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Organizing effects of adverse early-life condition on body mass, compensatory growth and reproduction: experimental studies in rock pigeons

Bin-Yan Hsu, Cor Dijkstra and Ton G. G. Groothuis

B.-Y. Hsu (<http://orcid.org/0000-0002-3799-0509>) (biyahs@utu.fi), C. Dijkstra and T. G. G. Groothuis, Groningen Inst. for Evolutionary Life Sciences, Univ. of Groningen, the Netherlands. Present address of BYH: Section of Ecology, Dept of Biology, Univ. of Turku, Finland.

Early-life food conditions can have profound impact on adult behavioural performance. In song birds, early-life food conditions affect adult physiology and cognitive performance such as song learning and spatial learning. However, effects on reproductive behaviour other than song, such as visual courtship display, pair formation, and egg laying, which are all important determinants of fitness, received hardly any attention. In this study, rock pigeons *Columba livia* were raised either in a food ad-libitum or at impoverished (quality) and restricted (quantity) food conditions, in which the latter was applied for either 26 or 8 d after hatching and in slightly different severity. Their growth and reproductive behaviour in adulthood was analysed under semi-natural conditions. Impoverished and restricted food (IRF) negatively affected adult body mass, pair-bonding behaviour, courtship (males) and being courted (females), and induced incomplete compensatory growth. Further analyses suggest that the effects of IRF on behaviour could result from the strong effects on body mass, and perhaps also from detrimental effects of compensatory growth. These results provide evidence that adverse early-life condition can negatively impact on reproductive success, as suggested by the significant effect on egg production, which will very likely lead to a lower life-time fitness. The detrimental effects on male courtship indicate that IRF can affect sexual displays via other pathways than by impaired cognition as has been suggested for bird song, since courtship in the pigeons is not learned.

Because many crucial developmental processes are still ongoing after birth, conditions at the early postnatal stage can have important effects on the phenotype even into adulthood, influencing fitness (Lindström 1999, Monaghan 2008, Boersma et al. 2014). The effects of early-life conditions, however, do not simply dominate the variation of life-history related traits. Instead, the effects can strongly depend on the adult environment. This is relevant regarding the question to what extent later environmental factors can reverse early detrimental effects.

Among all crucial factors of early-life conditions, food is undoubtedly a critical element. For a developing young animal, food provides the essential nutrients that it relies on for development and growth. To date, studies that investigated the effects of early-life food conditions have suggested profound effects in various traits later in life, including adult body mass and size (de Kogel 1997, Tschirren et al. 2009), metabolism (Verhulst et al. 2006, Schmidt et al. 2012), immune function (Verhulst et al. 2005, de Coster et al. 2011), stress response (Pravosudov and Kitaysky 2006), timing of reproduction (Alonso-Alvarez et al. 2006, Blount et al. 2006), senescence (Boonekamp et al. 2014) and cognition (e.g. song learning in songbirds, Nowicki et al. 2002, Spencer et al. 2003, Farrell et al. 2012, Schmidt et al. 2013; size of some

brain nuclei and spatial learning, Pravosudov et al. 2005). These studies applied diverse methodologies and many of them manipulated post-hatching brood size, in which the nestlings in an enlarged brood usually face tougher sibling competition and thus comparably lower food availability than nestlings from a reduced brood. Despite the relevance of brood-size manipulation, such an experiment manipulates multiple factors simultaneously (e.g. food availability, social environment and competition, parental efforts, etc), and the separate role of each factor is hard to be teased apart (Monaghan 2008). Studies that manipulated food availability directly, such as by food restriction in the nestling phase, would thus provide the most direct evidence on how early food conditions influence phenotype in adulthood. Since in the wild, food resources very likely vary in both quantity and quality simultaneously, manipulating food quality together with food quantity might provide a more accurate estimate on the actual effects of early-life food condition. Previous studies of food restriction have mostly focused on later cognitive performance or compensatory growth and related consequences. In several song bird species, food restriction (65–70% of ad-libitum) in the nestling phase significantly reduced the brain area of song control (HVC and RA) and song production (Nowicki et al. 2002, Buchanan et al. 2004,

MacDonald et al. 2006, Farrell et al. 2012, Schmidt et al. 2013). In western scrub-jays *Aphelocoma californica*, the similar scheme of food restriction also led to reduced hippocampal volume and number of neurons in the hippocampus (Pravosudov et al. 2005), and decreased performance of spatial memory (Pravosudov et al. 2005). Studies on compensatory growth have found that early food manipulation can lead to a higher growth rate after food restriction (Krause and Naguib 2011, Killpack et al. 2014). Such compensatory growth comes with costs, which can affect life span, locomotory activity, metabolism, oxidative resistance, exploratory behaviour and cognitive performance, and aspects of reproduction (Fisher et al. 2006, Alonso-Alvarez et al. 2007, Criscuolo et al. 2008, 2011, Krause and Naguib 2011, reviewed by Metcalfe and Monaghan 2001, Monaghan 2008).

Although such a wide range of traits can be organized by early-life growth conditions, whether and how reproductive behaviour such as courtship, pair formation, mate choice, intra-sexual aggression and egg production is affected is still underexplored, despite being important determinants of fitness. In this study, rock pigeon *Columba livia* nestlings were raised either under an impoverished and restricted food conditions (IRF hereafter) or ad-libitum condition since hatching by foster parents. We purposely manipulated the food condition in both quantity and quality to imitate a very poor food condition. With this we aim to test whether the poor early-life food condition would lead to post-fledging compensatory growth (accelerated growth rate or catching up with control birds in adulthood), and influence body mass and reproductive behaviour in adulthood. In one experiment (in 2012), the food treatment lasted for 26 d, while in the other (in 2013) only until d 8 after hatching. Because the nutritional stress in early life may have delayed their development or set up a constraint for proper reproduction, or have made them prioritize survival and self-maintenance over current reproductive effort, we expected that the birds experiencing IRF early in life would show lower levels of reproductive behaviour, such as courtship and aggression, than those reared in ad-libitum condition. Furthermore, we expect a stronger magnitude of this reproduction-depressing effect for IRF birds from 2012 because of its longer period of food treatment. Since we expected that IRF in early life would have strong effects on compensatory growth and body mass in adulthood, we were also interested in how these would explain the variation in reproductive performance.

Materials and methods

Study species and housing condition

In this study, the experimental pigeons *Columba livia* were from two previous experiments that aimed to investigate the differential effects of maternal testosterone under different post-hatching food conditions (Müller 2013, Hsu 2016). All pigeons included in previous experiments and this study were descendants of out-bred wild-caught individuals from our pigeon colony. All birds showed the same wild-type 'blue bar' plumage pattern (Johnston and Janiga 1995) and white

rump feathers. Morphologically, they are visibly distinct from domestic racing pigeons because of their smaller body size and operculum.

In the previous experiments, pigeon eggs were injected with either testosterone or vehicle solution. In this study, only those birds from the 'vehicle' group were included. In these experiments, breeding pairs were housed in identical standard aviaries (4.01 m long × 1.67 m wide × 2.2 m high) with 1–2 pairs per aviary in the animal facility of the Centre for Life Sciences, Univ. of Groningen. Eggs were collected and returned to other pairs for incubation after injection. Every pair of foster parents only received two eggs of different egg injection treatment, as pigeons mostly only lay two eggs per clutch. On the hatching day, chicks were re-arranged among foster nests to make sure that two chicks in the same nest hatched on the same day, had similar body mass, but hatched from opposite hormone treatments. In the meanwhile, every brood, along with the foster parents, was randomly assigned to one of the two post-hatching food treatments (IRF versus ad-libitum) and the nestling growth was tracked until fledging. After that, all pigeons (parents and young) were transferred to a large outdoor aviary (45 m long × 9.6 m wide × 3.75 m high) and housed there together with pigeons belonging to other studies and non-experimental adults. In the large aviary, ad-libitum food (seed mixture for *Streptopelia* species, KASPER™ 6721, + seed mixture for *Columba* species, KASPER™ 6712 + pellets for pigeons, KASPER™ P40, for nutrition details, see Supplementary material Appendix 1 Table A1), grit, and water were always provided.

In this study, we analysed the survival of the experimental birds (from birth to the start of behavioural observation in 2014, $n = 43$ from 2012 experiment and 64 from 2013 experiment) and the reproductive behaviour of those birds that survived into adulthood ($n = 55$). In most cases, these survived pigeons were raised by different foster parents, except for 5 nests. We thus randomly selected one pigeon in each of these 5 nests to avoid pseudo-replication (final $n = 50$, for the composition of their age and sex, see Table 1). Overall, pigeons from the IRF group had a relatively high early mortality (see Results), which is reflected in their lower sample size relative to those from ad-libitum group (Table 1). A potential survivor bias in the poor food treatment by those that could deal with it is thus inevitable. Nevertheless, any detrimental effect of the food treatment on the survivors would still indicate long-lasting effects of early food stress.

Before the behavioural observations, all pigeons were caught in the large aviary to check their leg bands and to measure their body mass as described in Hsu et al. (2016b). After processing, all birds were released back to the aviary and provided with a 10-day period of acclimatization before the observation started.

Table 1. The number of pigeons used in this study.

Food	2012		2013		Total
	ad-libitum	impoverished and restricted	ad-libitum	impoverished and restricted	
Female	8	3	6	5	22
Male	14	3	9	2	28
Total	22	6	16	7	50

Food treatment

In 2012 and 2013, two different food treatments were applied on the parental pigeons while they were raising chicks. In both years the food treatment started 1–2 d before the chicks hatched, and ended at d 26 post-hatching in 2012, and at d 8 post-hatching in 2013. Our food treatment aimed to manipulate both food quantity and quality. To do so, in both years, the ad-libitum group was fed with ad-libitum mixtures of commercial pigeon food (Tortelduivenvoer + Sierduivenvoer + Duivenkorrel, see Supplementary material Appendix 1 Table A1 for nutrient facts) and supplemented with vitamin powder Supralith™, while the impoverished-and-restricted-food (IRF) group only received a limited amount of grain mixtures, which contains lower protein content ('grain mixture with broken corns' in Supplementary material Appendix 1 Table A1). In 2012 we fed the IRF group with 33 g per pair per day. According to our previous study, the exactly same food treatment significantly reduced egg and yolk mass but was not too severe to impair egg laying (Hsu et al. 2016a). In 2013, 5 g additional food per chick per day was provided to each pair of parental pigeons in order to reduce chick mortality that had been observed in 2012. Pigeon nestlings completely rely on the provisioning by both parents after hatching. Pigeon parents feed nestlings by regurgitating a nutrient-rich crop secretion, called 'crop milk' during the first week (Johnston and Janiga 1995). After that, the proportion of crop milk gradually decreases and the proportion of semi-digested food (mainly seeds) increases and the modal fledging age in our colony is around 26 d after hatching. Therefore, in the 2012 experiment, the duration of food treatment lasted for the whole nestling period and in the 2013 experiment, it covered a key period after hatching. The differences of food treatment in the IRF groups between two experiments are summarised in Supplementary material Appendix 1 Table A2. After the food treatment, all pigeons, including parents and fledglings, were fed with the normal ad-libitum pigeon food again.

Behavioural observations and classification

From April 10 to May 16, 2014, we used a group scanning protocol for behavioural observation and recorded behaviour from an observation corridor next to the large pigeon aviary. All pigeons were individually recognizable by unique colour ring combinations. The birds included in this study were observed together with the birds involved in another simultaneously-conducted study (Hsu et al. 2016b). In brief, the observers scanned the whole group of pigeons from one end of the aviary to the other and recorded the behaviour of each pigeon (Table 2), on 24 d during a 6 week period, with 2 to 4 observation bouts each day. The direction (from left to right or vice versa) of each observation bout was randomly determined every day and then alternated during that day. In total 5 observers were involved and all of them were well pre-trained by B.-Y. H. to ensure correct and consistent recordings and were kept blind from knowledge of the experimental treatments.

During the behavioural observations, we focussed on courtship, pair-bonding and aggressive behaviour, which were pre-defined according to literature (Johnston and Janiga 1995) and our own experience (Table 2). More than one behaviour could be performed by an individual pigeon at the same time, for example, tail-dragging and bowing, or tail-dragging and driving, and in such cases both were recorded. Before data analysis, tail-dragging, bowing, and the male driving the female were grouped as 'courtship'. Attacking and fighting were merged into 'aggression'. For females, being driven and being courted were grouped as 'being courted'. Female-specific courtship (Hsu et al. 2016b) and female aggression were not considered for analysis because they were only very rarely performed. Copulation, courtship feeding and reciprocal preening are usually seen in both sexes among established pairs and thus were grouped as 'pair-bonding'. In the aviary, 78 nest-boxes were provided for the whole group of pigeons but were not opened until the middle of the behavioural observation. We made additional observations to identify those pigeons that occupied a

Table 2. The definitions of pigeon behaviour, based on our own experience and Johnston and Janiga (1995). Some categories were further grouped before data analysis: TD + BW + D = Courtship; CP + CF + RP = Pair-bonding; C0 + D0 = Being courted; A1 + F = Active aggression.

Behaviour	Definition
Courtship-related:	
Tail-dragging (TD)	A pigeon spreads its tail and drags it on the ground.
Bowing (BW)	A pigeon puffs out its neck feathers, lowers its head and turns around in circles, accompanying with cooing sound.
Driving (D)	One pigeon runs closely behind another.
Copulation (CP)	A pigeon stands on top of another pigeon, attempting cloacal contact.
Courtship feeding (CF)	A pigeon puts its beak inside the beak of the other.
Reciprocal preening (RP)	Two pigeons stand/sit close together and preen the other with its bill.
Being courted (C0)	Another pigeon is doing TD, BW toward the targeted pigeon.
Being driven (D0)	Another pigeon is driving the targeted pigeon.
Aggression-related:	
Attacking (A1)	Active agonistic behaviour by a pigeon against another one, like pecking, chasing, beating with wings, or kicking with feet.
Fighting (F)	Two pigeons actively engage in fighting with each other.
Other behaviour:	
Nest-building (NB)	A pigeon brings nest materials to its nest-site or tries to make a nest.
Inactive (I)	Standing, sitting, and any other inactive behaviour
Other (O)	Any other behaviour that is not defined above, for example, self-preening, eating, walking, and so on.

nest-box or a nesting site on the ground and checked them for egg production every morning.

Statistical analysis

All statistical analyses were conducted with R 3.3.1 (R Core Team). We used the package OIurv (Diez 2013) for the survival analysis. Due to the small sample sizes when higher-order interaction are considered, we did not include sex in this analysis in order to get more robust results concerning the effects of food treatment and year difference. Significance tests were conducted by Gehan-Wilcoxon test with $\rho = 0$.

All other analyses were conducted by general or generalised linear models (GLM). Food treatment (ad-libitum versus IRF) and the experimental run (2012 and 2013) were included as independent variables in all models. Sex was also included in those models in which the data of both sexes were included (body mass, nest occupation, pair-bonding behaviour).

The factor 'experimental run' is potentially confounded by the age of the birds, as we performed the observations of all birds in spring 2014, when the birds from the first experiment (2012, with longer and more severe food treatment) were two years old and the birds of the second experiment (2013, with shorter and less severe food treatment) one year. Plus, some year differences, like ambient temperatures, were inevitably confounded between the two experiments. Therefore, the factor experimental run should be regarded as a proxy representing a mixture of differences in the severity of food treatment and year. However, since in both experiments we used age matched control birds, we thus still can analyse whether food treatment showed different effects between two experiments by testing the interaction between food treatment and experimental run, without age as a confounding variable. Therefore, we included this interaction in all models. In models where sex was included because of known sex differences in behaviour for this species, we also tested the interaction between food treatment and sex.

The data of body mass, the total frequencies of male courtship and females being courted were analysed with GLMs, where Gaussian error distribution was assumed. Model diagnostics did not detect significant deviation of residual distribution from normality (Shapiro-Wilk tests, all p values > 0.2). Visual inspection on residual distribution also did not suggest any heterogeneity. The total frequency of male aggression was not normally-distributed and thus was first square-root-transformed to ensure a normally-distributed residual distribution (Shapiro-Wilk test on model residuals, $p = 0.385$). The data of pair-bonding were zero-inflated, and thus were re-coded as 1/0 (pair-bonding behaviour was observed or not) and analysed by binomial GLMs. The data of nest-box occupation and egg laying were similarly treated.

For the model of body mass, we additionally included the mass of the eggs from which the birds originally hatched. This was because egg mass often relates to chick body mass (Krist 2011) and egg mass in 2013 was significantly lower than that in 2012 (mean \pm SD: 2012, 17.33 ± 1.47 g; 2013, 16.56 ± 0.87 g, t test, $t_{48,207} = -2.42$, $p = 0.019$). We therefore included egg mass to, at least partially, account for

the substantial year difference that may be reflected in body mass.

In order to test whether compensatory growth occurred, we used the data of body mass at d 8 (the end point of food treatment in 2013) and d 26 (the end point of food treatment in 2012 and also the approximate fledging age for ad-lib fed nestlings) from our previous studies together with the body mass measured in 2014 to calculate the body mass gain between 1) d 8 and d 26 and 2) d 26 and 2014. The first one was for testing the potential immediate compensatory growth after food treatment in 2013 chicks. The second one was for testing the post-fledging compensatory growth. We used GLMs including only food treatment, experimental run, sex, and their interactions.

As food treatment significantly influenced body mass (see Results), which may influence behaviour, and compensatory growth may incur costs in terms of behaviour, too, we additionally applied GLMs to test the predictability of body mass and compensatory growth on reproductive behaviour. The post-fledging body mass gain (between d 26 and 2014) was used as an index of compensatory growth and entered in the model together with body mass in 2014. Body mass in 2014 was negatively correlated with the post-fledging body mass gain ($r = -0.276$, $n = 48$), which did not lead to strong collinearity in the models (all variance inflation factors < 1.2). No clear violation against model assumptions was detected.

In all models, multi-collinearity was checked and all variance inflation factors were < 2 . Effect sizes are presented in the supplementary materials.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.018pt> (Hsu et al. 2017).

Results

Survival into adulthood

The food treatment significantly led to a higher mortality in the IRF birds ($\chi^2 = 29$, $p < 0.001$) than in the ad-lib fed birds. This effect remained significant when we separately analysed the data within each year (2012, $\chi^2 = 16.4$, $p < 0.001$; 2013, $\chi^2 = 10.2$, $p = 0.001$; Fig. 1). In addition, there was also a significant difference between experimental runs, indicating that pigeons in the 2013 experiment had a significantly lower survival rate than those in the 2012 experiment ($\chi^2 = 14.1$, $p < 0.001$, Fig. 1). We further tested the survival curve for both years, but separately for the IRF and ad-libitum groups and found that in both groups birds in 2013 always had a lower survival than in 2012 (ad-libitum, $\chi^2 = 7.4$, $p = 0.006$; IRF, $\chi^2 = 4.6$, $p = 0.032$).

Body mass

The food treatment at the post-hatching stage significantly reduced body mass in adulthood ($p = 0.003$, Fig. 2, Table 3). Males were significantly heavier than females ($p = 0.022$, Table 3), but there was no sex-specific effect of food treatment on adult body mass ($p = 0.744$). The experimental

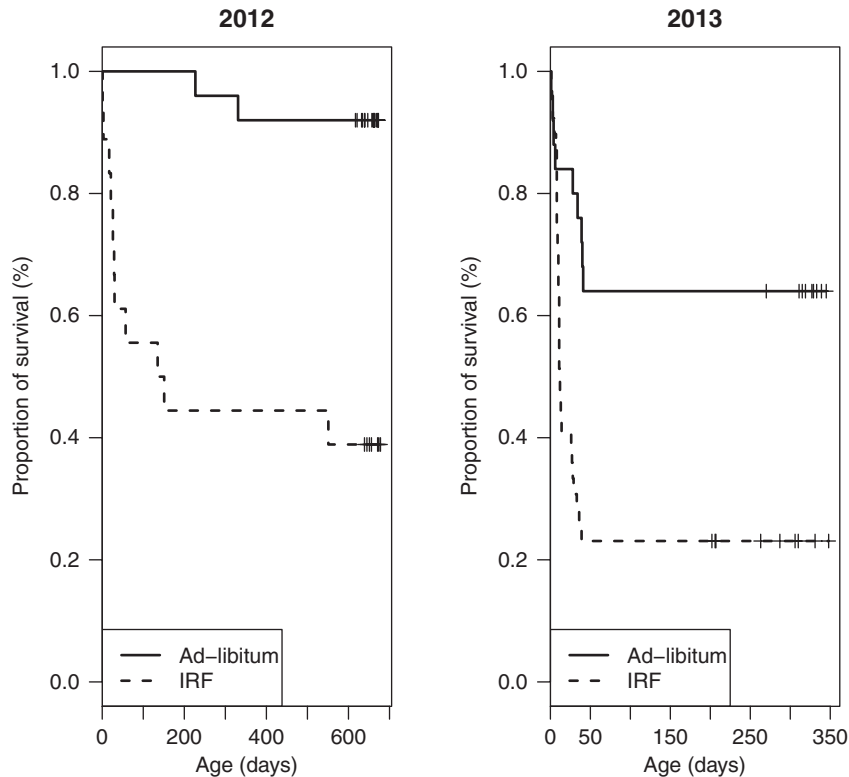


Figure 1. Survival curves of pigeons from the food impoverishment and restriction (IRF) experiments in 2012 and 2013. Solid line: ad-lib fed pigeons; dashed line: IRF pigeons. Data are right-censored, marked by the small crosses on the survival curves for those that were still alive in the end of the study period.

run (2012 versus 2013, see Food treatment) did not show a significant effect on adult body mass ($p = 0.536$). The interaction between food treatment and the experimental run was not significant ($p = 0.147$), although the difference

of body mass in 2014 between two food treatment groups seemed larger in the birds from 2012 experiment than those from 2013 group (Fig. 2).

Compensatory growth

For the body mass gain of chicks between d 8 and d 26, the interaction between food treatment and the experimental run was significant (Table 4). In the experiment of 2013, the body mass gain of chicks between d 8 and d 26 did not show a significant difference between control and IRF birds, despite the fact that the food treatment had ended after d 8 (Tukey HSD, $p = 0.981$, see the almost parallel increase in Fig. 2). This suggests lack of compensatory growth during the first few weeks after the food treatment in the 2013 experiment. During the same nestling stage in 2012, the chicks were still under the food treatment, leading to a much lower body mass gain until fledging for IRF chicks than control chicks (Tukey HSD, $p < 0.001$, Fig. 2).

Between d 26, after the food treatment had ended for all groups, and the 2014 breeding season, we observed an overall significant difference of body mass gain between the controls and IRF birds: pigeons from the IRF group gained more weight than pigeons from the control group (Table 4, Fig. 2). This compensatory growth was stronger in the 2012 birds than in the 2013 birds, as indicated by the significant interaction effect between food treatment and the experimental run (Table 4, Fig. 2). Indeed, post hoc analyses showed that the group difference was only significant in 2012 (Tukey HSD, 2012, $p < 0.001$, 2013, $p = 0.463$).

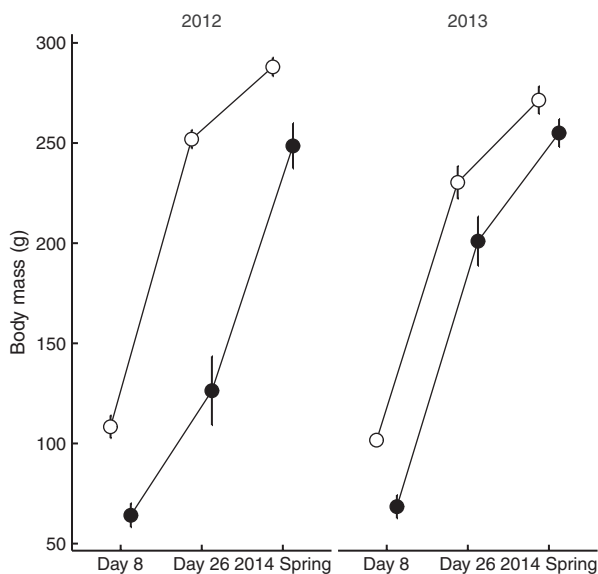


Figure 2. Mean \pm SE of pigeon body mass at 8 d and 26 d after hatching, and in adulthood (2014 spring). The left side showed the data from the 2012 experiment and the right side from the 2013 experiment. Filled circles: food impoverished and restricted pigeons; open circles: ad-lib fed pigeons.

Table 3. Results of the general linear model on adult pigeon body mass and reproductive behaviour. Data of body mass, male courtship and female being courted conformed normality and no data transformation was needed. The total frequencies of male aggression were square-root-transformed to ensure the normality of the model residuals. Nest-box occupation, egg-laying, and pair-bonding behaviour were coded as 1 or 0 and binomial error distribution with a logit link function was specified in the models; in these models z values instead of t values were presented. All p values for main factors were derived from the model without any interaction term.

Variables	Estimates	SE	t or z	p
Body mass (n = 49)^a				
Experimental run (2012)	4.074	6.532	0.624	0.536
Food (IRF ^c)	-23.329	7.472	-3.122	0.003
Sex (male)	15.300	6.448	2.373	0.022
Original egg mass	6.193	2.684	2.308	0.026
Food × sex	-5.096	15.514	-0.328	0.744
Food × experimental run	-22.399	15.165	-1.477	0.147
Nest-box occupation and pair formation (n = 50)				
Experimental run (2012)	-0.376	0.683	-0.551	0.582
Food (IRF ^c)	-0.996	0.735	-1.354	0.176
Sex (male)	-0.480	0.700	-0.686	0.493
Food × sex	0.853	1.525	0.560	0.576
Food × experimental run	-0.800	1.460	-0.548	0.584
Egg-laying (n = 22)				
Experimental run (2012)	-0.453	1.005	-0.451	0.652
Food (IRF ^c)	-2.127	1.056	-2.014	0.044
Food × experimental run	-18.566	3765.848 ^b	-0.005	0.996
Total frequency of male courtship (n = 28)				
Experimental run (2012)	0.173	0.162	1.073	0.294
Food (IRF ^c)	-0.512	0.206	-2.488	0.020
Food × experimental run	-0.652	0.408	-1.596	0.124
Total frequency of being courted in females (n = 22)				
Experimental run (2012)	0.109	0.091	1.197	0.246
Food (IRF ^c)	-0.316	0.095	-3.337	0.003
Food × experimental run	-0.349	0.178	-1.964	0.065
Pair-bonding behaviour (n = 50)				
Experimental run (2012)	-0.392	0.624	-0.629	0.530
Food (IRF ^c)	-1.806	0.773	-2.335	0.020
Sex (male)	-0.147	0.630	-0.233	0.816
Food × experimental run	-0.342	1.573	-0.218	0.828
Food × sex	-0.009	1.592	-0.006	0.995
Total frequency of male aggression (n = 28)				
Experimental run (2012)	-0.029	0.082	-0.350	0.729
Food (IRF ^c)	-0.231	0.105	-2.198	0.037
Food × experimental run	-0.280	0.212	-1.326	0.197

^aThere was one missing value in body mass.

^bThis unusually large standard error was likely caused by the fact that all food-impooverished females in 2012 did not lay any eggs during the observational period in 2014. Therefore, one must interpret the estimate of this interaction with caution.

^cIRF: impooverished and restricted food.

Nest-box occupation, pair formation, and egg laying

Among the 50 pigeons included in the analysis, 37 of them formed a stable pair with another bird and successfully occupied a nest-box or a nest-site on the ground, and the remaining 13 did not. The binomial GLM showed that post-hatching food treatment did not affect the odds of pair formation and nest occupation ($p = 0.176$, Table 3). Sex and the experimental run also did not have significant effects ($p = 0.493$, 0.582 , respectively). Moreover, the interaction of food treatment by sex and food treatment by experimental run were both non-significant ($p > 0.5$, Table 3).

Over the course of the observation, 12 out of the 22 females laid eggs while the other 10 did not. The binomial regression suggested that IRF females were less likely to lay eggs compared to control females (proportion of females laying eggs: ad-libitum 10/14; IRF 2/8, $p = 0.044$, Table 3). The experimental run and its interaction with food treatment did not show significant effects ($p > 0.6$, Table 3). Although the sample size was small and the p value was only borderline significant, the effect size was not small (Yule's $Q = -0.76$, Supplementary material Appendix 1 Table A3).

Frequencies of reproductive behaviour

We found that food impooverishment and restriction negatively impacted on the total frequency of all four reproductive behaviours we measured (Table 3). IRF males showed a significantly lower level of courtship and aggression than control males ($p = 0.020$, 0.037 , respectively, Table 3, Fig. 3A, D). IRF females were also significantly less courted by males than control females (Fig. 3B, $p = 0.003$, Table 3). For pair-bonding behaviour, which is typically seen in both sexes, the binomial GLM showed significantly lower odds for IRF pigeons to perform such behaviour ($p = 0.020$, Table 3) than for control pigeons. A Mann-Whitney U test also confirmed that IRF pigeons performed lower frequencies of pair-bonding behaviour ($p = 0.026$, Fig. 3C) than control pigeons. Pigeons of different sexes did not show significant difference on the observed performance of pair-bonding behaviour ($p = 0.816$). There was also no significant sex-specific effect of food treatment on pair-bonding behaviour ($p = 0.995$). In all four reproductive behaviours, neither the experimental run nor its interaction with food treatment showed any significant effects ($p > 0.06$ in all cases). Moreover, the effect sizes of food treatment for all reproductive behaviours were large (Supplementary material Appendix 1 Table A4).

Relationships between behaviour, body mass and compensatory growth

The models testing the effect of adult body mass and post-fledging body mass gain on the performance of reproductive behaviour showed that adult body mass was a significant predictor for male courtship ($p = 0.013$) and aggression ($p = 0.022$), and how often a female was courted ($p = 0.004$), but not for pair-bonding behaviour ($p = 0.221$). This indicates that heavier males courted more often and were more aggressive than lighter males and heavier females were being courted more often than lighter females. To analyse whether this relationship held within groups, we further tested this association only among the ad-libitum-fed birds as the sample size is larger, and body mass still significantly predicted the frequencies of all three behaviours ($p < 0.05$ in all cases). As for the post-fledging body mass gain, interestingly, it consistently showed opposite association from body mass with all behaviours, although it only approached significance for male courtship ($p = 0.088$) and the effect sizes were small (Supplementary material Appendix 1 Table A5).

Table 4. Results of general linear models on body mass gain between d 8 and d 26, and between d 26 and 2014 breeding season. Residuals of both models conformed normal distributions (Shapiro-Wilk test, $p > 0.1$). The interactions of interest were tested simultaneously but the results of all main effects were derived from the models leaving out all two-way interactions.

Variables	Estimates	SE	t	p
Body mass gain between d 8 and d 26 (n = 49) ^a				
Experimental run (2013)	9.478	9.411	1.007	0.319
Food (IRF ^c)	-37.011	10.677	-3.466	0.001
Sex (male)	9.552	9.473	1.008	0.319
Food × experimental run	88.653	17.143	5.171	<0.001
Food × sex	8.540	17.455	0.489	0.627
Body mass gain between d 26 and the 2014 breeding season (n = 48) ^{a,b}				
Experimental run (2013)	-11.047	7.261	-1.522	0.135
Food (IRF ^c)	44.966	8.341	5.391	<0.001
Sex (male)	6.347	7.261	0.874	0.387
Food × experimental run	-65.069	14.156	-4.597	<0.001
Food × sex	2.194	14.156	0.155	0.878

^aAmong the 50 pigeons included in this study, one individual did not have body mass data at d 8 and d 26, and was therefore removed from this analysis.

^bOne individual whose body mass data in 2014 was missing and was removed from this analysis.

^cIRF: impoverished and restricted food

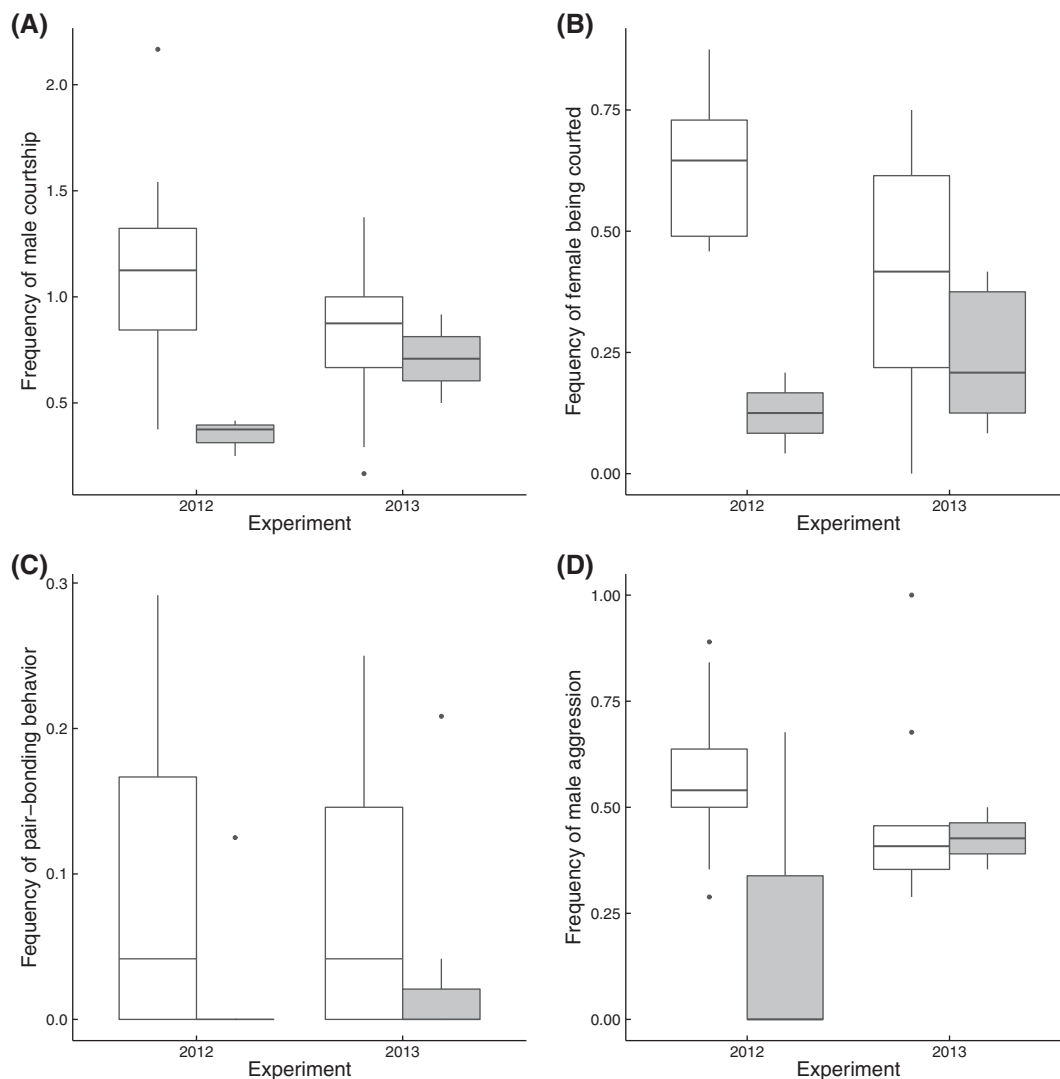


Figure 3. Boxplots of pigeon behavioural frequencies: (A) male courtship, (B) female being courted, (C) pair-bonding behaviour and (D) male aggression. Filled boxes depict food-impooverished and restricted pigeons, and empty box ad-lib fed pigeons. The upper and lower borders of the box correspond to the first and third quartiles and the lines within boxes to the median. Dots refer to extreme values. The whiskers extend to the highest and lowest value that is within the inter-quartile range. In two experiments (2012 versus 2013), food treatment was conducted with different duration and severity.

Evaluation of the confounding effects from uncontrolled year difference

In the above models for body mass and all reproductive behaviour, the main effects of experimental run and its interactions with our food treatment were all non-significant (Table 3), suggesting that the uncontrolled year difference did not seem to bias our results. To further confirm this, we ran all models in Table 3 again but restricted to the birds raised under food ad-libitum condition, and no significant difference between the two experimental runs were detected (in all cases, $p > 0.075$).

Discussion

Among the growing interest of the impact of early-life conditions on later life, their effects on reproductive behaviour is surprisingly neglected. In this study, by manipulating food quantity and quality simultaneously, we demonstrate that adverse early-life food conditions not only reduced the survival and the body mass of the survivors in adulthood, but also postural male display, female attractiveness, pair-bonding, and male aggression. Despite of the different duration and severity of food treatment between the two experimental runs (see Food treatment and Supplementary material Appendix 1 Table A2), not only we detected no main effects between the two experiments, but also no statistically significant interactions between the experimental run and the food treatment. There are several possible explanations for the lack of significant interaction between the food treatment and the experimental run. First of all, in 2013, the food treatment was only conducted in the first week after hatching. The lack of difference in the effects from the more endured and severe treatment in 2012 experiment suggests that the condition in the first week after hatching is probably of utmost importance for later-life phenotype. Second, the survivor bias might have blurred the difference between the two experimental runs, as those that could not deal with the poor food condition after hatching likely have died already. Third, the year differences might have confounded the interaction effects by amplifying the effects of the less endured and severe IRF in 2013. Such confounding effects by year differences are unfortunately not possible to be completely eliminated with our experimental design. Nevertheless, the year difference seems unlikely to bias our results regarding food treatment as the effects are similar between the two years and the experimental run itself did not result in significant difference on body mass and behaviour of those raised under ad-libitum food condition. Our results are thus still most likely explained by our food treatment and we therefore will focus on this in our discussion.

Food-impooverished and restricted pigeons had significantly lighter body mass in adulthood than control pigeons, indicating that they were unable to fully compensate for the depressed growth in their early life, despite the presence of ad-libitum food later on. We did detect remarkable compensatory growth of pigeons from the 2012 experiment but at two years of age they were still significantly lighter than the ad-lib fed counterparts (Fig. 2). This is consistent with a recent meta-analysis that in spite of the ability to accelerate

growth after food restriction, animals may not be able to fully 'catch-up' (Hector and Nakagawa 2012).

Compared to the ad-lib fed birds, the birds that received post-hatching food impoverishment and restriction showed reduced levels in almost all behavioural parameters. Along with adult body mass, these results are consistent with the predictions of the 'silver spoon hypothesis', in the sense that the poor condition in the early developmental period would yield long-term carry-over effects in adulthood, no matter whether the condition has improved (Grafen 1988, van de Pol et al. 2006, Monaghan 2008). Adult body mass was also a strong positive predictor for male courtship, male aggression, and female attractiveness. This perhaps reflects the fact that in many species larger males are advantaged over smaller ones in male-male competition (Andersson 1994), explaining the negative effect of food treatment on aggression. Also, our data on females being courted indicate that low quality females are relatively unattractive. Since food treatment also had a significant negative effect on egg production, male preference for heavier females seems adaptive. Because pigeons tend to maintain a life-long pair-bond unless the mate disappears (Johnston and Janiga 1995), this lower attractiveness of females will very likely lead to a reduced life-time reproductive success and fitness return, as will a lower male status in this colonial breeding species. This is in line with several field studies that have linked the quality of the natal environment and life-time reproductive success (Reid et al. 2003, van de Pol et al. 2006, Wilkin and Sheldon 2009).

Food impoverishment and restriction in early life also negatively affected pair-bonding behaviour, but adult body mass did not correlate with it. This suggests that the impact of early-life food condition is not fully translated by the corresponding change in body mass, although the small sample size warrants some caution. When analysing the combined effect of body mass and compensatory growth on adult behaviour, compensatory growth was, as predicted, negatively related to behavioural parameters, but was only approaching significance for courtship behaviour. This suggests that adult body mass is a better indicator than the potential costs of compensatory growth for adult behaviour.

The social environment probably plays an important role in explaining the long-term effects of early-life food condition we observed. The rock pigeon is a social species that forages and breeds in large groups. If lighter individuals, because of their adverse condition in early life, have become subordinate to heavier individuals, one would expect lower performance in both reproduction and aggression, as we observed in this study. It would be therefore of interest to analyse behavioural performance of IRF individuals while the ad-lib fed ones are removed from the population. Although such an experiment would not reflect the natural situation, it may reveal whether the effects of early-life condition would be conveyed by the social structure instead of solely explained by physiological mechanisms.

As far as behaviour is concerned, early-life food condition in birds has mainly been analysed in terms of cognition-based behaviours, focussing on song development (Nowicki et al. 2002, Spencer et al. 2003, Farrell et al. 2012, Schmidt et al. 2013) and spatial foraging and memory (Pravosudov et al. 2005, Farrell et al. 2012, Kriengwatana et al. 2015).

Song has partly the same function as male courtship behaviour in the pigeons, but in contrast to songbirds, postural and vocal displays in sub-oscines are not learned (Groothuis 1993, Gahr 2000). This suggests another pathway than impaired cognition for poor food condition affecting sexual displays. We could not record in detail the vocal displays in our large colony but a detailed analysis of the form of the postural and vocal displays after food treatment may be worthwhile for future work.

A proximate mechanism underlying the reduced reproductive behaviour due to early-life food treatment may be organizational changes of brain areas. Bird studies have shown evidence that brain areas related to song learning and spatial learning (e.g. the song control nuclei HVC and RA, and hippocampus, Nowicki et al. 2002, Buchanan et al. 2004, Pravosudov et al. 2005, MacDonald et al. 2006, Schmidt et al. 2013) can be affected by early-life food conditions. However, such areas have been attributed to learning whereas pigeon courtship is independent of at least imitation. Moreover, similar changes in brain areas relevant for the postural and vocal displays in the pigeons, or more generally, the areas controlling courtship in non-passerines, are less well known and we did not sacrifice birds for brain measurements.

Reduced performance of reproductive behaviour in the IRF birds could also be a consequence of altered neuro-endocrine function. Several studies have found that early food restriction can increase circulating baseline corticosterone levels (Pravosudov and Kitaysky 2006, Kriengwatana et al. 2014, but see Schmidt et al. 2014), suggesting enhanced activity of the hypothalamus-pituitary-adrenal (HPA) axis. As reproductive behaviour is very much testosterone-dependent (Adkins-Regan 2005, Hau and Goymann 2015), and the activation of HPA axis may inhibit the secretion of testosterone (Toufexis et al. 2014), the increased activity of HPA axis as a result of early-life food restriction might to some extent inhibit the performance of reproductive behaviour. Whether such effects will dampen over time, and how the interaction between HPA axis and HPG (hypothalamus-pituitary-gonad) axis is modulated by early-life food conditions requires more studies.

In addition to the effects of early-life food condition on nestling brain development or its endocrine function, at least part of the effects may have been realised by the fact that the parents were also food impoverished and restricted. During the first week after hatching, both parents of pigeons feed chicks with crop milk (Johnston and Janiga 1995). Apart from the reduced amount of crop milk due to food restriction, the composition of crop milk, for example, the amount of carotenoids (Eraud et al. 2008) and antibodies of parental origin (Engberg et al. 1992, Jacquin et al. 2012), may have been affected and thus brought effects to nestlings. Whether or not crop milk contains hormones of parental origin, especially stress hormones, and thereby influences offspring phenotype would be also very interesting for future studies. Finally, food impoverishment and restriction might have negatively affected parental brooding behaviour leading to more energy expenditure by the chicks. All in all, as the first week of crop milk feeding might be of utmost importance of pigeon nestlings, this might be an explanation for the finding that no significant interaction between food treatment and

the experimental run was observed, despite a more endured and severed food impoverishment was applied in only the first experimental run.

Among the different proposed hypotheses of how early life conditions may influence late life phenotype (reviewed in Monaghan 2008, Groothuis and Taborsky 2015), our results are clearly in line with the silver spoon hypothesis, showing additional detrimental long term effects on courtship, pair-bonding and reproduction. This study was, however, only testing behavioural and reproductive parameters of food-impoverished and restricted birds under an ad-libitum condition in adulthood. Therefore, the possibility that the negative effects of poor early-life food condition are due to 'mismatch' with adult environment cannot be ruled out. Besides, our experimental design also limits us to assess or control the potential effects of the offspring age. In recent years, accumulating evidences suggest the context at a later time point in life may be of vital importance in modulating the effects of conditions in an earlier life stage (Monaghan 2008, Henriksen et al. 2011, Groothuis and Taborsky 2015, Hsu 2016). We thus suggest that a full factorial design should be considered for future studies to fully represent different contexts at both age classes and disentangle such interactions (Monaghan 2008, Groothuis and Taborsky 2015).

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Supplementary material (Appendix JAV-01172 at <www.avianbiology.org/appendix/jav-01172>). Appendix 1.