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RESEARCH ARTICLE

The effect of food quality during growth on spatial memory consolidation in adult pigeons

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ABSTRACT

Poor environmental conditions experienced during early development can have negative long-term consequences on fitness. Animals can compensate for negative developmental effects through phenotypic plasticity by diverting resources from non-vital to vital traits such as spatial memory to enhance foraging efficiency. We tested in young feral pigeons (*Columba livia*) how diets of different nutritional value during development affect the capacity to retrieve food hidden in a spatially complex environment, a process we refer to as 'spatial memory'. Parents were fed with either high- or low-quality food from egg laying until young fledged, after which all young pigeons received the same high-quality diet until memory performance was tested at 6 months of age. The pigeons were trained to learn a food location out of 18 possible locations in one session, and then their memory of this location was tested 24 h later. Birds reared with the low-quality diet made fewer errors in the memory test. These results demonstrate that food quality during development has long-lasting effects on memory, with a moderate nutritional deficit improving spatial memory performance in a foraging context. It might be that under poor feeding conditions resources are redirected from non-vital to vital traits, or pigeons raised with low-quality food might be better in using environmental cues such as the position of the sun to find where food was hidden.

KEY WORDS: *Columba livia*, Diet, Early development, Learning, Nutrition, Foraging, Nutritional deficit, Sleep, Timing of learning

INTRODUCTION

Early development is crucial in shaping life history traits (Huchard et al., 2016; Lindström, 1999; Metcalfe and Monaghan, 2001). Conditions experienced during early life, when all physiological and morphological traits are developing, can have long-lasting effects on the individual phenotypes (Krause et al., 2011; Metcalfe and Monaghan, 2001; Monaghan, 2008; Romero-Haro and Alonso-Alvarez, 2015). Under natural conditions, food availability during growth can be highly variable. However, developing individuals can respond to periods of food shortage by accelerating growth once the environmental conditions improve, a form of phenotypic plasticity that result in costs such as reduced lifespan and fecundity (Hector and Nakagawa, 2012; Metcalfe and Monaghan, 2001).

Few researchers have investigated the effects of poor conditions during early development on cognitive processes in an ecological context. A previous study in western scrub jays (*Aphelocoma californica*) has shown that diet restriction to 65% of *ad libitum* food, a level commonly observed in wild birds during early post-hatching development, impairs spatial memory in foraging tasks at adulthood (Pravosudov et al., 2005). It is not only the amount of food, but the type of diet that matters. For example, blue tit (*Cyanistes caeruleus*) nestlings supplemented with taurine (an amino acid important for early development) performed better as adults in a spatial memory task compared with taurine-deprived blue tits (Arnold et al., 2007). However, other studies in rats (*Rattus norvegicus*) have found the opposite result. One showed that a dietary restriction (70% of *ad libitum* food intake) protected individuals from age-related cognitive declines, particularly in spatial memory tasks (Gyger et al., 1992). In addition, adult female Sprague–Dawley rats fed with a low caloric diet (reduced by 15% compared with the standard diet) during adolescence showed improved spatial memory as adults (Kaptan et al., 2015). This suggests that if animals do not obtain sufficient nutrition in early life, resources can be diverted to key brain areas related to survival in preference over less important ones to protect from deleterious cognitive effects (Lukas and Campbell, 2000; Nowicki and Searcy, 2005; Schew and Ricklefs, 1998). Accordingly, Wistar rats fed with low-quality food during development had a lower body mass at 45 days of age compared with conspecifics fed with high-quality food, but brain mass did not differ, suggesting that some mechanisms protect brain tissue during periods of nutritional deficit (de Souza et al., 2012).

The influence of nutrition in early life on memory performance as adults might be mediated by differences in memory consolidation. There is accumulating evidence that sleep can improve memory consolidation in mammals (Boyce et al., 2016; Diekelmann and Born, 2010; Genzel et al., 2012; McDevitt et al., 2015; Ramadan et al., 2009; Rasch and Born, 2013). Prenatal malnourished rats were shown to differ in their sleep–wake cycle as adults compared with normally nourished conspecifics (Datta et al., 2000). The timing and amount of sleep after learning are critical factors determining the level of improvement in memory performance (e.g. Diekelmann et al., 2009; Hagewoud et al., 2010; Tucker et al., 2006; Van der Werf et al., 2009). For instance, white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) show a decrease in performance in a repeated-acquisition task after one night of experimental sleep deprivation (Rattenborg et al., 2004). Another study examined the performance of adult starlings (*Sturnus vulgaris*) in an auditory discrimination task following retention intervals primarily containing either sleep (night) or wakefulness (day) (Brawn et al.,

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2013; Brawn and Margoliash, 2014). When tested in the evening, after a daytime period of wakefulness, mean performance showed a small, non-significant decrease. But when tested in the morning after a night-time period, when sleep was prominent, performance increased significantly. It was also shown that sleep plays a role in the consolidation of imprinting memories in chickens (*Gallus gallus domesticus*; Horn, 2004; Jackson et al., 2008), and sleep has been implicated in song learning in zebra finches (*Taeniopygia guttata*, reviewed in Margoliash and Schmidt, 2010). However, the role of sleep in spatial memory consolidation in birds has not yet been examined (Rattenborg et al., 2011) and the interaction with differences in early nutrition and sleep has not been investigated.

Our aim was to test whether a moderate deficit in nutritional condition at the nestling stage has negative or positive long-term effects on a spatial memory task in feral pigeons (*Columba livia*). To test for the impact of the time of learning, and therefore for the influence of sleep and wakefulness, learning took place either in the morning or evening. Based on previous studies of pigeons, the amount of sleep at night is higher than during the day (Martinez-Gonzalez et al., 2008; Tobler and Borbély, 1988; Walker and Berger, 1972). The memory consolidation period consisted of a 24 h period and differed only in the sequence of light and dark phases. We used a food treatment shown to not induce differences in fledging success (Costantini, 2010). Pigeons with nestlings received either a low- or high-quality diet. After fledging, all offspring received the same high-quality food and they were tested for spatial memory performance at an age of 6 months.

MATERIALS AND METHODS

Food treatments during growth

In January 2010, we captured 120 pigeons (60 males, 60 females) in three locations in Paris and assigned them randomly to outdoor aviaries (each aviary contained six males and six females) measuring 2×2×3 m for breeding at the biological station 'Foljuif' (CEREEP-Ecotron Ile-de-France, UMS 3194 ENS CNRS, Saint-Pierre-les-Nemours, France). Half of the parents were fed *ad libitum* with a high protein and lipid diet composed of mixed corn, wheat and peas (hereafter referred to as high-quality diet). The other half of the pigeons were fed each 30 g wheat per day, which corresponds to a basal food quantity to maintain domestic pigeons (Hawkins et al., 2001); this diet is less rich in proteins and lipids (hereafter referred to as low-quality diet). The high- and low-quality food treatments consisted, respectively, of 15.1 and 12.5% protein, 3.2 and 1.9% fat, 6.3 and 2.0% fibre and 61.6 and 60.2% carbohydrates. Previous studies have shown that such differences between low- and high-quality diets are large enough to induce differential growth (Jacquin et al., 2012) and differences in oxidative stress levels in young pigeons, but fledging success remains the same in both food treatments (Costantini, 2010). The food treatment might have had an impact on prenatal development (Ismail et al., 2013). Because the parents were feeding the young with the different quality of food, we cannot rule out the possibility that differences in parental care affected the development of the young. Pigeons feed nestlings with crop milk until approximately day 12 post-hatching, and they may be able to adjust the composition of their crop milk (Vandeputte-Poma, 1980). Although structural body size was not affected by food treatment, as shown by tarsus length at the age of 6 months [two-way ANOVA with tarsus size as the dependent variable and sex and treatment as independent variables, n=29, food treatment (low-quality food): $F_{1,9.18}$=2.30, estimate=−0.58±0.38, P=0.14; sex (male): $F_{1,8.30}$=2.08, estimate=0.55±0.38, P=0.16], offspring fed with low-quality food tended to be lighter in body mass at the age of 6 months than those raised with high-quality food [two-way ANOVA with body mass as the dependent variable and sex and food treatment as independent variables, n=29, food treatment (low-quality food): $F_{1,3246}$=3.65, estimate=−10.90±5.70, P=0.07; sex (male): $F_{1,1756}$=1.98, estimate=8.02±5.70, P=0.17]. This suggests that the parents were not able to fully compensate for the dietary deficiency through adjusting their crop milk composition or other measures of parental care.

Pigeons laid eggs approximately 2 months after the start of the food treatment. As part of another study (Ismail et al., 2013), the eggs were cross-fostered immediately after clutch completion to nests with similar laying dates (±1 day). Therefore, offspring differed in pre- and post-hatching food treatment. The two food treatments were given from the pre-breeding period until the offspring fledged at an age of 30 days. All birds were provided with mineral grit and vitamin-supplemented water. In 2010, 88 offspring fledged (46 males, 42 females; from 60 breeding pairs) and we used 29 unrelated offspring in the memory experiments conducted from January to March 2011. Of these 29 birds, 10 birds had experienced the 'pre-hatching low-quality food treatment' and 'post-hatching high-quality food treatment'; three birds received the 'pre- and post-hatching low-quality food treatments'; 12 birds received the 'pre-hatching high-quality food treatment' and 'post-hatching low-quality food treatment'; and four birds received the 'pre- and post-hatching high-quality food treatments'. In the present study, we considered only the 'post-hatching food treatment' as this determines the environment of the growing nestlings. Furthermore, when adding the 'pre-hatching food treatment' into the model, this factor was not significant and did not explain any part of the variation of the memory performance (see Table S1). For this reason, we did not include it as fixed effect into the analyses.

After fledging, at an age of 34 days, all young were moved to aviaries consisting of a random group of 10–12 birds of the two post-hatching food treatments and they were all fed *ad libitum* with the high-quality diet until memory testing began at an age of 6 months. After this experiment, at the age of 1 year, birds raised on the low-quality post-hatching food treatment were significantly lighter in body mass compared with conspecifics raised with the high-quality food treatment [two-way ANOVA with body mass as the dependent variable and sex and treatment as independent variables, food treatment (low-quality food): $F_{1,3133}$=5.77, estimate=−11.46±4.77, P=0.02; sex (male): $F_{1,3760}$=6.93, estimate=12.60±4.79, P=0.01].

Memory test

We tested 15 unrelated pigeons (nine males, six females) raised post-hatching in the low-quality food treatment and 14 unrelated birds (six males, seven females, one unknown) from the high-quality food treatment. Birds were housed in groups of four to six individuals from both treatment groups during the duration of the experiments. Pigeons were habituated to the experimental outdoor aviary (2×2×3 m) for several weeks and trained to remove an opaque plastic lid from a food bowl. The experimental aviary was similarly structured as the outdoor aviaries, with a transparent roof, one side closed by a wall and one side closed with a plastic cover (Fig. 1A). The front and one side of the aviary consisted of wire-mesh and allowed a view of the landscape around the aviary without giving visual access to other experimental pigeons. Birds stayed in acoustic contact with other pigeons. Two days before the start of the experiment, we began to mildly food-deprive the pigeons to increase their motivation to search for food in the memory test. Birds were fed individually (in transport boxes into which they were

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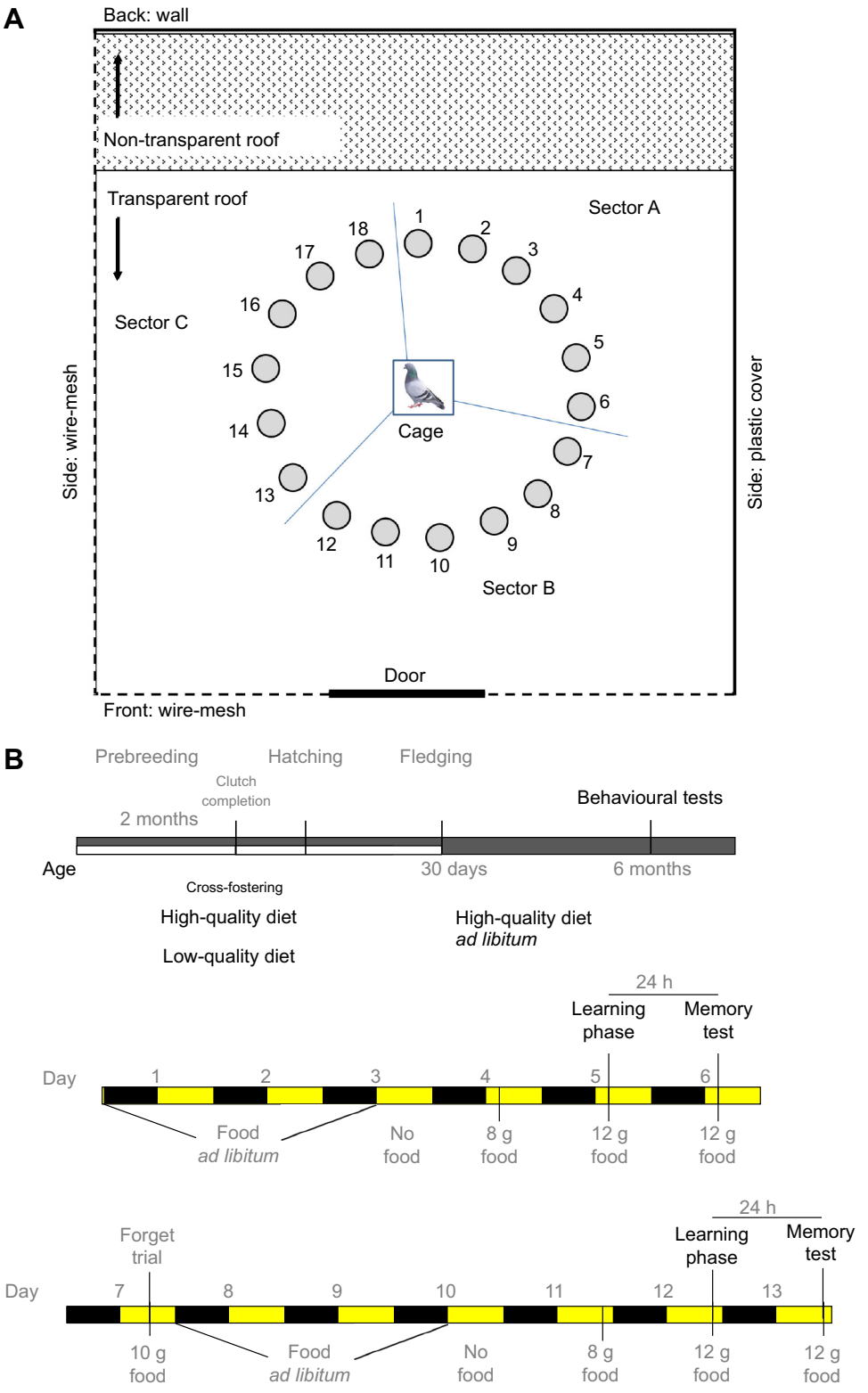

Fig. 1. Experimental setup and schedule of a spatial memory test using pigeons raised with low- or high-quality food. (A) Experimental setup of the spatial memory test. The aviary had wire-mesh in the front and at one side, a plastic cover at another side and a wall at the back, as well as a transparent roof. Pigeons were released from the centre of a circle with 18 food bowls, had to learn one rewarded food location and were tested 24 h later. (B) Experimental schedule showing food treatments during growth, and learning and testing phases in a spatial memory test with one session of learning in the morning and one in the evening and testing 24 h later. Half of the pigeons received high-quality diet and the other half low-quality diet from pre-breeding until offspring fledged, after which all offspring were fed with the high-quality diet until behavioural tests occurred at 6 months of age. Birds were food-deprived before the test to increase motivation to search for food. The sequence of the time of learning was randomized for each bird.

trained to go by themselves) to control the food intake of each bird, and each bird received a reduced amount of food before the experiment (Fig. 1B). Pigeons lost 2.2±0.32% (mean±s.e.) of their mean body mass from the beginning of the food deprivation until the end of the memory tests (paired *t*-test: t_{28}=5.28, P<0.0001). The loss in body mass did not differ between pigeons raised with a low- or high-quality diet (Student's *t*-test: t_{26}=0.83, P=0.41).

During the learning session, we trained the pigeons to find the food location. Each pigeon had to learn in which location, out of 18 positions, food was hidden (see Fig. 1 and Movie 1). We used 18 positions, ensuring that the memory test would be sufficiently difficult to detect between-individual variation in memory performance. This was necessary, because in preliminary experiments with other pigeons, individuals made almost no

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errors when tested with fewer locations (six or nine locations). One randomly chosen bowl contained high-quality food and the others were empty. The 18 bowls were positioned in a circle of 150 cm diameter and each pigeon was released into the centre of the circle. During the learning session with uncovered bowls, pigeons appeared to be motivated to perform the task, as they moved directly to the bowl with food in 5.0±1.1 s and ate all of the grains. Immediately after the food had been consumed, the bird was removed from the aviary and 2 min later it was released again into the experimental aviary, this time with all bowls covered with lids. This was done to ensure that the pigeon searched in the same location for food as when the bowls were uncovered. The same bowl as in the previous session contained food. The bird was allowed to find the food by removing the lids and each bird found the food rapidly (within 27.8±3.7 s). We recorded the time it took each bird to reach and touch the first lid and compared this latency with that during the memory test to compare the motivation to find the food. Additionally, we tested whether pigeons from both post-hatching food treatments differed in the number of errors made during learning. After the bird found and ate the food, we brought it back to the home aviary. To minimize stress during transport between the home aviary and the experimental arena, a distance of approximately 5 m, the birds were trained to enter a small cage. The cage was placed in the middle of the experimental aviary and the birds were released untouched on the ground via a remote mechanism that lifted the cage, but not the cage floor (see Movie 1). The cage lifted up completely, so that the pigeon had 360 deg of free motion when released. With this method the stress level was kept at a minimum, as pigeons did not need to be captured and handled. After the experiment, we placed a small amount of food inside the cage to motivate the pigeon to go back into it for transportation back to the home aviary.

Twenty-four hours later, we tested whether the pigeons remembered the specific position in which food had been located during the learning session (memory test). We counted the number of lids removed until the food was found. The number of errors made before finding the correct location was used as a measure of memory performance. Additionally, we recorded the time each bird needed from the start of testing until it found the rewarded bowl. Often in memory tests the correct location is not rewarded (i.e. no food is placed in the correct bowl) to exclude olfactory cues, but as we wanted to keep the birds motivated for a second trial, we placed the food during the test phase in the covered bowl. Similar foraging tasks are often used to assess spatial memory performance in birds (e.g. Cristol et al., 2003).

Two memory tests per individual (except one individual that died 4 days after the first memory test for unknown reasons) were conducted to study the impact of the time of learning on memory performance, once in the morning (AM session) starting 30 min after sunrise, and once in the evening (PM session) ending 30 min before sunset. The order of the morning and evening tests was randomly chosen (14 birds were first tested in the morning and 15 first in the evening, balanced for the food treatment groups). Two adjacent aviaries with birds of both food treatments were tested in parallel and one started with the morning session, whereas the other aviary started with the evening session; the learning time was chosen randomly. We included a 24 h period after learning until testing to control for differences in activity levels between light and dark phases. With this setup, each memory consolidation phase includes the same amount of activity and sleep, with the only difference being the sequence of sleep and wakefulness (Jackson et al., 2008). We expected the birds to spend most of the time asleep after learning in the evening, whereas after learning in the morning we expected the birds to spend a large amount of time awake and active, as shown in previous studies using electroencephalograms. In these studies, captive pigeons spent 79.8–81.6% of the time asleep (non-REM+REM sleep) during the dark phase and spent 37.7–51.3% of the time asleep during the light phase, indicating a diurnal activity pattern (Martinez-Gonzalez et al., 2008; Tobler and Borbély, 1988).

Before the second trial, all pigeons went through a ‘forget’ trial to prevent them from remembering the food location from the first experiment. To this end, we placed food in all 18 open bowls and each pigeon was allowed to eat all the food. This forget trial proved to be adequate, as in the second learning session birds did not preferentially visit the bowl where food had been placed during the first memory test (only one out of 28 birds visited the same bowl first). After the forget trial, pigeons were kept in their home aviary for 2 days, during which they were fed *ad libitum*. Two days before conducting the second test, we mildly food-deprived the pigeons again. In the second memory test, we placed food in a randomly chosen bowl other than the one used in the first memory test (this was done for all birds, but one pigeon got the same food bowl rewarded as in the first test owing to experimenter error).

Ethical approval

This research adhered to the National Institutes of Health standards regarding the care and use of animals in research. All protocols were approved by the French Veterinary Department of Seine-et-Marne (authorization no. 77-05).

Statistical procedure

Because some locations may be easier to learn than others, depending on where the external cues such as a wall, a tree or the entrance door of the aviary are located, we pooled bowls 1 to 6 in a sector called A, bowls 7 to 12 in sector B and bowls 13 to 18 in sector C. We aimed for three sectors and defined first the section opposite of the door as bowl 1 and then counted clockwise. We used this approach rather than comparing the performance at individual bowls, because the repetitions per bowl were too low for statistical comparisons. The sector thus described the spatial location of the food reward and was added as a variable into the models. To control for possible motivational differences when learning in the morning or evening, we compared the time from the start of a trial until the bird found the food during the learning phase (with open bowls) using a linear mixed-model ANOVA [restricted maximum likelihood (REML) with Kenward–Roger correction]. Motivation was set as the dependent variable, bird identity as a random variable, and food treatment, time of day, sector and second-order interactions were included as response variables. We used linear mixed models with bird identity as a random variable, because each individual was tested twice. We included the number of errors in the memory test as a dependent variable (linear mixed-model ANOVA, REML with Kenward–Roger correction), and time of learning (AM or PM), sector with the food reward (A, B, or C), food treatment during growth, trial number (1 or 2), as well as second-order interactions as response variables. In preliminary analyses, sex was not associated with memory, and hence we did not include this variable in the final models. Additionally, we used the time (log-transformed) of each bird from the start of the memory test until it found the covered, rewarded bowl as a dependent variable to test for an influence of the speed of solving the task. Non-significant terms of the full model were stepwise backward eliminated based on Akaike’s information criterion (AIC; Burnham and Anderson,

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2004), starting with statistical interactions, to find the best-fitting models. Models were compared and we chose the one with the lowest AIC, but still including all significant terms. We conducted *post hoc* analyses when statistically significant differences were found. The residuals of all models were checked for normality. Means are quoted ±s.e. Tests are two-tailed and *P*-values smaller than 0.05 are considered significant.

RESULTS

All birds showed high motivation to learn the food location as they touched the first lid during learning within 2.0±3.7 s and during testing within 2.2±4.3 s, a difference that was not significantly different (paired *t*-test: t_{56}=0.38, *P*=0.7). They needed on average 31.0±4.3 s to find the food during the memory test. Motivation during learning, measured as the time it took each bird to reach the open bowl where food was located, did not differ significantly between post-hatching food treatment groups, sectors where food was located (A, B or C), and whether learning occurred in the morning or evening (linear mixed-model ANOVA: food treatment: $F_{1,24.99}$=2.79, *P*=0.11; time of learning: $F_{1,19.71}$=2.70, *P*=0.12; sectors: $F_{1,37.52}$=0.16, *P*=0.86; all interactions were not significant). Pigeons from both food treatments did not differ in the number of errors made during learning (Student's *t*-test: t_{54}=−0.54, *P*=0.59).

The number of lids removed before finding food 24 h after the learning phase was associated with the post-hatching food treatment during growth, the sector where food was hidden, and the interaction between treatment and sector (food treatment: $F_{1,21.27}$=13.85, *P*=0.001; sector: $F_{2,45.8}$=12.49, *P*<0.0001; interaction: $F_{2,45.46}$=7.78, *P*=0.001; Table 1, Fig. 2A). Pigeons raised on a low-quality diet made significantly fewer errors compared with pigeons raised on a high-quality diet (Fig. 3A). The overall effect of food treatment was primarily due to significantly more errors in sector A (mean number of errors was 10.59), with individuals raised with high-quality food making twice as many errors as birds raised with low-quality food (mean number of errors: 14.27 versus 6.91, Tukey's HSD, *P*=0.0004; Fig. 2A). In the two other sectors, where the number of errors was lower (mean number of errors in sectors B and C: 7.76 and 5.14, respectively), we found no significant association between the number of errors and food treatment (Tukey's HSD, sector B: *P*=0.88, sector C: *P*=0.36; Fig. 2A). Mean body mass or the percentage of body mass loss during the tests did not have an impact on memory performance (body mass: $F_{1,19.26}$=0.80, *P*=0.38; % loss in body mass: $F_{1,29.15}$=0.38, *P*=0.92). The time needed to reach the rewarded bowl during learning was not related to the number of errors (for learning with open bowls: $F_{1,40.63}$=1.26, *P*=0.27; for learning with closed bowls: $F_{1,45.15}$=0.90, *P*=0.35).

Table 1. Linear mixed-model ANOVA for the number of errors made during memory tests of pigeons raised on low- and high-quality diets and for which the learning session occurred either in the morning or in the evening

R^2=0.44	Testing errors	
Parameter	*F*	*P*
Time of learning (morning or evening)	$F_{1,25.04}$=3.09	0.09
Sector (A, B or C)	$F_{2,45.8}$=12.49	<0.0001
Food treatment (low or high quality diet)	$F_{1,21.27}$=13.85	0.001
Trial number (first or second)	$F_{1,24.78}$=1.07	0.31
Sector×Food treatment	$F_{2,45.46}$=7.78	0.001
Time of learning×Trial number	$F_{1,21.52}$=4.25	0.05
Time of learning×Food treatment×Trial number	$F_{1,21.54}$=14.98	0.0009

Individual identity was a random effect.

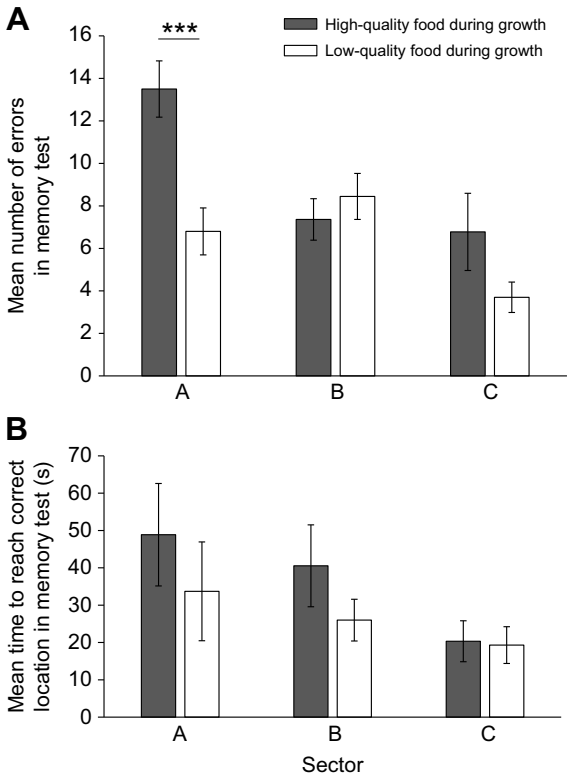

Fig. 2. The performance in a spatial memory test of pigeons raised with low- or high-quality food during growth in the three parts of an experimental area. (A) Mean (±s.e.m.) number of errors during memory tests performed by feral pigeons when the reward was placed in the three different sectors of the experimental area. Each sector contained six food positions. Pigeons raised with high-quality food (grey bars) during growth made more errors in sector A of a memory test compared with pigeons raised on a low-quality diet (white bars) (Tukey's HSD, ***P=0.0004). There was no difference in the mean number of errors in sectors B and C (sector B and C: P>0.3, linear mixed-model ANOVA: sector×food treatment, P=0.001). Sample sizes in the three sectors for the high- and low-quality food treatments were: sector A, 8 and 10; sector B, 11 and 9; sector C, 9 and 10 birds, respectively. (B) Mean (±s.e.m.) time to reach the correct location during memory tests performed by feral pigeons when the reward was placed in the three different sectors of the experimental area. Pigeons raised with high- and low-quality food during growth did not differ in the time needed to reach the correct location, but birds were faster to find the rewarded location when food was located in sector C compared with sector A or B (Tukey's HSD, sector A versus B: P=0.5, sector A versus C: P=0.007; sector B versus C: P=0.09) (linear mixed-model ANOVA, sector: P=0.009). Sample sizes are as in A.

Overall, birds performed similarly in the first and second trials (trial number: $F_{1,24.78}$=1.07, *P*=0.31; Table 1). Pigeons differed in the number of errors made at testing, depending on the food treatment in interaction with the time of learning and trial number (time of learning×food treatment×trial number: $F_{1,21.54}$=14.98, *P*=0.0009; Table 1). A *post hoc* analysis revealed that during the first trial, birds that had been raised on a low-quality diet and were learning in the evening performed significantly better (mean number of errors 4.39) compared with birds raised on a high-quality diet and learning in the evening (mean number of errors 10.31, Tukey's HSD, *P*=0.0005; Fig. 3B). During the first trial, birds learning in the morning did not differ in their memory performance between food treatments (Tukey's HSD, *P*=1.00; Fig. 3B). In the second trial, pigeons raised on a high-quality diet when learning in the morning made more errors at testing (mean number of errors 12.88) compared with when learning in the

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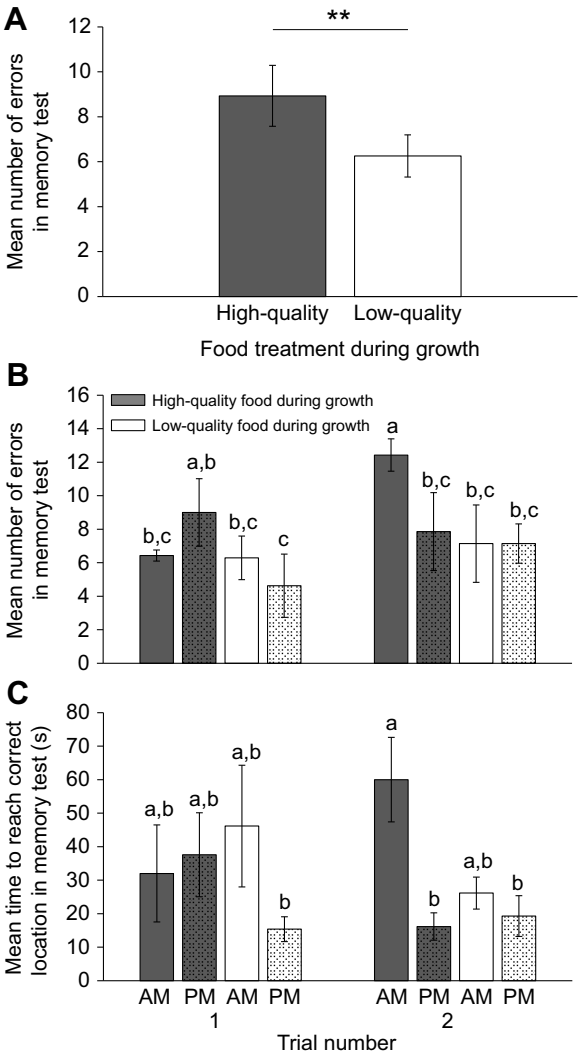

Fig. 3. The performance in a memory task of pigeons raised with low- or high-quality food during growth. (A) Mean (±s.e.m.) number of errors of feral pigeons during memory tests when learning had occurred either in the morning (AM) or in the evening (PM) with testing 24 h later. Pigeons were raised with a high- (n=14, grey bars) or low-quality diet (n=15, white bars) and tested twice. Pigeons raised on low-quality food made fewer errors in a memory task compared with pigeons raised on high-quality food (mixed-model ANOVA: food treatment, ***P=0.001). (B) Mean (±s.e.m.) number of errors of feral pigeons during two memory trials (on day 6 and day 13) when learning had occurred either in the morning (AM) or in the evening (PM, dark pattern) with testing 24 h later. Pigeons were raised with a high- (grey bars) or low-quality diet (white bars) and had been randomly assigned to start with either a morning or evening trial. Pigeons raised with a high-quality diet made significantly more errors when learning had occurred in the morning in their second test compared with all other treatments and learning times (linear mixed-model ANOVA: time of learning×food treatment×trial number, P=0.0009). (C) Mean (±s.e.m.) time to reach the correct food location during two memory trials (on day 6 and day 13) when learning had occurred either in the morning (AM) or in the evening (PM, dark pattern) with testing 24 h later. Pigeons were raised with a high- (grey bars) or low-quality diet (white bars) and had been randomly assigned to start with either a morning or evening trial. Pigeons raised with a high-quality diet took significantly longer to reach the correct location in a spatial memory test when learning had occurred in the morning in their second test compared with all other treatments and learning times (linear mixed-model ANOVA: time of learning×food treatment×trial number, P=0.008). For B and C, the sample size for each test condition was seven; for the group tested in the evening in trial 1 it was eight birds. Different letters above columns indicate significant differences.

Table 2. Linear mixed-model ANOVA for the time each bird needed to find the correct food location during the memory test of pigeons raised on low- and high-quality diets and for which the learning session occurred either in the morning or in the evening

R^2=0.49	Time to find correct location during test	
Parameter	F	P
Time of learning (morning or evening)	$F_{1,25.98}$=9.81	0.004
Sector (A, B or C)	$F_{2,46.08}$=5.18	0.009
Food treatment (low or high quality diet)	$F_{1,23.21}$=1.26	0.27
Trial number (first or second)	$F_{1,25.45}$=0.10	0.76
Sector×Food treatment	$F_{2,46.56}$=1.21	0.30
Time of learning×Trial number	$F_{1,23.46}$=2.72	0.11
Time of learning×Food treatment×Trial number	$F_{1,23.48}$=8.25	0.008

Individual identity was a random effect.

evening (mean number of errors 4.39, Tukey's HSD, P=0.002; Fig. 3B). They performed worse compared with pigeons raised on a low-quality diet and learning in the morning (mean number of errors first test 7.42, second test 6.97; Tukey's HSD, P=0.009 and P=0.0005, respectively) or evening for both trials (mean number of errors first test 4.39, second test 6.77; Tukey's HSD, P=0.0001 and P=0.003, respectively; Fig. 3B). Pigeons raised on a high-quality diet made more errors in the second trial (mean number of errors 12.88) compared with the first trial when learning in the morning (mean number of errors 7.28, Tukey's HSD, P=0.006), but they did not differ between trials when learning in the evening (Tukey's HSD, P=0.22; Fig. 3B). Birds raised on a low-quality diet did not differ in their performance between trials (Tukey's HSD, P>0.4; Fig. 3B).

The number of errors in the memory test was positively correlated with the time needed to reach the correct location (Spearman correlation, r_S=0.67, P<0.0001). The time needed to reach the rewarded food bowl during memory tests was significantly related to the time of learning and to the sector in which the reward was located (linear mixed-model ANOVA: time of learning: $F_{1,25.98}$=9.81, P=0.004; sector: $F_{2,46.08}$=5.18, P=0.009; Table 2, Fig. 2B). Pigeons learning in the morning took longer to find the correct bowl than when learning in the evening (on average 41±7 s versus 22±4 s), and they needed the same amount of time when the food location was in sector A or B (on average 40±9 and 34±6 s, respectively; Tukey's HSD, P=0.5), but were faster to find the food in sector C (20±3 s; Tukey's HSD, sector A versus C: P=0.007; sector B versus C: P=0.09; Fig. 2B). Food treatment did not influence the speed of solving the memory task (food treatment: $F_{1,23.21}$=1.26, P=0.27), but the interaction between time of learning, trial number and food treatment was significant (time of learning×food treatment×trial number: $F_{1,23.48}$=8.25, P=0.008; Table 2, Fig. 3C). Pigeons raised on high-quality food took significantly longer to reach the correct location in trial 2 when learning in the morning compared with learning in the evening (mean latency 60±12 s versus 16±4 s, Tukey's HSD, P=0.002) and compared with pigeons raised on a low-quality food that learned in the evening for both trials (mean latency trial 1: 15±4 s, Tukey's HSD, P=0.01; mean latency trial 2: 19±6 s, Tukey's HSD, P=0.04; Fig. 3C).

DISCUSSION

Pigeons fed with low-quality food during growth made fewer errors and were faster at locating the food during the memory tests than pigeons fed with high-quality food. This shows that a moderate deficit in nutritional condition at the nestling stage has positive

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long-term effects in a spatial memory task. This further suggests that pigeons experiencing a deficit in the nutritive food value when they are young put more effort into memorizing the location in which food is located later in life.

The memory performance differed depending on the sector of the aviary. Testing took place in an outdoor aviary where spatial cues were non-randomly distributed. Therefore, it might be that some feeding locations were easier to remember (i.e. sectors B and C) than others (i.e. sector A), because pigeons rely on environmental cues when remembering food patches (Spetch and Edwards, 1988). Pigeons from the low-quality food treatment were significantly better at remembering the location in which food had been located in sector A compared with sector B or C than pigeons from the high-quality food treatment. Pigeons are known to use olfaction for navigation (Gagliardo et al., 2011), but it is unlikely that differences in olfaction led to our results. If birds raised with the low-quality diet invested more effort in finding the food using olfaction, they would have outperformed pigeons raised with high-quality food in all three sectors. Because birds did not differ in the number of errors in the two other sectors of the experimental setup, we conclude that olfaction did not influence our findings. Furthermore, pigeons of both food treatments did not differ in the number of errors made during learning. Our result also cannot be explained by pigeons from the high-quality treatment being distracted or avoiding sector A owing to neophobia, because during learning, the time to find the food did not differ between treatments or sectors. In fact, the perceived risk of predation may have contributed to the differences in the number of errors in sector A between pigeons raised on low- and high-quality food. This is the sector in which the birds had their back oriented towards the door and the side of the aviary with wire-mesh (Fig. 1). It might be that they perceived potential threats as more likely to come from the area opposite to sector A and, therefore, anti-predator vigilance may have distracted them when searching for the food. It has been shown that in captivity, pigeons sleeping with one eye closed have this eye oriented towards where the risk of predation is the lowest, leaving the open eye oriented towards where predators are most likely to emerge (Rattenborg et al., 2001). Furthermore, foraging individuals were shown to be slower in reaction to a predator compared with when not foraging, indicating that individuals are indeed less attentive at watching whether a predator is around while foraging (Bohórquez-Herrera et al., 2013). This appears to be particularly the case for birds raised on low-quality food, which may invest less in vigilance and more in remembering the place where food is hidden within a risky food patch. Nevertheless, we cannot exclude alternative interpretations to explain differences in learning between areas, such as the sunlight or other environmental cues that are related to orientation (Bingman and Jones, 1994; Gagliardo et al., 1996). It had been shown that pigeons can rely on the sun compass when learning a spatial memory test (Gagliardo et al., 1996). Therefore, it might be that differences in the ability to use the sun compass could have contributed to our result. Birds that were raised on the low-quality food treatment might have been better able to use the sun compass to memorize the position of the food, which might have helped them to find the food with fewer mistakes and in shorter time. However, this might further indicate that specific brain areas could have been favoured during development of the individuals from the low-quality food treatment. However, we did not find better memory abilities of the birds from the low-quality food treatment in the two other areas of the memory task, as would be expected if the pigeons are using the sun compass to remember the placement of the food.

Interestingly, pigeons raised with a high-quality diet made significantly more errors and took approximately 45 s longer to find the location in which food had been hidden when learning had occurred in the morning in their second test compared with all other treatments and learning times. This suggests that it is more difficult to remember where a food patch is located if the learning phase takes place in the early morning before pigeons are distracted by their daily activities compared with when learning takes place just before sleeping at night. This difficulty appears to be apparent only in pigeons fed with high-quality food, further indicating that pigeons from the low-quality food treatment invest more effort in learning where food is located. Even though both learning groups had the same amount of time to be dedicated to sleep, the birds learning in the evening had less interference after learning owing to the close temporal proximity of evening training to the major nocturnal sleep period (Talamini et al., 2008). However, pigeons raised on a high-quality diet did not differ in performance from birds raised on a low-quality diet when learning took place in the morning for the first trial. It might be that the second trial is perceived as being more difficult, as birds need to focus on finding the correct location of learning phase two and not the location of learning phase one. Therefore, differences in memory performance depending on the time of learning might arise only when the task is sufficiently difficult. Indeed, the performance of birds raised on low- and high-quality diets did not differ during learning, when the retention interval was short (a few minutes) and therefore the task presumably easier than after the retention interval of 24 h. It is plausible that pigeons fed with low-quality food may differentially invest in sleep than pigeons fed with high-quality food, which could explain the different performances of birds from both food treatments. This is what was observed in rats, in which malnourished individuals spent 20% more time in non-REM sleep and 61% less time in REM sleep compared with well-nourished individuals (Datta et al., 2000). Studies using electroencephalogram to study avian sleep architecture are needed to test for an effect of different nutrition during development on sleep in adult birds. Our results do not show a strong improvement in memory performance during all trials when learning took place in the evening, but they suggest that sleep can improve memory only under specific conditions (when the task is sufficiently difficult).

Overall, foraging is a costly activity, especially when the perceived risk of predation is increased (Lemon, 1991). Because memory consolidation increases the costs of enhanced neural processing power and maintenance of neural structures (Isler and van Schaik, 2006), foraging and memory performance might be traded off differently with other traits such as immunity or reproduction in pigeons raised on low- and high-quality diets. Individuals raised on a low-quality diet might have invested more resources into key brain areas important for foraging to improve cognitive performance (Nowicki and Searcy, 2005). This investment might have come with costs such as reduced life span or reproductive output, which we did not consider. Previous studies in other bird species found that a deficit in the nutritive value of the food given to nestlings impaired cognitive processes at adulthood (Arnold et al., 2007; Bonaparte et al., 2011; Pravosudov et al., 2005). Another study in zebra finches found that post-fledging nutritional stress enhanced performance in an associative learning task (Kriengwatana et al., 2015). However, at the same time, the treatment impaired performance in a hippocampus-dependent spatial memory task (Kriengwatana et al., 2015). Understanding the discrepancy between studies, with some finding a reduction and others an enhancing effect of low-quality diets on memory performance, requires an experimental approach where animals

are fed with a range of diets from very high to low nutritive value. Experiments using nutritional stress in natural ranges should test species-specific ecologically important traits and long-term consequences (Drummond and Ancona, 2015). Furthermore, more studies on memory cues are needed to understand why some locations in which food was hidden were more difficult to memorize. Therefore, when testing spatial learning, the environment needs to be taken into account, and especially behavioural differences in different parts of the experimental setup should be carefully investigated. Whatever the exact mechanism underlying our results, our study shows that pigeons can display improved spatial memory abilities as a response to limit the long-lasting effects of poor rearing conditions.

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Author contributions
A.R., C.M.-H., J.G., M.F.S. and N.C.R. designed the study. L.J. and M.F.S. conducted the experiments. A.R. and M.F.S. performed the statistical analyses. A.R., M.F.S. and N.C.R. wrote the paper. A.R., J.G. and N.C.R. contributed equally. All authors discussed the results and commented on the manuscript. All authors read and approved the final manuscript.

Competing interests
The authors declare no competing or financial interests.

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References
Arnold, K. E., Ramsay, S. L., Donaldson, C. and Adam, A. (2007). Parental prey selection affects risk-taking behaviour and spatial learning in avian offspring. *Proc R. Soc. B Biol. Sci.* **274**, 2563-2569.
Bingman, V. P. and Jones, T. J. (1994). Sun compass-based spatial learning impaired in homing pigeons with hippocampal lesions. *J. Neurosci.* **14**, 6687-6694.
Bohórquez-Herrera, J., Kawano, S. M. and Domenici, P. (2013). Foraging behavior delays mechanically-stimulated escape responses in fish. *Integr. Comp. Biol.* **53**, 780-786.
Bonaparte, K. M., Riffle-Yokoi, C. and Burley, N. T. (2011). Getting a head start: diet, sub-adult growth, and associative learning in a seed-eating passerine. *PLoS ONE* **6**, e23775.
Boyce, R., Glasgow, S. D., Williams, S. and Adamantidis, A. (2016). Causal evidence for the role of REM sleep theta rhythm in contextual memory consolidation. *Science* **352**, 812-816.
Brawn, T. P. and Margoliash, D. (2014). A bird's eye view of sleep-dependent memory consolidation. In *Sleep, Neuronal Plasticity and Brain Function* (ed. P. Meerlo, R. M. Benca, T. Abel), pp. 207-237. Berlin; Heidelberg: Springer.
Brawn, T. P., Nusbaum, H. C. and Margoliash, D. (2013). Sleep consolidation of interfering auditory memories in starlings. *Psychol. Sci.* **24**, 439-447.
Burnham, K. P. and Anderson, D. R. (2004). Multimodel inference understanding AIC and BIC in model selection. *Sociol. Methods Res.* **33**, 261-304.
Costantini, D. (2010). Effects of diet quality on growth pattern, serum oxidative status, and corticosterone in pigeons (*Columba livia*). *Can. J. Zool.* **88**, 795-802.
Cristol, D. A., Reynolds, E. B., Leclerc, J. E., Donner, A. H., Farabaugh, C. S. and Ziegenfus, C. W. S. (2003). Migratory dark-eyed juncos, *Junco hyemalis*, have better spatial memory and denser hippocampal neurons than nonmigratory conspecifics. *Anim. Behav.* **66**, 317-328.
Datta, S., Patterson, E. H., Vincitore, M., Tonkiss, J., Morgane, P. J. and Galler, J. R. (2000). Prenatal protein malnourished rats show changes in sleep/wake behavior as adults. *J. Sleep Res.* **9**, 71-79.
de Souza, A. S., Rocha, M. S. and Tavares do Carmo, M. G. (2012). Effects of a normolipidic diet containing trans fatty acids during perinatal period on the growth, hippocampus fatty acid profile, and memory of young rats according to sex. *Nutrition* **28**, 458-464.
Diekelmann, S. and Born, J. (2010). The memory function of sleep. *Nat. Rev. Neurosci.* **11**, 114-126.
Diekelmann, S., Wilhelm, I. and Born, J. (2009). The whats and whens of sleep-dependent memory consolidation. *Sleep Med. Rev.* **13**, 309-321.
Drummond, H. and Ancona, S. (2015). Observational field studies reveal wild birds responding to early-life stresses with resilience, plasticity, and intergenerational effects. *Auk* **132**, 563-576.
Gagliardo, A., Mazzotto, M. and Bingman, V. P. (1996). Hippocampal lesion effects on learning strategies in homing pigeons. *Proc. R. Soc. B Biol. Sci.* **263**, 529-534.
Gagliardo, A., Ioalè, P., Filannino, C. and Wikelski, M. (2011). Homing pigeons only navigate in air with intact environmental odours: a test of the olfactory activation hypothesis with GPS data loggers. *PLoS ONE* **6**, e22385.
Genzel, L., Quack, A., Jäger, E., Konrad, B., Steiger, A. and Dresler, M. (2012). Complex motor sequence skills profit from sleep. *Neuropsychobiology* **66**, 237-243.
Gyger, M., Kolly, D. and Guigoz, Y. (1992). Aging, modulation of food intake and spatial memory: a longitudinal study. *Arch. Gerontol. Geriatr.* **15**, 185-195.
Hagewoud, R., Havekes, R., Novati, A., Keijser, J. N., Van Der Zee, E. A. and Meerlo, P. (2010). Sleep deprivation impairs spatial working memory and reduces hippocampal AMPA receptor phosphorylation. *J. Sleep Res.* **19**, 280-288.
Hawkins, P., Morton, D. B., Cameron, D., Cuthill, I., Francis, R., Freire, R., Gosler, A., Healy, S., Hudson, A., Inglis, I., et al. (2001). Laboratory birds: refinements in husbandry and procedures. *Lab. Anim.* **35** Suppl. 1, 97-103.
Hector, K. L. and Nakagawa, S. (2012). Quantitative analysis of compensatory and catch-up growth in diverse taxa. *J. Anim. Ecol.* **81**, 583-593.
Horn, G. (2004). Pathways of the past: the imprint of memory. *Nat. Rev. Neurosci.* **5**, 108-120.
Huchard, E., English, S., Bell, M. B. V., Thavarajah, N. and Clutton-Brock, T. (2016). Competitive growth in a cooperative mammal. *Nature* **533**, 532-534.
Isler, K. and van Schaik, C. (2006). Costs of encephalization: the energy trade-off hypothesis tested on birds. *J. Hum. Evol.* **51**, 228-243.
Ismail, A., Jacquin, L., Haussy, C., Legoupi, J., Perret, S. and Gasparini, J. (2013). Food availability and maternal immunization affect transfer and persistence of maternal antibodies in nestling pigeons. *PLoS ONE* **8**, e79942.
Jackson, C., McCabe, B. J., Nicol, A. U., Grout, A. S., Brown, M. W. and Horn, G. (2008). Dynamics of a memory trace: effects of sleep on consolidation. *Curr. Biol.* **18**, 393-400.
Jacquin, L., Récapet, C., Bouche, P., Leboucher, G. and Gasparini, J. (2012). Melanin-based coloration reflects alternative strategies to cope with food limitation in pigeons. *Behav. Ecol.* **23**, 907-915.
Kaptan, Z., Akgün-Dar, K., Kapucu, A., Dedeakayoğulları, H., Batu, , Ş. and Üzüm, G. (2015). Long term consequences on spatial learning-memory of low-calorie diet during adolescence in female rats; hippocampal and prefrontal cortex BDNF level, expression of NeuN and cell proliferation in dentate gyrus. *Brain Res.* **1618**, 194-204.
Krause, E. T., Steinfartz, S. and Caspers, B. A. (2011). Poor nutritional conditions during the early larval stage reduce risk-taking activities of fire salamander larvae (*Salamandra salamandra*). *Ethology* **117**, 416-421.
Kriengwatana, B., Farrell, T. M., Aitken, S. D., Garcia, L. and 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**, 195-218.
Lemon, W. C. (1991). Fitness consequences of foraging behaviour in the zebra finch. *Nature* **352**, 153-155.
Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends Ecol. Evol.* **14**, 343-348.
Lukas, W. D. and Campbell, B. C. (2000). Evolutionary and ecological aspects of early brain malnutrition in humans. *Hum. Nat.* **11**, 1-26.
Margoliash, D. and Schmidt, M. F. (2010). Sleep, off-line processing, and vocal learning. *Brain Language* **115**, 45-58.
Martinez-Gonzalez, D., Lesku, J. A. and Rattenborg, N. C. (2008). Increased EEG spectral power density during sleep following short-term sleep deprivation in pigeons (*Columba livia*): evidence for avian sleep homeostasis. *J. Sleep Res.* **17**, 140-153.
McDevitt, E. A., Duggan, K. A. and Mednick, S. C. (2015). REM sleep rescues learning from interference. *Neurobiol. Learn. Mem.* **122**, 51-62.
Metcalfe, N. B. and Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.* **16**, 254-260.
Monaghan, P. (2008). Early growth conditions, phenotypic development and environmental change. *Philos. Trans. R Soc. B Biol. Sci.* **363**, 1635-1645.
Nowicki, S. Searcy, W. A. (2005). Adaptive priorities in brain development: theoretical comment on Pravosudov et al. (2005). *Behav. Neurosci.* **119**, 1415-1418.
Pravosudov, V. V., Lavenex, P. and Omanska, A. (2005). Nutritional deficits during early development affect hippocampal structure and spatial memory later in life. *Behav. Neurosci.* **119**, 1368-1374.
Ramadan, W., Eschenko, O. and Sara, S. J. (2009). Hippocampal sharp wave/ripples during sleep for consolidation of associative memory. *PLoS ONE* **4**, e6697.
Rasch, B. and Born, J. (2013). About sleep's role in memory. *Physiol. Rev.* **93**, 681-766.

Rattenborg, N. C., Amlaner, C. J. and Lima, S. L. (2001). Unilateral eye closure and interhemispheric EEG asymmetry during sleep in the pigeon (*Columba livia*). *Brain Behav. Evol.* **58**, 323-332.

Rattenborg, N. C., Mandt, B. H., Obermeyer, W. H., Winsauer, P. J., Huber, R., Wikelski, M. and Benca, R. M. (2004). Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *PLoS Biol.* **2**, e212.

Rattenborg, N. C., Martinez-Gonzalez, D., Roth, T. C. and Pravosudov, V. V. (2011). Hippocampal memory consolidation during sleep: a comparison of mammals and birds. *Biol. Rev.* **86**, 658-691.

Romero-Haro, A. A. and Alonso-Alvarez, C. (2015). The level of an intracellular antioxidant during development determines the adult phenotype in a bird species: a potential organizer role for glutathione. *Am. Nat.* **185**, 390-405.

Schew, W. A. and Ricklefs, R. E. (1998). Developmental plasticity. In *Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum* (ed. J. M. Starck and R. E. Ricklefs), pp. 288-304. New York: Oxford University Press.

Spetch, M. L. and Edwards, C. A. (1988). Pigeons', *Columba livia*, use of global and local cues for spatial memory. *Anim. Behav.* **36**, 293-296.

Talamini, L. M., Nieuwenhuis, I. L. C., Takashima, A. and Jensen, O. (2008). Sleep directly following learning benefits consolidation of spatial associative memory. *Learn. Mem.* **15**, 233-237.

Tobler, I. and Borbély, A. A. (1988). Sleep and EEG spectra in the pigeon (*Columba livia*) under baseline conditions and after sleep deprivation. *J. Comp. Physiol. A* **163**, 729-738.

Tucker, M. A., Hirota, Y., Wamsley, E. J., Lau, H., Chaklader, A. and Fishbein, W. (2006). A daytime nap containing solely non-REM sleep enhances declarative but not procedural memory. *Neurobiol. Learn. Mem.* **86**, 241-247.

Vandeputte-Poma, J. (1980). Feeding, growth and metabolism of the pigeon, *Columba livia domestica*: duration and role of crop milk feeding. *J. Comp. Physiol. B* **135**, 97-99.

Van Der Werf, Y. D., Altena, E., Schoonheim, M. M., Sanz-Arigita, E. J., Vis, J. C., De Rijke, W. and Van Someren, E. J. W. (2009). Sleep benefits subsequent hippocampal functioning. *Nat. Neurosci.* **12**, 122-123.

Walker, J. M. and Berger, R. J. (1972). Sleep in the domestic pigeon (*Columba livia*). *Behav. Biol.* **7**, 195-203.