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A trade-off between reproductive investment and maternal cerebellum size in a precocial bird

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Abstract

Natural selection favours increased investment in reproduction, yet considerable variation in parental investment is observed in natural populations. Life history theory predicts that this variation is maintained by a trade-off between the benefits of increased reproductive investment and its associated costs for the parents. The nature of these costs of reproduction, however, remains poorly understood. The brain is an energetically highly expensive organ and increased reproductive investment may therefore negatively affect brain maintenance. Using artificial selection lines for high and low prenatal maternal investment in a precocial bird, the Japanese quail (*Coturnix japonica*), we provide experimental evidence for this hypothesis by showing that increased prenatal provisioning negatively affects the size of a particular brain region of the mother, the cerebellum. Our finding suggests that cognitive demands may constrain the evolution of parental investment, and vice versa, contributing to the maintenance of variation in reproductive behaviour in animal populations.

Keywords: life-history evolution; trade-off; brain size; parental care; cost of reproduction; reproductive investment

Introduction

Conditions experienced during the first stages of life have long-lasting consequences for an individual's fitness [1]. Because early life conditions are strongly influenced by the parents in most taxa, natural selection will favour increased parental provisioning. Yet, considerable variation in parental investment is observed in natural populations [2], suggesting that costs of reproduction constrain the evolution of parental care [3]. The nature of these costs of reproduction, however, is still poorly understood [4].

The brain is one of the most energetically expensive organs in vertebrates [5]. Parental investment of limited resources into reproduction may therefore negatively affect brain maintenance, and vice versa. In line with this idea, brain size is negatively associated with fecundity within [6] and across [7, 8] species. Moreover, in humans, there is anecdotal evidence that resources are plastically reallocated from the brain to reproduction during pregnancy, with a woman's brain shrinking by up to 7% during the course of gestation [9]. To date, this trade-off has only been considered in terms of the brain as a single unit, despite the brain being a highly differentiated organ. No study has, therefore, been able to demonstrate whether such a trade-off involves the brain as a whole, or only specific brain regions.

If there is a trade-off between reproductive investment and brain maintenance, we predict that individuals that invest more in reproduction experience a stronger reduction in the size of the brain, or specific regions thereof. Here we experimentally tested this hypothesis using artificial selection lines for divergent maternal investment in a precocial bird, the Japanese quail (*Coturnix japonica*) [10]. In precocial birds, offspring are largely independent after birth and little post-hatching care is provided by the parents. Prenatal maternal provisioning, in the form of differential resource allocation to the eggs, therefore plays a key role in mediating offspring performance [11, 12]. Because offspring provisioning is limited to females in this species, we predict that resource-based trade-offs between reproductive investment and brain maintenance will be found in females, but not in males. Furthermore, we predict that females selected for high maternal investment will experience higher costs of reproduction (i.e. a stronger reduction in the mass of the brain or specific brain regions) than females selected for low maternal investment.

Material and Methods

Selection lines for divergent maternal investment

We artificially selected Japanese quail for high (H-line) and low (L-line) prenatal maternal investment using relative egg mass (i.e. egg mass corrected for female body mass and size) as the selection criterion (see [10] for details). After four generations of directional selection, the replicated H- and L-lines differed in egg mass by > 1 SD (ESM1), whereas there was no evidence for a line difference in the number of eggs laid [10]. For this study, we used males and females from the fourth and fifth generation of the selection experiment.

Brain measures

Breeding pairs were kept in cages (122 x 50 x 50cm) for reproduction. After breeding, 68 H-line females, 76 H-line males, 54 L-line females, and 79 L-line males were euthanized. We measured body mass and removed the brain from the skull. We then separated the cerebellum, which is involved in diverse cognitive functions in birds (ESM2), from the rest of the brain (ROB; total brain – cerebellum), and weighed both parts separately to the nearest 0.001 g (wet mass). A pilot study showed that wet and dry brain masses are strongly positively correlated ($r = 0.750$, $P < 0.001$, $N = 18$).

Statistical analysis

We used linear mixed effect models to test for differences in cerebellum mass, the mass of the ROB, and the proportion (%) of the cerebellum in the total brain mass between selection lines and sexes. Sex, selection line, the interaction between sex and selection line, generation and line replicate were included as fixed effects, and family ID was included as a random effect.

We ran the analyses without (i.e. absolute cerebellum mass) and with (i.e. relative cerebellum mass) body mass included as a covariate. Cerebellum mass, the mass of the ROB and body mass were $\log_{10}$ transformed and proportional cerebellum mass was arcsine transformed before analysis. The interaction term was removed from the final models if it was non-significant. *P* values were obtained by comparing two nested models, with and without the variable of interest, using likelihood ratio tests. Analyses were performed in R using the package lme4 [13].

Results

Consistent with a trade-off scenario, we observed a significant interaction effect between selection line and sex on cerebellum size (absolute cerebellum size: $\chi^2 = 9.824$, $P = 0.002$, Fig. 1A; body size-corrected cerebellum size: $\chi^2 = 10.010$, $P = 0.002$, Fig. 1B). Females selected for high maternal investment had a significantly smaller cerebellum compared to both males from the high investment lines ($\chi^2 = 23.962$, $P < 0.001$) and females selected for low maternal investment ($\chi^2 = 4.754$, $P = 0.029$; ESM1). In contrast, the difference in cerebellum size between males and females from the low investment lines was considerably smaller and statistically non-significant ($\chi^2 = 2.801$, $P = 0.094$). Furthermore, no significant difference in cerebellum size between males from the divergent lines was found ($\chi^2 = 0.007$, $P = 0.935$; ESM3). When considering the ROB, we observed an overall sexual dimorphism with females having a smaller ROB, both absolutely ($\chi^2 = 7.347$, $P = 0.007$) and relatively to their (larger) body size ($\chi^2 = 16.999$, $P < 0.001$). However, unlike for the cerebellum, the strength of this sex difference was similar across selection lines (sex x line interaction: $\chi^2 = 0.334$, $P = 0.563$ for absolute, and $\chi^2 = 0.375$, $P = 0.540$ for body size corrected brain size). Furthermore, no overall difference between the lines was observed ($\chi^2 = 0.5892$, $P = 0.443$). Consequently, females selected for high maternal investment had not only absolutely, but also proportionally (i.e. relative to the rest of the brain) a smaller cerebellum than males ($\chi^2 = 17.820$, $P < 0.001$), whereas females and males from the low maternal investment lines did not differ in proportional cerebellum size ($\chi^2 = 0.287$, $P = 0.592$; sex x line interaction: $\chi^2 = 10.214$, $P = 0.001$, Fig. 1C). Furthermore, females selected for high maternal investment had a proportionally smaller cerebellum than females from the low investment lines ($\chi^2 = 4.227$, $P = 0.040$). These results show that it is specifically individuals that invest heavily in reproduction (i.e. H-line females) that experience a reduction in absolute, relative as well as proportional cerebellum size.

Discussion

Life history theory predicts that the benefits of reproductive investment are balanced by their associated costs for the parents [3]. These costs have been suggested to involve physiological processes such as immunosupression [14] or oxidative stress [15]. Our study shows that in addition, impaired maintenance of specific brain regions, and the likely associated reduction in cognitive capacity [6, 16], may represent a significant cost of reproduction that may contribute to the maintenance of variation in parental provisioning.

Currently, we can only speculate why it was specifically the cerebellum, but not the ROB, that was affected by differential maternal investment. Because the ROB consists of number of different brain regions, we may lack the power to detect reductions of specific ROB regions, or they might be masked by reallocations within the ROB. Alternatively, the specific size reduction of the cerebellum may be explained by particularly high maintenance costs of this brain region in birds. Further studies are needed to test this hypothesis.

The cerebellum is involved in diverse cognitive functions such as sensory-motor control, memory and learning [17, 18]. Although, very little is known about the relationship between cerebellum size and cognitive capacity in non-human species (ESM2), in humans the cerebellum is known to be particularly vulnerable to age-related loss of mass [19], and its volume is related to cognitive performance [20]. These findings suggest that the smaller cerebellum in females that invest heavily in reproduction may have negative consequences for their cognitive capacity (see also [6]), potentially affecting their survival. In line with this idea, guppy (*Poecilia reticulata*) females artificially selected for small brain size have recently been found to survive significantly worse in an environment with high predation risk than large-brained females [21], suggesting that females with a large brain have a cognitive advantage that allows them to avoid predation [22]. Ultimately, the novelty and predictability of the environment will determine the costs and benefits associated with cognitive capacity [23, 24], and may thereby indirectly shape the optimal level of reproductive investment.

Conclusions

Our study provides the first experimental evidence that increased reproductive investment results in a mass reduction of a specific brain region, the cerebellum. Together with evidence from comparative studies that show a negative relationship between brain size and fecundity across species [7, 8], and the finding that artificial selection for large brain size leads to a reduced fecundity within species [6], it suggests that impaired cognitive capacity may be a significant cost of reproduction that contributes to the maintenance of variation in reproductive behaviour in animal populations.

Ethics

Experimental procedures were conducted under licences provided by the Veterinary Office of the Canton of Zurich, Switzerland (195/2010; 14/2014; 156).

Data Accessibility

Data are available from Dryad [25].

Competing interests

We have no competing interests.

Authors’ Contributions

JLP performed the selection experiment, CE performed the brain dissections, BT conceived the study, analysed the data and wrote the paper. All authors revised the manuscript critically, gave final approval for publication and agreed to be accountable for all aspects of the work.

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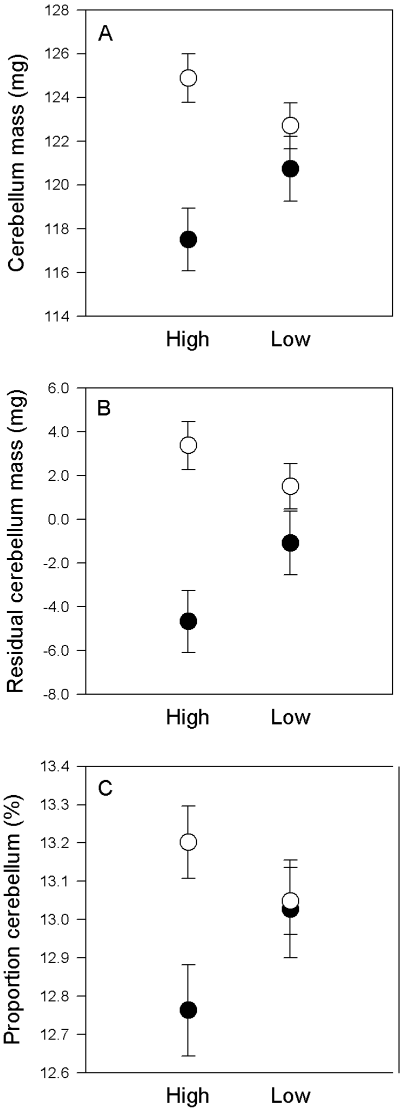
Figure 1 Cerebellum mass of males and females selected for high and low prenatal maternal investment.

Cerebellum mass (A), residuals of a linear regression of cerebellum mass on body mass (B), and proportional cerebellum mass (C) of females (filled-circles) and males (open-circles) from selection lines for high (High) and low (Low) prenatal maternal investment. Means ± SE are shown.



Electronic supplementary material

A trade-off between reproductive investment and maternal cerebellum size in a precocial bird

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EMS1. Additional analyses

Differences in maternal investment between the selection lines

We used a linear mixed effects model to test for a difference in egg size between females from the divergent lines used in our study. Selection line, generation, line replicate were included as fixed effects, and family ID was included as a random effect. Females selected for high maternal investment laid significantly larger eggs (mean ± SD: 12.6 ± 1.1g) than females selected for low maternal investment (11.2 ± 0.9g; $\chi^2 = 39.154$, $P < 0.001$; see also [1]).

Eggs from the high investment lines contained more yolk and albumen (i.e. more resources [1]). Furthermore, females from the high investment lines had larger reproductive organs and a higher resting metabolic rate than females from the low investment lines [2]. This, together with the lack of a response in the number of eggs laid [1], demonstrates that females from the high investment lines showed an increased investment in reproduction.

Relationship between egg size and cerebellum size

In addition to the analysis presented in the main text, we tested for a relationship between cerebellum size and egg investment using a linear mixed effects model that included generation as a fixed effect, family ID as a random effect, and average egg size of a female (in g), instead of line, and female body mass as covariates. There was a negative relationship between egg size and cerebellum size across all females ($\chi^2 = 4.539$, $P = 0.033$; controlling for female body mass), further strengthening the conclusion that increased maternal investment is associated with a reduced cerebellum size.

EMS2. The role of the cerebellum in cognition

The cerebellum is involved in diverse cognitive functions such as sensory-motor control, memory and learning [3-5]. In birds, there is a correlation between cerebellum size or foliation and bower [6] and nest complexity [7], as well as tool use [8] across species. In humans the cerebellum is known to be particularly vulnerable to age-related loss of mass [9], and its volume is related to cognitive performance [10]. To date, little is known, however, about the relationship between cerebellum size and cognitive capacity within non-human species.

Unfortunately, it was not possible to further separate other candidate brain regions within the rest of the brain because of practical limitations.

EMS3. Lack of a difference in males' cerebellum size

Because no difference in the males' cerebellum size was observed between the lines, our results suggest that the reduction in cerebellum size in females, and in particular in females from the high investment lines, was due to a plastic reallocation of resources during reproduction (see also [11]). However, the cerebellum of birds in pre-reproductive state would have to be measured to completely rule out alternative explanations. Furthermore, the lack of a difference in males highlights that developing in a large egg has no significant long-term effects on brain size (but see e.g. [12] for a different pattern across species).

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