental, cognitive, behavioural and mental health impairments following childhood malnutrition: A systematic review. *BMJ Global Health*, *7*(7). https://doi.org/10.1136/bmjgh-2022-009330

Kotrschal, A., Corral-Lopez, A., & Kolm, N. (2019). Large brains, short life: Selection on brain size impacts intrinsic lifespan. *Biology Letters*, *15*(5), 20190137. https://doi.org/10.1098/rsbl.2019.0137

Kotrschal, A., & Taborsky, B. (2010). Environmental change enhances cognitive abilities in fish. *PLOS Biology*, *8*(4), e1000351. https://doi.org/10.1371/journal.pbio.1000351

Kriengwatana, B., Farrell, T. M., Aitken, S. D. T., Garcia, L., & MacDougall-Shackleton, S. A. (2015). Early-life nutritional stress affects associative learning and spatial memory but not performance on a novel object test. *Behaviour*, *152*(2), 195–218. https://doi.org/10.1163/1568539X-00003239

Landys, M. M., Goymann, W., & Slagsvold, T. (2011). Rearing conditions have long-term consequences for stress responsiveness in free-living great tits. *General and Comparative Endocrinology*, *174*(2), 219–224. https://doi.org/10.1016/j.ygcen.2011.08.022

Le Galliard, J. -F., Paquet, M., & Mugabo, M. (2015). An experimental test of density-dependent selection on temperament traits of activity, boldness and sociability. *Journal of Evolutionary Biology*, *28*(5), 1144–1155. https://doi.org/10.1111/jeb.12641

Lemaître, J.-F., Berger, V., Bonenfant, C., Douhard, M., Gamelon, M., Plard, F., & Gaillard, J.-M. (2015). Early-late life trade-offs and the evolution of ageing in the wild. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1806), 20150209. https://doi.org/10.1098/rspb.2015.0209

Lendvai, Á. Z., Bókony, V., Angelier, F., Chastel, O., & Sol, D. (2013). Do smart birds stress less? An interspecific relationship between brain size and corticosterone levels. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1770). https://doi.org/10.1098/rspb.2013.1734

Linden, M., Gustafsson, L., & Part, T. (1992). Selection on fledging mass in the Collared Flycatcher and the Great Tit. *Ecology*, *73*(1), 336–343. (WOS:A1992HC84200030). https://doi.org/10.2307/1938745

Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, *14*(9), 343–348. https://doi.org/10.1016/S0169-5347(99)01639-0

Menezes, J., Souto das Neves, B.-H., Gonçalves, R., Benetti, F., & Mello-Carpes, P. B. (2020). Maternal deprivation impairs memory and cognitive flexibility, effect that is avoided by environmental enrichment. *Behavioural Brain Research*, *381*, 112468. https://doi.org/10.1016/j.bbr.2020.112468

Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: Grow now, pay later? *Trends in Ecology & Evolution*, *16*(5), 254–260. https://doi.org/10.1016/S0169-5347(01)02124-3

Monrós, J. S., Belda, E. J., & Barba, E. (2002). Post-fledging survival of individual great tits: The effect of hatching date and fledging mass. *Oikos*, *99*(3), 481–488.

Naef-Daenzer, B., Widmer, F., & Nuber, M. (2001). Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology*, *70*(5), 730–738. (WOS:000171128800003). https://doi.org/10.1046/j.0021-8790.2001.00533.x

Norte, A. C., Ramos, J. A., Sampaio, H. L., Sousa, J. P., & Sheldon, B. C. (2010). Physiological Condition and Breeding Performance of the Great Tit. *The Condor: Ornithological Applications*, *112*(1), 79–86. https://doi.org/10.1525/cond.2010.080071

Nowicki, S., Searcy, W. A., & Peters, S. (2002). Brain development, song learning and mate choice in birds: A review and experimental test of the" nutritional stress hypothesis". *Journal of Comparative Physiology A*, *188*(11–12), 1003–1014.

Perrins, C. M., & McCleery, R. H. (1985). The effect of age and pair bond on the breeding success of Great Tits Parus major. *Ibis*, *127*(3), 306–315. (WOS:A1985AMH3600002).

Pickett, S. R. A., Weber, S. B., McGraw, K. J., Norris, K. J., & Evans, M. R. (2013). Environmental and parental influences on offspring health and growth in Great Tits (Parus major). *PLOS ONE*, *8*(7), e69695. https://doi.org/10.1371/journal.pone.0069695

Pigeault, R., Cozzarolo, C.-S., Glaizot, O., & Christe, P. (2020). Effect of age, haemosporidian infection and body condition on pair composition and reproductive success in Great Tits Parus major. *Ibis*, *162*(3), 613–626. https://doi.org/10.1111/ibi.12774

Prado, E. L., & Dewey, K. G. (2014). Nutrition and brain development in early life. *Nutrition Reviews*, *72*(4), 267–284. https://doi.org/10.1111/nure.12102

Pravosudov, V. V., Lavenex, P., & Omanska, A. (2005). Nutritional deficits during early development affect hippocampal structure and spatial memory later in life. *Behavioral Neuroscience*, *119*(5), 1368–1374. https://doi.org/10.1037/0735-7044.119.5.1368

Preiszner, B., Papp, S., Pipoly, I., Seress, G., Vincze, E., Liker, A., & Bókony, V. (2017). Problem-solving performance and reproductive success of great tits in urban and forest habitats. *Animal Cognition*, *20*(1), 53–63. https://doi.org/10.1007/s10071-016-1008-z

Reader, S. M., & Laland, K. N. (2003). *Animal innovation: An introduction*. Oxford University Press.

Reader, S. M., & MacDonald, K. (2003). Environmental variability and primate behavioural flexibility. In S. M. Reader & K. N. Laland (Eds), *Animal Innovation* (pp. 83–116). Oxford University Press.

Rödel, H. G., & Meyer, S. (2011). Early development influences ontogeny of personality types in young laboratory rats. *Developmental Psychobiology*, *53*(6), 601–613. https://doi.org/10.1002/dev.20522

Rodenburg, T. B., Komen, H., Ellen, E. D., Uitdehaag, K. A., & van Arendonk, J. A. M. (2008). Selection method and early-life history affect behavioural development, feather pecking and cannibalism in laying hens: A review. *Applied Animal Behaviour Science*, *110*(3), 217–228. https://doi.org/10.1016/j.applanim.2007.09.009

Rodríguez, S., van Noordwijk, A. J., Álvarez, E., & Barba, E. (2016). A recipe for postfledging survival in great tits Parus major: Be large and be early (but not too much). *Ecology and Evolution*, *6*(13), 4458–4467. https://doi.org/10.1002/ece3.2192

Ronget, V., Gaillard, J.-M., Coulson, T., Garratt, M., Gueyffier, F., Lega, J.-C., & Lemaître, J.-F. (2018). Causes and consequences of variation in offspring body mass: Meta-analyses in birds and mammals. *Biological Reviews*, *93*(1), 1–27. https://doi.org/10.1111/brv.12329

Schoech, S. J., Rensel, M. A., & Heiss, R. S. (2011). Short- and long-term effects of developmental corticosterone exposure on avian physiology, behavioral phenotype, cognition, and fitness: A review. *Current Zoology*, *57*(4), 514–530. https://doi.org/10.1093/czoolo/57.4.514

Sol, D., Ducatez, S., & Sayol, F. (2016). Cognitive Buffer Hypothesis, The. In V. Weekes-Shackelford, T. K. Shackelford, & V. A. Weekes-Shackelford (Eds), *Encyclopedia of Evolutionary Psychological Science* (pp. 1–6). Springer International Publishing. https://doi.org/10.1007/978-3-319-16999-6_897-1

Sol, D., Timmermans, S., & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour*, *63*(3), 495–502. https://doi.org/10.1006/anbe.2001.1953

Sonnenberg, B. R., Heinen, V. K., Pitera, A. M., Benedict, L. M., Branch, C. L., Bridge, E. S., Ouyang, J. Q., & Pravosudov, V. V. (2022). Natural variation in developmental condition has limited effect on spatial cognition in a wild food-caching bird. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1984), 20221169. https://doi.org/10.1098/rspb.2022.1169

Soravia, C., Ashton, B. J., Thornton, A., Bourne, A. R., & Ridley, A. R. (2024). High temperatures during early development reduce adult cognitive performance and reproductive success in a wild animal population. *Science of The Total Environment*, *912*, 169111. https://doi.org/10.1016/j.scitotenv.2023.169111

Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews*, *85*(2), 301–325. https://doi.org/10.1111/j.1469-185X.2009.00103.x

Svensson, L. (1992). *Identification guide to European passerines*. British Trust for Ornithology.

Szabo, B., Valencia-Aguilar, A., Damas-Moreira, I., & Ringler, E. (2022). Wild cognition – linking form and function of cognitive abilities within a natural context. *Current Opinion in Behavioral Sciences*, *44*, 101115. https://doi.org/10.1016/j.cobeha.2022.101115

Tilgar, V., Mänd, R., Kilgas, P., & Mägi, M. (2010). Long-term consequences of early ontogeny in free-living Great Tits Parus major. *Journal of Ornithology*, *151*(1), 61–68. https://doi.org/10.1007/s10336-009-0426-y

Tinbergen, J. M., & Boerlijst, M. C. (1990). Nestling weight and survival in individual Great Tits (Parus major). *Journal of Animal Ecology*, *59*(3), 1113–1127.

Urhan, U., Mårdberg, M., Isaksson, E., van Oers, K., & Brodin, A. (2023). Blue tits are outperformed by great tits in a test of motor inhibition, and experience does not improve their performance. *Royal Society Open Science*, *10*(2), 221176. https://doi.org/10.1098/rsos.221176

Veenema, A. H. (2009). Early life stress, the development of aggression and neuroendocrine and neurobiological correlates: What can we learn from animal models? *Frontiers in Neuroendocrinology, Hormones & Social Behavior*, *30*(4), 497–518. https://doi.org/10.1016/j.yfrne.2009.03.003

Verboven, N., & Visser, M. E. (1998). Seasonal variation in local recruitment of great tits: The importance of being early. *Oikos*, *81*(3), 511–524. (WOS:000072934100009). https://doi.org/10.2307/3546771

Verhulst, S. (2026). Age dependent reproductive effort in great tits. *Journal of Avian Biology*, *2026*(1), e03541. https://doi.org/10.1002/jav.03541

Visser, M. E., & Verboven, N. (1999). Long-term fitness effects of fledging date in great tits. *Oikos*, *85*(3), 445–450. https://doi.org/10.2307/3546694