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Fitness consequences of environmental conditions at different life stages in a long-lived vertebrate

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The predictive adaptive response (PAR) hypothesis proposes that animals adjust their physiology and developmental trajectory during early life in anticipation of their future environments. Accordingly, when environmental conditions in early life match environmental conditions during adulthood, individual fitness should be greater. Here, we test this hypothesis in a long-lived mammal, the roe deer, using data from two contrasting populations, intensively monitored for more than 35 years. In the highly productive site, the fitness of female roe deer increased with the quality of environment during adulthood and, contrary to predictions of PAR, individuals born in good conditions always outperformed those born under poor conditions. In the resource-limited site, the fitness of female roe deer born in poor years was better than those born in good conditions in poor years when the animals were adult, but not in good years. Although consistent with predictions of PAR, we showed that this pattern is likely to be a consequence of increased viability selection during the juvenile stage for animals born in poor years. While PARs are often advanced in evolutionary medicine, our findings suggest that detailed biological processes should be investigated before drawing conclusions about the existence of this phenomenon.

1. Introduction

Although the role of environment in the development of an individual has been recognized for a long time [1], understanding the interplay between the developing individual and its environment continues to be a major challenge for evolutionary biologists [2]. Previous studies, conducted on a large range of taxa including humans, have shown that environmental conditions early in life, when the architecture of the body is being established [3], can have long-term effects on life-history traits [4–6]. The question is whether these long-term, environmentally induced changes represent an adaptive response to different environments, or are a consequence of constraints on development imposed by food resource availability [7,8].

Building on the concepts of 'fetal programming' [9] and of 'thrifty phenotype' [10] issued from human medicine, the predictive adaptive response (PAR) hypothesis posits that a young animal should adjust its physiology during early development in anticipation of its future environment [2,11,12]. Gluckman and co-workers have proposed that the capacity of individuals to adjust their development in response to early environments has evolved via natural selection, in a similar way to adaptive phenotypic plasticity [13–15]. The proximate

mechanisms underlying PARs include epigenetic changes in gene regulation, variation in organ structure or alteration in cell number [11,16]. Ultimately, fitness benefits would arise from a slower metabolism increasing survival in food-limited environments, or from a higher metabolism allowing greater reproductive success when food resources are plentiful [2].

PAR is thus a form of developmental plasticity where fitness benefits of the developmental responses to early-life environment are not immediate, but postponed to the adult stage [12]. The adaptive value of the PAR depends, however, on the strength of the correlation between environmental conditions experienced during early life and environmental conditions experienced during adulthood, as mismatching may lead to fitness disadvantages and disease [11]. For instance, a mismatch between pre- and post-natal nutrient availability increased the risk for cardiovascular disorder in sheep (*Ovis aries*) [17]. Hence, a key aspect of the PAR hypothesis is that fitness should be the highest for individuals for whom early-life conditions match conditions during adulthood (figure 1*a*). The most obvious competing hypothesis is that harsh early-life environmental conditions can constrain body development, leading individuals born under favourable conditions to outperform consistently those born in adverse conditions (figure 1*b*), also known as the 'silver spoon' effect [18].

While long-term consequences of early-life conditions have long been recognized in animal populations in the wild [19,20], most studies have focused on testing for 'silver spoon' effects without including possible effects of environmental conditions during adulthood. On the other hand, the PAR hypothesis is currently much debated [21–25]. This hypothesis is often advanced in the medical and epidemiological literature for explaining the occurrence of metabolic diseases, but empirical support for PARs remains scarce in long-lived species [17]. Moreover, tests of the PAR hypothesis assessing consequences for fitness itself are currently lacking. Comparing the fitness of individuals when early conditions either match environmental conditions during adulthood or do not is a key requirement for testing the PAR hypothesis [23].

Long-term monitoring of a large number of known-age animals in two contrasting roe deer (*Capreolus capreolus*) populations provided a unique opportunity to test the PAR hypothesis in a long-lived, wild, mammalian species. After exploring the correlation of environmental conditions during adulthood with those in early life, we quantified the effects of the conditions in early-life and current environmental conditions on annual adult survival, annual adult reproductive success and mean individual fitness of different cohorts. Under the PAR hypothesis, early and current environmental conditions should interact to affect adult performance: individuals should perform better when they experienced similar conditions during early life and adulthood than when they experienced mismatched conditions (figure 1*a*).

2. Material and methods

(a) Roe deer as a biological model

The European roe deer is a medium-sized, forest-dwelling herbivore (adult body mass ranges between 20 and 30 kg) with weak sexual size dimorphism [26]. Roe deer can live up to 18 years of age in the wild [27] and are weakly polygynous [28]. Females are iteroparous (one reproductive attempt per year) and can give birth to one to three fawns each year in May–June from 2 years
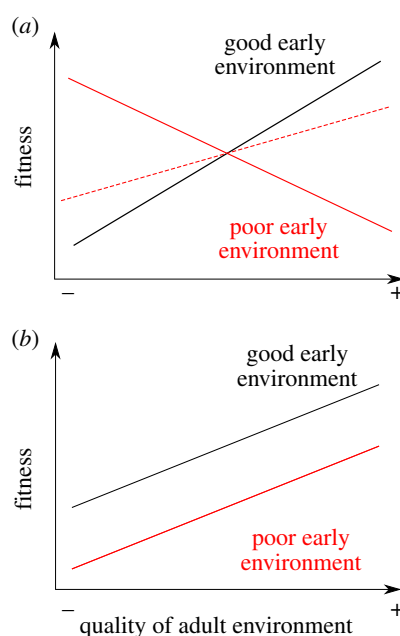

Figure 1. Variation in mean fitness as a function of environmental conditions during early life and adulthood under two different scenarios. (*a*) Predictive adaptive response (PAR). For individuals born in good environmental conditions, mean fitness increases as the adult environment improves. For individuals born in poor environmental conditions, mean fitness may increase weakly (dotted red lines) or decrease (solid red lines) with improvement of the adult environment. In poor environmental conditions during adulthood, however, individuals born in poor conditions perform better than those born in good conditions. By contrast, individuals born under favourable conditions have higher mean fitness than those born under poor conditions when environmental conditions during adulthood are good. (*b*) 'Silver spoon' effect. Here, there is no environmental matching. Mean fitness increases with the quality of adult environment and individuals born in good environmental conditions always have higher mean fitness than those born in poor environmental conditions. (Adapted from [2,7].)

of age onwards (triplets are exceedingly rare in our study areas; see below). Weaning occurs in late summer, and dispersing individuals generally leave their mothers at 1 year of age. Being income breeders (*sensu* [29]), female roe deer rely almost exclusively on available food resources during breeding rather than on body reserves to meet the energetic costs of reproduction [30]. Hence, growth rates and survival of fawns directly depend on food resources during the spring and summer of birth [31–33].

(b) Study areas and populations

The study was carried out in two fenced forests managed by the Office National des Forêts: the 2614 ha Réserve Biologique Intégrale of Chizé (CH) located in western France and the 1360 ha Territoire d'Étude et d'Expérimentation of Trois-Fontaines (TF) in eastern France. Primary production in the CH forest is quite low owing to poor soils and frequent summer droughts, whereas TF is a rich and productive forest owing to high-quality soils and infrequent summer droughts (electronic supplementary material, table S1). No predator of roe deer occurred in either site and the few roe deer hunted at TF were right-censored from the dataset. Both populations have been intensively monitored by using capture–mark–recapture (CMR) methods since 1976 at TF and 1978 at CH. About half the roe deer present in a given population were captured every year (between 8 and 12 days of captures, mostly in January–February) using drive nets. At capture, all animals are sexed and weighed to the nearest 100 g. Since 1985, newborn fawns

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have also been captured and marked around the time of birth, from 15 April to 15 June [32]. In addition to captures, intensive observations took place every year in both study sites during summer and autumn to assess the reproductive success of marked females (see [34] for details).

(c) Roe deer life-history traits

All females included in this study were of known age, because they had been marked as newborn fawns during spring, or as fawns in their first winter (eight to nine months of age), when age can be reliably established on the basis of the presence of milk teeth [35]. We considered reproductive and survival characteristics of prime-aged females (2–8 years) before senescence; these parameters do not vary with age in prime-aged females [36,37]. We divided annual reproductive success into three categories: (i) 'no offspring weaned', (ii) 'one offspring weaned' and (iii) 'two or three offspring weaned' [38]. Triplets were absent at CH and accounted for only 1.8% of litters at TF.

(d) Measures of environmental variation

Previous studies in roe deer have shown that average body mass of weaned offspring is an integrator of environmental conditions around the time of birth (i.e. in spring–summer) for which weather variables and population size are only proxies [33,39]. Thus, we used the average body mass of roe deer fawns in January–February (about eight months of age) of each year, adjusted for possible confounding effects (see below), as a measure of environmental conditions during the previous year (see [40,41] for a similar approach). Hence, environmental conditions experienced each year by juveniles and adults were measured by the average body mass of roe deer fawns the next winter. We estimated year-specific body mass of fawns with linear models (one per site), including sex (to account for the weak sexual size dimorphism of roe deer [26]), month of capture (to control for fawn growth over the winter catch season [35]) and habitat type at CH only (to control for possible confounding effects of habitat quality; see the electronic supplementary material, table S1 and [42] for further details). No heterogeneity of habitat occurred at TF at the home range scale. The adjusted year-specific body masses of roe deer fawns are shown in the electronic supplementary material, figure S1.

(e) Statistical analysis

As a first step, we used linear models to investigate relationships between environmental conditions during early (i.e. year of birth) and adult (i.e. the average environment between 2 and 8 years of age) stages. Then, we performed analyses on life-history traits with environmental conditions in early life characterized as a two-level factor, dichotomized by a median split (bad conditions: below median value of year-specific fawn body mass; good conditions: above or equal median value of year-specific fawn body mass). This allowed us to test explicitly the predictions displayed in figure 1 (i.e. an interaction for PAR and an additive effect for silver spoon hypothesis; see [25] for a similar approach). Interpretation of the results did not change when we considered the quality of early-life conditions as a continuous variable (electronic supplementary material, table S2).

To test the PAR hypothesis for shaping variation in reproductive success of female roe deer, we used multinomial mixed models [43] of annual reproductive success, such that the cumulative probability that a female weaned 0, 1 and 2 or more fawns in a given year is equal to 1. Environmental conditions experienced during year of birth and at a given breeding year plus the interaction between these two variables were entered as fixed effects. Female identity was entered as a random effect, controlling for the non-independence of repeated measures on the same

female. Parameters were estimated by maximum-likelihood using the package 'ordinal' of the software R v. 2.14 [44]. We tested the PAR hypothesis for causing variation in annual adult survival of female roe deer using CMR modelling [45] with E-SURGE [46]. Our models included environmental conditions experienced during year of birth and at a given survival event plus their two-way interactions. Following previous CMR analyses in both populations [47,48], we estimated time-dependent capture probabilities (three periods at TF: 1976–1999, 2000 and 2001–2010; 13 periods at CH: 1978–1985, 1986–1999 and annual capture probabilities from 2000 to 2010). In all models, we used a backward selection procedure, testing successively the first-order interactions and, if not statistically significant, the main effects of covariates. Statistical significance was assessed by likelihood ratio test. Estimates (mean ± s.e.) and sample sizes (n) are given in parentheses.

Finally, we quantified the fitness consequences of early and adult conditions of life as a final test of the PAR. At both TF and CH, we built two sets of Leslie matrix models [49], one for each type of environmental conditions in early life (two groups: bad versus good). We entered the predicted values of reproduction and survival rates according to their relationship with environmental conditions during adulthood (represented as lines in figure 2 and the electronic supplementary material, figure S4) in matrix models (electronic supplementary material, figure S2) to obtain the predicted mean fitness, measured as the asymptotic growth rate [50], of each of these groups facing different adult conditions. We did the same using observed reproduction and survival rates (represented as points in figure 2 and the electronic supplementary material, figure S4) to get the observed mean fitness of each of these groups facing different adult conditions.

3. Results

(a) Environmental variability and predictability

At TF, average body mass of fawns was highly variable among years ($F_{(d.f. = 36,1770)} = 12.68$, $p < 0.001$; coefficient of variation = 6.5%), ranging from 14.80 ± 0.32 kg in 2005 to 20.27 ± 0.28 kg in 1977 (electronic supplementary material, figure S1a). At CH, average body mass of fawns was also highly variable among years ($F_{(d.f. = 34,1757)} = 27.19$, $p < 0.001$; coefficient of variation = 10.0%), ranging from 12.17 ± 0.36 kg in 2011 to 17.72 ± 0.34 kg in 1995 (electronic supplementary material, figure S1b). Environmental conditions were extremely harsh between 1983–1987 and since 2003 at CH, with all average annual body masses less than 14.5 kg.

The correlation between the environmental conditions in early and adult stages was high and positive in the highly productive population of TF ($\beta = 0.43 \pm 0.10$, $p < 0.001$, $R^2 = 0.40$; electronic supplementary material, figure S3a), but non-existent in the food-restricted population of CH ($\beta = 0.17 \pm 0.19$, $p = 0.37$, $R^2 = 0.03$; electronic supplementary material, figure S3b). Thus, PAR could only occur at TF, because without a reliable cue of future environmental conditions, there is no basis for an adaptive scenario in the long run [22,25,51,52]. However, this prediction must be viewed with caution because the observed environmental variability during the study period does not necessarily represent the long-term and past environment in which PAR could have been favoured by natural selection.

(b) Testing the predictive adaptive response hypothesis

Contrary to expectations from PAR, we found no evidence for an interaction between early-life and current environmental
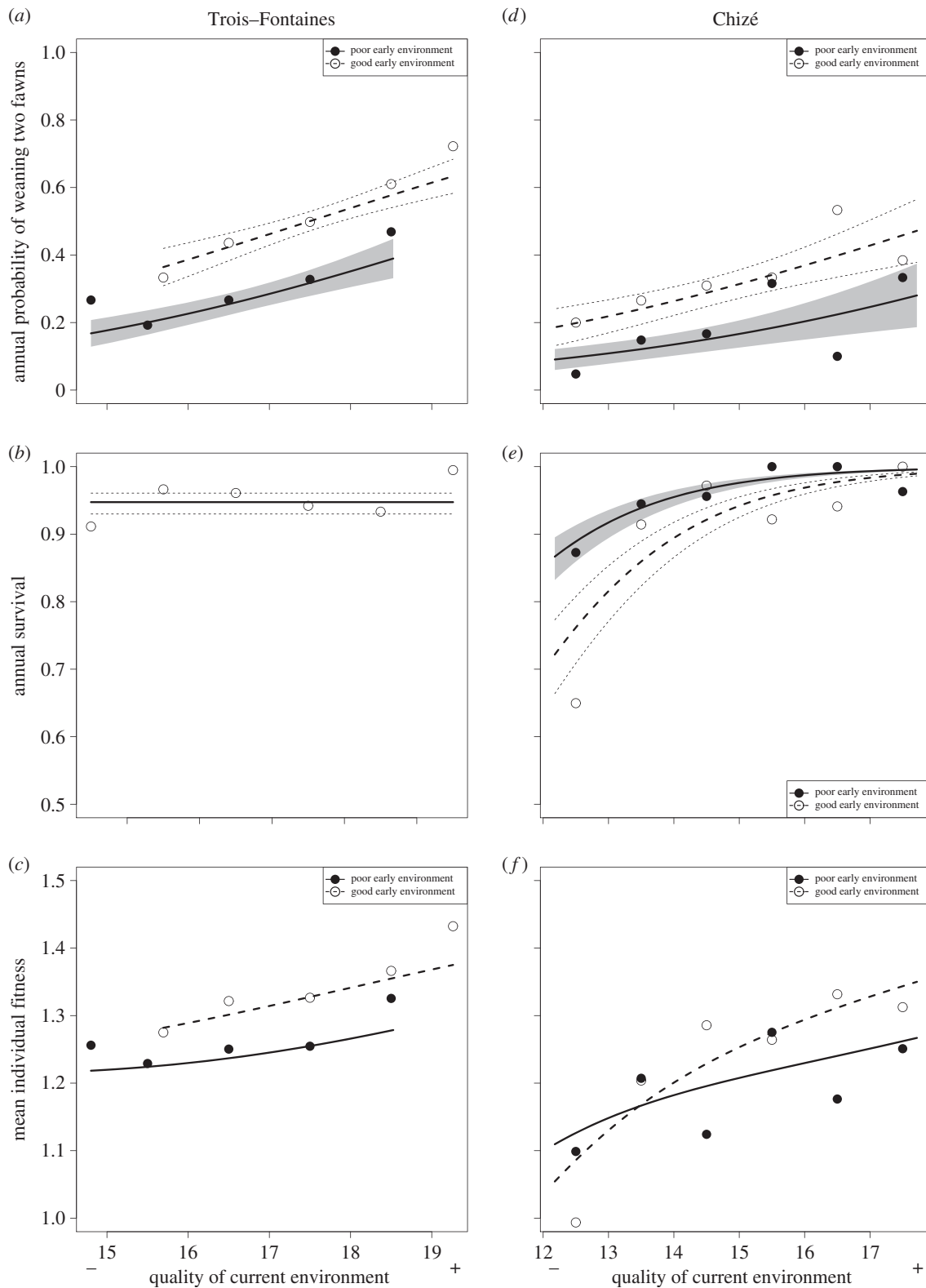
Figure 2. Influence of early-life and current environmental conditions on annual fitness components and mean annual fitness of adult female roe deer in both sites. Variation in (a,d) the annual probability of weaning two fawns, (b,e) annual survival and (c,f) mean annual fitness are shown. The average body mass of roe deer fawns in January–February was used as an annual measure of environmental conditions experienced by female roe deer during the previous year (see Material and methods). The lines represent model predictions with their 95% CIs and points indicate the observed means for each class of 1 kg average fawn body mass. See also the electronic supplementary material, figure S4 for effects of early-life and current environmental conditions on the annual probability to wean 0 fawns or 1 fawn.

conditions on annual reproductive success at TF ($n = 656$, $\chi^2_{(\text{d.f.} = 1)} = 0.07$, $p = 0.79$) or at CH ($n = 275$, $\chi^2_{(\text{d.f.} = 1)} = 0.10$, $p = 0.76$). In both populations, the annual reproductive success of adult females increased with the quality of the current

environment (TF: $\chi^2_{(\text{d.f.} = 1)} = 3.48$, $p = 0.06$, $\beta = 0.19 \pm 0.10$; CH: $\chi^2_{(\text{d.f.} = 1)} = 4.10$, $p = 0.04$, $\beta = 0.18 \pm 0.09$). Being income breeders, female roe deer do not accumulate significant body reserves for reproduction [29,30], so reproductive success

strongly depends on changes in food resources during the last weeks of gestation and early lactation, when reproductive energetic costs peak [53]. Overall, females born in favourable conditions had a consistently higher reproductive output than those born in poor conditions (TF: $\chi^2_{(d.f. = 1)} = 9.95$, $p = 0.001$, $\beta = 0.62 \pm 0.20$; CH: $\chi^2_{(d.f. = 1)} = 5.82$, $p = 0.01$, $\beta = 0.64 \pm 0.26$). For instance, females born in good environmental conditions had 2.15 and 2.29 times higher chances of rearing two fawns to weaning than females born under poor conditions at TF and CH, respectively (figure 2a,d). This probably resulted from long-term positive consequences of early environmental conditions on body mass [54], which in turn influenced reproductive performance of females [41,55].

As for reproduction, no interaction between early-life and current environmental conditions could be detected for annual adult survival rate (TF: $n = 322$, $\chi^2_{(d.f. = 1)} = 0.14$, $p = 0.71$; CH: $n = 331$, $\chi^2_{(d.f. = 1)} = 0.15$, $p = 0.70$). Annual survival of adult females was high and quite constant at TF (figure 2b), irrespective of the environmental conditions experienced early in life ($\chi^2_{(d.f. = 1)} = 0.94$, $p = 0.33$) and in the current year ($\chi^2_{(d.f. = 1)} = 0.1$, $p = 0.75$). At CH, annual adult survival was positively influenced by the quality of current environment ($\chi^2_{(d.f. = 1)} = 31.16$, $p < 0.001$; figure 2e) but, unexpectedly, females born in favourable conditions consistently showed a lower survival than those born in poor conditions ($\chi^2_{(d.f. = 1)} = 11.71$, $p < 0.001$; figure 2e).

At CH, as female roe deer born in poor conditions have lower reproduction, but higher survival rates than females born in good conditions, the overall effect of early conditions on mean fitness depends on the relative effects of the environment on these two demographic rates. We found that under favourable adult conditions, females born in good conditions had a higher mean fitness than those born in poor conditions (figure 2f). However, when adult conditions became very harsh (as observed in 6 years) at CH, the negative effects of early-life conditions on adult survival counteracted their positive influence on reproduction, because females born under poor environmental conditions showed a higher mean fitness than those born under good conditions (figure 2f). At TF, female roe deer born in poor conditions had lower fitness than females born in good conditions independent of the environmental conditions during adulthood (figure 2c).

(c) The confounding effect of viability selection on detection of predictive adaptive response

That the mean fitness curves of good and bad cohorts crossed when environmental conditions during adulthood were harsh at CH (figure 2f) could be interpreted as support for the PAR hypothesis (figure 1a). However, a more parsimonious explanation may involve a difference in viability selection (*sensu* [50]) during the earliest stage of life. Indeed, early body development of roe deer was highly constrained by poor early nutrition in this population [33,39] such that cohorts born under poor conditions may have experienced high condition-dependent mortality. This resulted in a 'filtering effect', so that under poor early-life environmental conditions only the best roe deer survived to adulthood, leading to a high survival in adulthood for these cohorts. For long-lived species such as roe deer, juvenile survival is indeed highly variable and sensitive to environmental conditions [55]. For instance, only 18% of newborns survived until eight to nine months of age during the severe spring–summer drought in 2005 at CH.
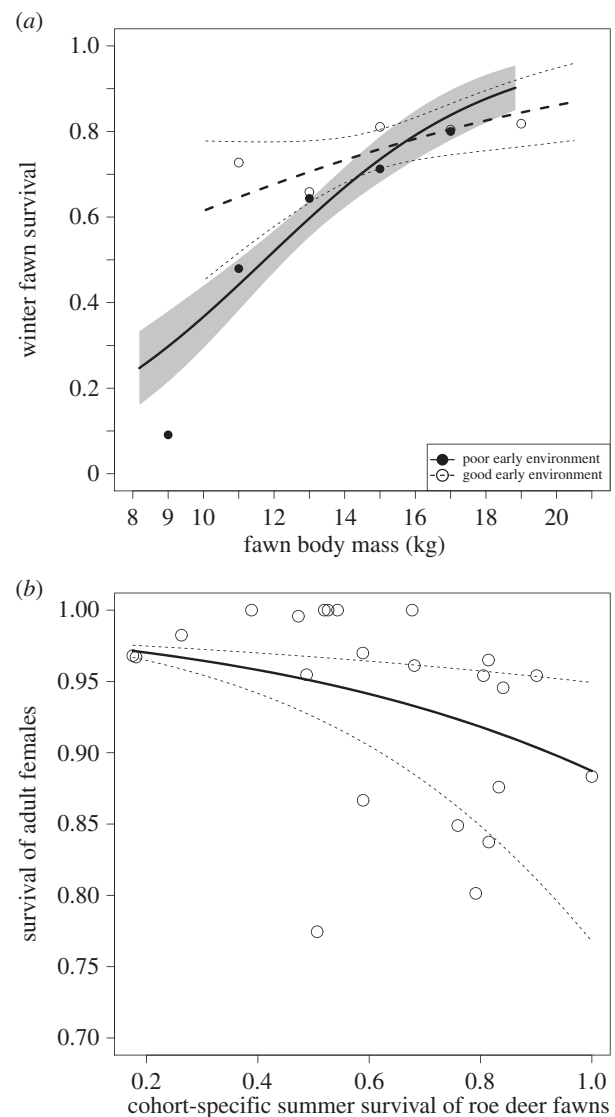

Figure 3. Viability selection during juvenile stage and its consequences on adult survival in the population of Chizé, France. (a) Relationship between winter fawn survival (between 8–9 and 20–21 months of age) of female roe deer and their body mass at eight to nine months of age (adjusted for date of capture) in relation to the quality of early-life environmental conditions. (b) Relationship between survival of adult female roe deer and their cohort-specific summer fawn survival (between 0 and 8–9 months of age). The lines represent model predictions with their 95% CIs.

Conversely, cohorts born under favourable conditions may have experienced a weak viability selection in early life, so weaker individuals can be recruited into the population as adults, but then suffer from increased mortality when meeting harsh environmental conditions during adulthood. In support of this 'filtering effect', the strength of viability selection favouring large body mass decreased with the quality of the environment in early life at CH ($\chi^2_{(d.f. = 1)} = 4.62$, $p = 0.03$; figure 3a). In addition, cohorts suffering from high juvenile mortality showed subsequently higher survival in adulthood ($\chi^2_{(d.f. = 1)} = 8.15$, $p = 0.004$; figure 3b). Nevertheless, no effect of viability selection was detectable on reproduction in this population, because females surviving harsh early-life conditions hardly reached the threshold body mass of 22 kg ($\chi^2_{(d.f. = 1)} = 23.01$, $p < 0.001$; figure 4), above which they raise two fawns successfully [56]. Strong viability selection is thus likely to explain the opposite effects of early-life conditions on reproduction and survival (figure 2d,e), and the resulting
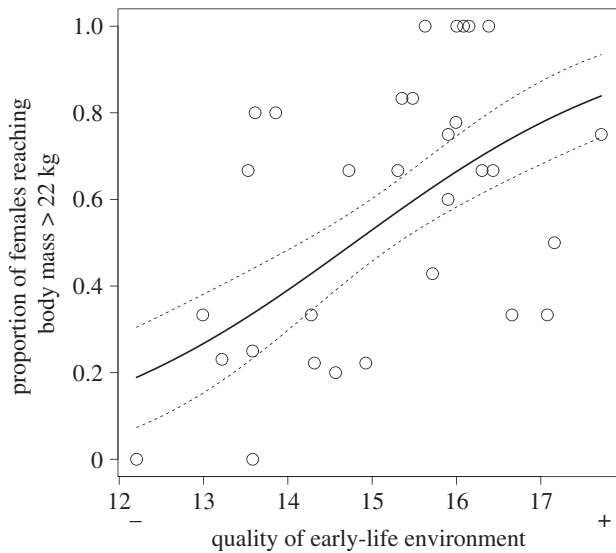
Figure 4. Relationship between the proportion of adult female roe deer with a body mass >22 kg and the quality of early-life environmental conditions at Chizé, France. The average body mass of roe deer fawns in January–February was used as an annual measure of environmental conditions experienced by female roe deer during the previous year (see Material and methods). The solid line represents the predicted relationship with 95% CIs (dotted lines).

interactive effects between environmental conditions during early life and adulthood on mean fitness (figure 2f) we observed in the food-limited population of CH.

In the highly productive forest of TF, even if the strength of viability selection is higher when early environmental conditions are poor ($\chi^2_{(d.f. = 1)} = 3.99$, $p = 0.04$; electronic supplementary material, figure S5), it was half as strong as the viability selection that bad cohorts suffered at CH (on a logit scale, $\beta = 0.32 \pm 0.06$ at CH versus $\beta = 0.17 \pm 0.07$ at TF). Consequently, a low juvenile survival was not associated with higher adult survival at TF ($\chi^2_{(d.f. = 1)} = 0.39$, $p = 0.53$), so the low viability selection during juvenile stage had no consequences on mean fitness of good and bad cohorts during adulthood in this population with abundant resources. Hence, not accounting for between-year differences in viability selection during the earliest stages of life can mimic an apparent support for PAR, in particular under harsh environmental conditions.

4. Discussion

Female roe deer do not adjust their phenotype during their first year of life in anticipation of their future environments, providing no support for the PAR hypothesis. Much of the empirical evidence in support of the PAR comes from short-lived species [57–59]. For instance, female butterflies experiencing food restriction during larval development change their body allocation via an increased thorax ratio (i.e. thorax mass/body mass) that leads to better flight performances during the adult stage, which in turn enhance dispersal into higher quality habitats [58]. However, the extrapolation of such results to long-lived species as done by Gluckman and co-workers in humans has often been questioned [21,22,51]. The evolution of PAR relies on the assumption that early environmental conditions generally predict adult environmental conditions. Simulations recently

performed by Nettle et al. [52] showed that environmental autocorrelation has to be very high to allow the occurrence of what they called 'external PAR'. While in short-lived species matching of the conditions of life at the juvenile and adult stages is likely to occur, the long life and the long time required to achieve reproductive maturity of large mammals make such matching less likely in these species [21]. Despite the marked difference in the correlation of environmental conditions during adulthood with those in early life ($R^2 = 0.40$ versus $R^2 = 0.03$ at TF and CH, respectively), our results rather support the 'silver spoon' hypothesis, which predicts that body development is constrained by poor early nutrition in both populations. Although the environmental predictability we recorded over the study period of more than 35 years does not necessarily represent the long-term and past environment in which PAR could have been evolved, past environments of roe deer populations are likely to have been highly variable. Like other polytocous deer species, the roe deer is indeed adapted to the dynamics of early stages of forest succession rather than to stable climax woodland [60].

Beyond the assumption that the environment in early life provides a reliable clue of the environmental conditions during adulthood, the PAR hypothesis requires that embryos are informed about the quality of environmental conditions during pregnancy. This assumption is questionable for some species. Tactics of energy allocation to reproduction vary along an income–capital continuum [61], which may have a central role for the evolution of adaptive responses to environmental variation during early life. In income breeders such as roe deer [30], the offspring developmental trajectory directly depends on resources available to the mother during the energetically costly periods of late gestation and early lactation. In poor years, embryos receive less energy from mothers and, in turn, should be informed on the environmental conditions. However, this is not the case in capital breeders, which use stored fat reserves to meet the high energy requirements of reproduction [29]. By using energy stored before reproduction, such as in humans, capital breeders buffer (at least partly) offspring dependency from environmental conditions during these critical periods.

Since the initial paper by Williams & Nesse [62], the field of 'evolutionary medicine' or 'Darwinian medicine' has progressed substantially and become an important component of public health (see [63] for a recent review). In humans, PARs are commonly invoked to account for observed associations between early-life conditions and health (as assessed by occurrence of diabetes or cardiovascular diseases) later in life [64]. The connection between PAR and human health is relatively straightforward. If the early-life environment matches the environment during adulthood, then the risk of diseases in late life is low. By contrast, if a mismatch occurs between environments during early life and adulthood, the risk of diseases increases, especially during the post-reproductive period when diseases become relatively invisible to natural selection [11,64]. Although fitness and health are distinct concepts [62], both should peak when early- and later-life environmental conditions match according to the PAR hypothesis. It is important to note that these predictions from the PAR hypothesis about adult health are exactly similar to those from 'the thrifty phenotype' hypothesis [10]. In contrast to the PAR hypothesis, the thrifty phenotype hypothesis posits that selection

favours developmental responses that improve immediate chances of survival at the expense of risking disease later in life [10]. Therefore, understanding the evolutionary processes underlying relationships between early-life conditions and adult health is necessary to discriminate among the competing hypotheses.

The results of our study, based on two populations of the same species living in contrasting environments, clearly demonstrate that harsh early-life conditions impose strong developmental constraints with major fitness consequences, and do not support the PAR hypothesis. Similarly, Hayward and co-workers recently provided the first empirical test of PAR in humans and found no support for it, because individuals experiencing low crop yields in early life showed lower survival and fertility during the famine than individuals experiencing high early-life crop yields in pre-industrial Finnish populations [24]. Moreover, and importantly, we show here that the strong viability selection imposed by very harsh environmental conditions in early life can lead to apparent support for the PAR hypothesis. Confounding effects of viability selection have so far been neglected when testing the PAR hypothesis. Although the PAR hypothesis requires more empirical tests, its validity in long-lived species is increasingly uncertain.

References

1. Hertwig O. 1900 *The biological problem of today: preformation or epigenesis? The basis of a theory of organic development.* New York, NY: Macmillan.

2. Bateson P *et al.* 2004 Developmental plasticity and human health. *Nature* **430**, 419–421. (doi:10.1038/nature02725)

3. Metcalfe NB, Monaghan P. 2001 Compensation for a bad start: grow now, pay later. *Trends Ecol. Evol.* **16**, 254–260. (doi:10.1016/S0169-5347(01)02124-3)

4. Lindström J. 1999 Early development and fitness in birds and mammals. *Trends Ecol. Evol.* **14**, 343–348. (doi:10.1016/S0169-5347(99)01639-0)

5. Lummaa V, Clutton-Brock TH. 2002 Early development, survival and reproduction in humans. *Trends Ecol. Evol.* **17**, 141–147. (doi:10.1016/S0169-5347(01)02414-4)

6. Beckerman AP, Benton TG, Ranta E, Kaitala V, Lundberg P. 2002 Population dynamic consequences of delayed life-history effects. *Trends Ecol. Evol.* **17**, 263–269. (doi:10.1016/S0169-5347(02)02469-2)

7. Monaghan P. 2008 Early growth conditions, phenotypic development and environmental change. *Phil. Trans. R. Soc. B* **363**, 1635–1645. (doi:10.1098/rstb.2007.0011)

8. Clutton-Brock TH, Sheldon BC. 2010 Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol.* **25**, 562–573. (doi:10.1016/j.tree.2010.08.002)

9. Lucas A. 1991 Programming by early nutrition in man. In *The childhood environment and adult disease* (eds GR Bock, J Whelan), pp. 38–55. Chichester, UK: Wiley.

10. Hales CN, Barker DJP. 1992 Type 2 (non-insulin dependent) diabetes mellitus: the thrifty phenotype hypothesis. *Diabetologia* **35**, 595–601. (doi:10.1093/ije/dyt133)

11. Gluckman PD, Hanson MA. 2004 Living with the past: evolution, development, and patterns of disease. *Science* **305**, 1733–1736. (doi:10.1126/science.1095292)

12. Gluckman PD, Hanson MA, Spencer H. 2005 Predictive adaptive responses and human evolution. *Trends Ecol. Evol.* **20**, 527–533. (doi:10.1016/j.tree.2005.08.001)

13. West-Eberhard MJ. 1989 Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* **20**, 249–278. (10.1146/annurev.es.20.110189.001341)

14. Pigliucci M, Murren CJ, Schlichting CD. 2006 Phenotypic plasticity and evolution by genetic assimilation. *J. Exp. Biol.* **209**, 2362–2367. (doi:10.1242/jeb.02070)

15. Nussey DH, Wilson AJ, Brommer JE. 2007 The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.* **20**, 831–844. (doi:10.1111/j.1420-9101.2007.01300.x)

16. Gluckman PD, Hanson MA, Spencer H, Bateson P. 2005 Environmental influences during development and their later consequences for health and disease: implications for the interpretation of empirical studies. *Proc. R. Soc. B* **272**, 671–677. (doi:10.1098/rspb.2004.3001)

17. Cleal JK *et al.* 2007 Mismatched pre- and postnatal nutrition leads to cardiovascular dysfunction and altered renal function in adulthood. *Proc. Natl Acad. Sci. USA* **104**, 9529–9533. (doi:10.1073/pnas.0610373104)

18. Grafen A. 1988 On the uses of data on lifetime reproductive success. In *Reproductive success: studies of individual variation in contrasting breeding systems,* (ed. TH Clutton-Brock), pp. 454–471. Chicago, IL: University of Chicago Press.

19. Albon SD, Clutton-Brock TH, Guinness FE. 1987 Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. *J. Anim. Ecol.* **56**, 69–81. (doi:10.2307/4800)

20. Madsen T, Shine R. 2000 Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. *J. Anim. Ecol.* **69**, 952–958. (doi:10.1111/j.1365-2656.2000.00477.x)

21. Wells JCK. 2006 Is early development in humans a predictive adaptive response anticipating the adult environment? *Trends Ecol. Evol.* **21**, 424–425. (doi:10.1016/j.tree.2006.05.006)

22. Wells JCK. 2007 Flaws in the theory of predictive adaptive responses. *Trends Endocrinol. Metab.* **18**, 331–337. (doi:10.1016/j.tem.2007.07.006)

23. Rickard IJ, Lummaa V. 2007 The predictive adaptive response and metabolic syndrome: challenges for the hypothesis. *Trends Endocrinol. Metab.* **18**, 94–99. (doi:10.1016/j.tem.2007.02.004)

24. Hayward AD, Rickard IJ, Lummaa V. 2013 Influence of early-life nutrition on mortality and reproductive success during a subsequent famine in a preindustrial population. *Proc. Natl Acad. Sci. USA* **110**, 13 886–13 891. (doi:10.1073/pnas.1301817110)

25. Hayward AD, Lummaa V. 2013 Testing the evolutionary basis of the predictive adaptive response hypothesis in a preindustrial human population. *Evol. Med. Public Health* **1**, 106–117. (doi:10.1093/emph/eot007)

26. Andersen R, Duncan P, Linnell JDC. 1998 *The European roe deer: the biology of success.* Oslo, Norway: Scandinavian University Press.

27. Loison A, Festa-Bianchet M, Gaillard JM, Jorgenson JT, Jullien JM. 1999 Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* **80**, 2539–2554. (doi:10.1890/0012-9658(1999)0802539:ASSIFP]2.0.CO;2)

28. Vanpé C, Gaillard JM, Morellet N, Kjellander P, Liberg O, Delorme D, Hewison AJM. 2009 Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer. *J. Mammal* **90**, 661–665. (doi:10.1644/08-MAMM-A-137R.1)

29. Jönsson IK. 1997 Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**, 57–66. (doi:10.2307/3545800)

8

rspb.royalsocietypublishing.org Proc. R. Soc. B **281**: 20140276

30. Andersen R, Gaillard JM, Linnell JDC, Duncan P. 2000 Factors affecting maternal care in an income breeder, the European roe deer. *J. Anim. Ecol.* **69**, 672–682. (doi:10.1046/j.1365-2656.2000.00425.x)

31. Gaillard JM, Delorme D, Jullien JM. 1993 Effects of cohort, sex, and birth date on body development of roe deer (*Capreolus capreolus*) fawns. *Oecologia* **94**, 57–61. (doi:10.1007/BF00317301)

32. Gaillard JM, Boutin JM, Delorme D, Van Laere G, Duncan P, Lebreton JD. 1997 Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* **112**, 502–513. (doi:10.1007/s004420050338)

33. Toïgo C, Gaillard JM, Van Laere G, Hewison AJM, Morellet N. 2006 How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography* **29**, 301–308. (doi:10.1111/j.2006.0906-7590.04394.x)

34. Gaillard JM, Festa-Bianchet M, Delorme D, Jorgenson J. 2000 Body mass and individual fitness in female ungulates: bigger is not always better. *Proc. R. Soc. Lond. B* **267**, 471–477. (doi:10.1098/rspb.2000.1024)

35. Hewison AJM, Gaillard JM, Angibault JM, Van Laere G, Vincent JP. 2002 The influence of density on post-weaning growth in roe deer *Capreolus capreolus* fawns. *J. Zool.* **257**, 303–309. (doi:10.1017/S0952836902000900)

36. Gaillard JM, Andersen R, Delorme D, Linnell JDC. 1998 Family effects on growth and survival of juvenile roe deer. *Ecology* **78**, 2878–2889. (doi:10.1890/0012-9658(1998)079[2878:FEOGAS]2.0.CO;2)

37. Gaillard JM, Viallefont A, Loison A, Festa-Bianchet M. 2004 Assessing senescence patterns in populations of large mammals. *Anim. Biodivers. Conserv.* **27**, 47–58.

38. Hamel S, Côté SD, Gaillard JM, Festa-Bianchet M. 2009 Individual variation in reproductive costs of reproduction: high-quality females always do better. *J. Anim. Ecol.* **78**, 143–151. (doi:10.1111/j.1365-2656.2008.01459.x)

39. Pettorelli N, Gaillard JM, Mysterud A, Duncan P, Stenseth N, Delorme D, Van Laere G, Toïgo C, Klein F. 2006 Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. *Oikos* **112**, 565–572. (doi:10.1111/j.0030-1299.2006.14447.x)

40. Festa-Bianchet M, Coltman D, Turelli L, Jorgenson JT. 2004 Relative allocation to horn and body growth in bighorn rams varies with resource availability. *Behav. Ecol.* **15**, 305–312. (doi:10.1093/beheco/arh014)

41. Hamel S, Gaillard JM, Festa-Bianchet M, Côté SD. 2009 Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology* **90**, 1981–1995. (doi:10.1890/08-0596.1)

42. Pettorelli N, Dray S, Gaillard JM, Chessel D, Duncan P, Illius A, Guillon N, Klein F, Van Laere G. 2003 Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. *Oecologia* **137**, 363–369. (doi:10.1007/s00442-003-1364-7)

43. Agresti A. 2002 *Categorical data analysis*, 2nd edn. New York, NY: Wiley.

44. Christensen RHB. 2013 Ordinal: regression models for ordinal data. R package version 2012–09–11. See http://cran.r-project.org/web/packages/ordinal/index.html.

45. Lebreton JD, Burnham KP, Clobert J, Anderson DR. 1992 Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118. (doi:10.2307/2937171)

46. Choquet R, Rouan L, Pradel R. 2009 Program E-SURGE: a software application for fitting multievent models. In *Modeling demographic processes in marked populations*, (eds DL Thomson, EG Cooch, MJ Conroy), pp. 845–865. New York, NY: Springer.

47. Pettorelli N, Gaillard JM, Duncan P, Maillard D, Van Laere G, Delorme D. 2003 Age and density modify the effects of habitat quality on survival and movements of roe deer. *Ecology* **84**, 3307–3316. (doi:10.1890/02-0602)

48. Choquet R, Viallefont A, Rouan L, Gaanoun K, Gaillard JM. 2011 A semi-Markov model to assess reliably survival patterns from birth to death in free-ranging populations. *Methods Ecol. Evol.* **2**, 383–389. (doi:10.1111/j.2041-210X.2011.00088.x)

49. Caswell H. 2001 *Matrix population models: construction, analysis, and interpretation*, 2nd edn. Sunderland, MA: Sinauer Associates.

50. Fisher RA. 1930 *The genetical theory of natural selection*. Oxford, UK: Clarendon Press.

51. Kuzawa CW. 2005 Fetal origins of developmental plasticity: are foetal cues reliable predictors of future nutritional environments? *Am. J. Hum. Biol.* **17**, 5–21. (doi:10.1002/ajhb.20091)

52. Nettle D, Frankenhuis WE, Rickard IJ. 2013 The evolution of predictive adaptive responses in human life history. *Proc. R. Soc. B* **280**, 20131343. (doi:10.1098/rspb.2013.1343)

53. Sadleir RMFS. 1987 Reproduction in female Cervids. In *Biology and management of the Cervidae* (ed. CM Wemmer), pp. 123–144. Washington, DC: Smithsonian Institution Press.

54. Douhard M, Gaillard JM, Delorme D, Capron G, Duncan P, Klein F, Bonenfant C. 2013 Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females. *Ecology* **94**, 1805–1814. (doi:10.1890/13-0034.1)

55. Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C. 2000 Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* **31**, 367–393. (doi:10.1146/annurev.ecolsys.31.1.367)

56. Gaillard JM, Sempéré AJ, Boutin JM, Van Laere G, Boisaubert B. 1992 Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). *Can. J. Zool.* **70**, 1541–1545. (doi:10.1139/z92-212)

57. Lee TM, Zucker I. 1988 Vole infant development is influenced perinatally by maternal photoperiodic history. *Am. J. Physiol.* **255**, R831–R838.

58. van den Heuvel J, Saastamoinen M, Brakefield PM, Kirkwood TBL, Zwaan BJ, Shanley DP. 2013 The predictive adaptive response: modeling the life-history evolution of the butterfly *Bicyclus anynana* in seasonal environments. *Am. Nat.* **181**, 28–42. (doi:10.1086/668818)

59. Dantzer B, Newman AEM, Boonstra R, Palme R, Boutin S, Humphries MM, McAdam AG. 2013 Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. *Science* **340**, 1215–1217. (doi:10.1126/science.1235765)

60. Bunnell FL. 1987 Reproductive tactics of cervidae and their relationships to habitat. In *Biology and management of the Cervidae* (ed. CM Wemmer), pp. 145–167. Washington, DC: Smithsonian Institution Press.

61. Warner DA, Bonnet X, Hobson KA, Shine R. 2008 Lizards combine stored energy and recently acquired nutrients flexibly to fuel reproduction. *J. Anim. Ecol.* **77**, 1242–1249. (doi:10.1111/j.1365-2656.2008.01442.x)

62. Williams GC, Nesse RM. 1991 The dawn of Darwinian medicine. *Q. Rev. Biol.* **66**, 1–22. (doi:10.1086/417048)

63. Stearns SC. 2012 Evolutionary medicine: its scope, interest and potential. *Proc. R. Soc. B* **279**, 4305–4321. (doi:10.1098/rspb.2012.1326)

64. Gluckman PD, Hanson MA. 2006 Adult disease echoes of the past. *Eur. J. Endocrinol.* **155**, S47–S50. (doi:10.1530/eje.1.02233)