

Survival & Reproduction versus the environment: a trade-off analysis

A comparison between the pace of life hypothesis and the silver spoon hypothesis

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The trade-off between survival and reproduction is central in life-history, and susceptible to environmental effects. Both survival and reproduction require resources which can be limited, thus forcing individuals to expend more energy into one than the other. For example, in passerine birds, the combination of harder developmental conditions (increased brood size) and increased foraging effort (less food availability) was found to reduce individuals' survival and lifespan. Due to there being a trade-off between survival and reproduction, this decrease in survival should affect reproduction. According to literature, there are currently two hypotheses that predict the effect of environmentally induced developmental factors on reproduction: the pace of life hypothesis, which argues reproductive success will increase, and the silver spoon hypothesis, which argues reproductive success will decrease. The extra foraging effort, on the other hand, is predicted to limit expendable energy, which could also influence survival or reproduction. In this paper we further analysed the survival versus reproduction trade-off to review which hypothesis fits the trade-off best. This was done by conducting two separate, yet interlinked studies on the passerine zebra finch (*Taeniopygia guttata*) focussing on both survival and reproduction separately. Although not entirely according to expectations, we generally found that individuals from a hard development and hard foraging treatment had a decreased survival and decreased reproductive output. These findings fit the silver spoon hypothesis much better and thus made us conclude that individuals of lesser quality have a lower reproductive success and are under the effect of the silver spoon hypothesis.

1. Introduction

Throughout one's life-history, individuals are constantly faced with choices which ultimately come down to trade-offs and how they deal with these trade-offs. In life-history evolution, the trade-off between reproduction and survival is arguably the most central (Stearns, 1992; Roff, 2002; Cox *et al.*, 2010). In essence, this trade-off is the choice between spending energy on oneself (survival) or into one's future (reproduction). The physiological reasoning behind the trade-off is based on the assumption that both survival and reproduction cost resources, such as energy and nutrients, and thus these two fitness elements are of competitive nature (Zera & Harshman, 2001; Harshman & Zera, 2007; Cox *et al.*, 2010). As these fitness elements are dependent on environmental factors such as nutrient availability, it becomes apparent that this trade-off can and needs to be quite flexible and adaptable (Cox *et al.*, 2010). However, precisely how and to what extent these environmental factors can influence this trade-off is as of yet still mostly unknown (Briga *et al.*, 2017).

This study reviewed two kinds of environmental factors (brood size and food availability) that together influence this trade-off. In recent studies it has been found that passerine birds individuals from enlarged broods have a decreased lifespan when these individuals are also subjected to low food availability, as compared to individuals from reduced broods (Briga *et al.*, 2017). Furthermore, other studies also found that sibling competition, food deprivation, elevated corticosterone levels, and a

whole host of other environmentally induced factors decreased lifespan (Ricklefs, 1993; Drummond & Anaconda, 2015). Because survival and reproduction are in a trade-off, this reduction in survival is predicted to have an effect on reproduction. The trade-off between survival and reproduction argues that individuals of lesser quality must spend more energy into somatic maintenance (survival) to retain their health. There are currently two hypothesis that predict how developmental environmental effects will alter the trade-off: the pace of life hypothesis and the silver spoon hypothesis.

One theory behind the trade-off predicts that selection rewards individuals to have a higher rate of reproduction to counter their shorter lifespan and still be able to reproduce a sufficient amount (Briga *et al.*, 2017). This in turn causes the individuals to spend less effort on their somatic maintenance (survival). This hypothesis is often referred to as the pace of life hypothesis (Réale *et al.*, 2010; Niemelä *et al.*, 2013). The alternative is that individuals are required to expend more energy on somatic maintenance in order to retain their health and be able to reproduce. Individuals of lesser quality are predicted to have to 'catch up' to higher quality individuals by investing into somatic maintenance before being able to successfully reproduce. This hypothesis is also known as the silver spoon hypothesis (Stamps, 2006).

The aforementioned environmental effects tested by Briga *et al.* (2017) are predicted to affect the trade-off by limiting individuals' expendable energy and fitness (Gustafsson, 1987; Kitaysky *et al.*, 2010). An increased brood size often leads to more competition amongst siblings (Neuenschwander *et al.*, 2003; Briga, 2016), which in turn causes a decrease in fitness (Gustafsson, 1987). Developmental effects like these are what the previous two hypotheses are based upon. Similarly, a long-term low food availability has been hypothesized to reduce fitness (Piatt *et al.*, 2007; Hunt *et al.*, 2008), but has also been suggested to decrease fecundity (Lack, 1966; Cairns, 1988). Due to the extra effort required to look for food when food availability is low, it is physiologically similar to individuals having to exert more effort to obtain food (Koetsier & Verhulst, 2011). The aforementioned hypothesis are only applicable to developmental environmental effects on the trade-off. The energy limitation introduced by this extra foraging effort can thus potentially alter what the hypotheses predict and thus affect the trade-off as a whole. Through these effects, these environmental factors can thus heavily influence the trade-off between survival and reproduction. However, as mentioned before, the precise impact on the trade-off is uncertain and less well studied due to the combination of developmental and foraging effort environmental effects.

This paper consists of two separate, yet connected analyses on both the survival and reproduction side of the trade-off conducted with two

2. Material and methods

As mentioned in the introduction, this paper consists of two separate, yet connected studies. These will be separately handled in the results and further on in the paper, but the methods of these two studies can overlap quite heavily.

2.1.: Survival Study

This study was conducted on a captive population of zebra finches from 2009 until 2015. Most individuals (N=162) were subjected to a developmental manipulation by having their clutch size altered. Afterwards during their adulthood some of these individuals were allowed to breed to test the potential costs of reproduction in combination to their aforementioned developmental manipulations on survival. This was the main experimental setup of the study, and thus when referring to individuals in the experiment, we mean the individuals separated in breeding and non-breeding groups.

2.1.1: Developmental manipulation – Cross-fostering

The birds used in the experiment were raised from healthy semi-randomly paired (non-experimental) individuals, housed in indoor breeding cages (L x W x H: 80 x 40 x 40 centimetre) with a nest-box and hay as nesting material inside. These aviaries were kept under constant conditions: a temperature of around 21°C, with a 60% humidity, and a Light:Dark cycle of 14:10 (07:00-21:00h light). Water, sepi, and a commercial tropical seed mixture were provided *ad libitum*. The birds were not given any extra supplemental egg food after eggs hatched, to standardise feeding conditions for the chicks. To ensure animal welfare and get a proper overview of the growing conditions of the eggs and chicks, the breeding cages and nest-boxes were checked daily.

Once the oldest chick in a nest reached 4-5 days, the cross-fostering manipulation was initiated. The chicks in this nest were cross-fostered

separate studies on the passerine Zebra Finch (*Taeniopygia guttata*). The first study reviews the trade-off from the survival perspective by altering individuals' early life development (hereafter "Survival study"). The second study is more reproduction focused than the first and reviews that side of the trade-off. After altering the early life development of individuals much like the survival study, this study also alters the adult life of the individuals by increasing or decreasing their required foraging effort (hereafter "Reproduction study").

Furthermore, as both studies are based on the same theory, the research question and hypotheses overlap, but the studies themselves simply view the question and hypotheses from a different angle: "How do developmental, foraging, and the combination of these manipulations affect the survival and reproductive success of Zebra Finches?". The hypotheses for this question originate from the aforementioned theories behind the trade-off between survival and reproduction: The pace of life hypothesis and the silver spoon hypothesis. This is combined with the limited expendable energy introduced by the extra foraging effort. According to the pace of life hypothesis, we expect to find that individuals from a hard development and hard foraging treatment have a decreased survival, but increased reproduction. Whereas in regards to the silver spoon hypothesis, we expect to find that individuals from a hard development and hard foraging treatment have both a decreased survival and decreased reproduction.

randomly with other nests where the oldest chick had also reached 4-5 days to create small (2, sometimes 3 hatchlings) and large (6, sometimes 5 hatchlings) broods. Observations in the wild showed that an increase in clutch size caused the chicks to beg more for food, meaning chicks in bigger clutches had to exert more effort to obtain food compared to chicks in small clutches and generally had an increased amount of sibling competition (Neuenschwander *et al.*, 2003; Briga, 2016). Individuals that grew up in a small nest are thus hereafter referred to as coming from an easy development, whereas individuals from a large nest are hereafter referred to as coming from a hard development. These brood sizes are within the natural range, as observed in the wild (Zann, 1996). When the birds reached 15 days of age, they were ringed for identification purposes. From the age of 35 days up until 120 (average of 105 days, between 90 and 120) days old, the birds were placed in large indoor aviaries (153 x 76 x 110 cm) together with (up to 40) same sex individuals and four adults (two male and two female) for sexual imprinting. This developmental manipulation is described in extended detail in Briga *et al.* (2017).

2.1.2: Adulthood and data collection

Once the birds reached an age of approximately 100 days, they were randomly evenly assigned over eight outdoor aviaries (310 x 210 x 150 cm) in semi-natural conditions. Each aviary contained one sex, a maximum of 25 birds, and an approximately evenly distributed amount of easy and hard development individuals. These eight aviaries were distributed over four breeding and four non-breeding aviaries as part of the experimental setup to test the cost of reproduction. As a result of this, the four breeding aviaries were checked three times a week to collect reproduction data. As the experiment ran for six years, it became ideal to test for the effects of development and breeding behaviour on survival. Thus, the longevity of individuals was recorded together with their birth date and the date the birds were placed in the experiment.

2.1.3: Statistical Analysis

Data was analysed using R 3.5.1 (Ihaka & Gentleman, 1996) inside RStudio 1.1.456 (RStudio Team, 2015). See the appendix for used packages and the script itself. Survival analyses were conducted using piece-wise exponential additive models (Bender & Scheipl, 2018). These models were created mainly to detect significant survival differences between breeding and non-breeding individuals, sex, and developmental categories. The time variable for these survival analyses (and thus also the response variable) was the years the individual spent in the experiment as a function of survival. This was corrected for by including the age the individual had when put into the experiment (henceforth: starting age). Moreover, some individuals were censored when they had, for example, died after the experiment had ended or were euthanised. This censoring allowed us to control these exceptions on survival, while still including the individuals in the analysis. The predictor variables for these models were, as previously mentioned, the individuals experimental group (breeding vs. non-breeding), sex, developmental category (small brood, large brood, no development), and starting age. Possible interactions between these variables were also tested for. Models were step-wise shortened using Ockham's razor (Jefferys *et al.*, 1992) to end up with a minimum adequate model. The summary function in R was used to test for significant predictor variables and/or interactions between them for these models.

2.2: Reproduction Study

The reproduction study is by all means a continuation of the survival study. Having been conducted from September 2017 onwards to June 2019, it both increased the environmental factors influencing the trade-off between survival and reproduction, and is also increasing the understanding of this trade-off by focussing more on reproductive success. The latter is done by keeping a better track of the reproduction of the birds. Moreover, the study has a more expanded fitness analysis by having frequent biometry measures of the produced chicks to get a proper understanding of the long lasting future effects of the environmental manipulations conducted in this study. Sadly however, due to data collection having stopped in the middle of the 2019 breeding season meant these later biometry measures were not yet conducted and thus not accounted for in this paper. Genetic parentage was also not able to be included due to this time constraint, and thus all parentage data is based on social parents.

2.2.1: Developmental manipulation – Cross-fostering

The developmental manipulation used in this experiment is the same as the one used in the survival study in 2.1.1. See Briga *et al.* (2017) for full details.

2.2.2: Adulthood manipulation – Foraging effort

At around 105 days of age (between 90 and 120 days), the individuals were placed in the adult outdoor foraging effort treatment. Birds from both easy and hard developments were placed in either an easy or a hard foraging environment (L x W x H: 310 x 210 x 150 centimetre) located in Groningen, The Netherlands (53.242945, 6.537672). All treatments were equally divided over both treatment and sex. Thus, each aviary had five (± 2) hard development females, five (± 2) hard development males, five (± 2) easy development females, and five (± 2) easy development males for a total of ~ 20 (± 4) birds per aviary (four aviaries, N= ~ 80).

The foraging effort manipulation was conducted in the same way as explained in Koetsier & Verhulst (2011). The essence of the technique

is that food is offered in a container (L x W x H: 120 x 10 x 60 centimetre) suspended in the air, with five holes in each side from which the birds can feed (figure 1). 'Easy' foraging aviaries have inner (/perching) tubes below the outer (/feeding) tubes, allowing the birds to perch and easily feed. In 'hard' foraging aviaries the perches were absent, forcing the birds to hover to obtain food and then fly back to a distant perch to consume the seeds, which is energetically more demanding and similar to a low food availability (Koetsier & Verhulst, 2011).

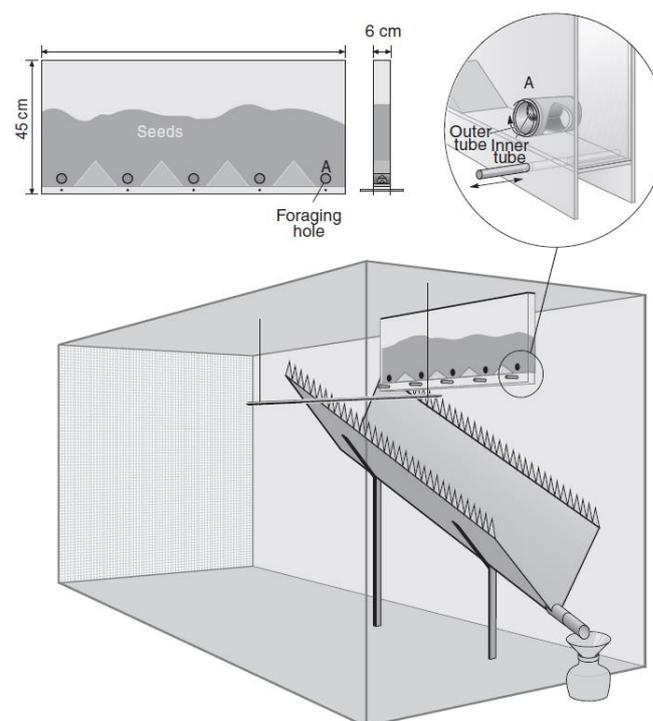


Figure 1. Setup of the foraging difficulty manipulation. At the bottom is an overview of the aviary with the food container hanging from the ceiling with a tray system designed to catch fallen seeds. At the top right is a detail of the tubes from which food is obtained and on which the birds can perch (which is removed for effortless foraging). At the top left is the food container viewed from the side and front (Koetsier & Verhulst, 2011).

Prior to being placed in the foraging effort manipulation, all birds were trained for the foraging protocol in two separate outdoor aviaries of the same size (L x W x H: 120 x 6 x 45 centimetre). The birds were initially placed in these aviaries to let the birds adjust from the indoor to the outdoor climate. After a minimum of 2 weeks, the training for the foraging effort manipulation started by gradually shortening the perching tubes by 0.5 centimetre every day over the course of ten days. The perching tubes initially reached five centimetres out of the box and were shortened to 0.5 centimetres before being removed altogether. After each shortening, the birds were observed to ensure that they were still feeding, which was especially critical in the last few centimetre-steps. If the birds did not feed, we did not shorten the tubes. The birds were then kept without any perching tubes for a week to let them adjust properly. This training was conducted for all birds, including the ones in the easy foraging group to ensure comparability between the treatment groups in case some birds were not able to cope with the effortful foraging condition. Finally, in the beginning of March, all individuals were blood sampled to establish genetic parentage. Again, however, this was not included in this paper due to time constraints.

2.2.3: Reproduction data collection

The breeding season of zebra finches housed in the Netherlands is mainly determined by the availability of nesting locations and nesting materials (Zann, 1996). This is because zebra finches originate from Australia, where humidity is the limiting factor (Zann, 1996). However, due to a higher humidity, this limitation is entirely removed in the Netherlands, thus the birds will breed year-round if location and materials are provided. The birds were offered nest boxes by the end of March 2019 to allow them to reproduce. Data was collected until June 2019. Instead of daily checks, the nests were checked 3 times a week (on the mornings of Monday, Wednesday, and Friday), to ensure the health and wellbeing of the birds, while simultaneously limiting disturbance. Next to welfare, we collected reproductive output data consisting of number of eggs and chicks in a nest. Prior to these checks, the birds were observed to establish the social parents of the chicks.

On day 1 (the same day the chick is found), the individual chicks were marked and weighed. The marking was done by removing one (or more) of the four feather patches on the chicks' heads. On day 12(\pm 1), we ringed all chicks in a nest for identification purposes. On day 15(\pm 1), the first biometry measurements were taken. These included weight, tarsus-length, wing-length, and headbill-length. Furthermore, blood was taken in order to establish genetic parentage. Then, on day 31(\pm 1) the same biometry measurements as on day 15 were taken again. During the entire breeding season, the aviaries were observed to determine the social parents of the nests.

2.2.4: Statistical analyses

Data was analysed using R 3.5.1 (Ihaka & Gentleman, 1996) inside RStudio 1.1.456 (RStudio Team, 2015). See the appendix for used packages and the script itself. Analyses were conducted from three different 'perspectives': 1. the offspring fitness, 2. maternal reproductive output, and 3. paternal reproductive output. It's important to note, however, that in principle, these 'perspectives' are all still from the perspective of the parents. After all, the offspring fitness is being tested to view whether it's affected by the developmental- and foraging treatment of the parents.

For the chicks, we mainly looked at the effect of the parental development and foraging effort on their growth. This was done by using mass and structural size as the main growth variables. The latter of which was calculated with the following formula: "Structural size =

(standardized headbill length + standardized tarsus length) / 2". This calculation has previously also been used by Briga (2016). As mentioned before, biometry was measured on both day 15 and day 30. The data is thus split over these two days and separate analyses were conducted for both. These analyses were conducted using linear models with mixed effects. The response variables for these models were mass and structural size on day 15 or day 30, with the development of both the father and mother, the foraging treatment, and the clutch size as fixed predictor variables. These variables were initially also given interactions with one another to test for significant interactions. Aviary, nest number, and season were added to the models as random predictor variables to control for variance between these variables. Models were then step-wise shortened using Ockham's razor (Jefferys *et al.*, 1992) to end up with a minimum adequate model. ANOVA's were used to test for significant predictor variables and/or interactions between them.

Analyses for the maternal and paternal effects were conducted in a rather similar fashion to one another. Using generalized linear models, the reproductive output of an individual was checked with three separate response variables: the proportion of eggs that hatched, and the proportion of chicks that made it to both day 15 and 30 respectively. These proportions were all accounted for by including the appropriate weight variable in the model (e.g. clutch size for hatched proportion, and amount of hatched chicks for day 15/30 chicks). The fixed predictor variables for these models were the development and foraging treatment of the individual, which were given an interaction with each other in the model. These models were then also step-wise shortened using Ockham's razor (Jefferys *et al.*, 1992) to end up with a minimum adequate model. Chi-square test ANOVA's were used to test for significant predictor variables and/or interactions between them.

Lastly, we tested for selective mortality of the chicks given their parent's developmental treatment and the foraging treatment. This was done using generalized linear mixed models with as response variable whether a chick had survived until day 30 as a binary variable. The fixed predictor variables were the development of the father and mother, the foraging treatment, and clutch size. The random predictor variables were the aviary nest number to control for variation. Like before, models were step-wise shortened using Ockham's razor (Jefferys *et al.*, 1992) to end up with a minimum adequate model. Chi-square test ANOVA's were used to test for significant predictor variables and/or interactions between them.

3. Results

Most graphs in the results section are survival plots and boxplots. The boxplots show Q1, Q3, the median, the average (diamond shape) and the whiskers, which are 1.5 times the standard deviation from the mean. Most irrelevant non-significant results were left out of the main results, but can still be viewed within the appendix when noted as '(AX)', where X represents the number in the appendix itself.

3.1: Survival Study results

For individual survival, we found that whether individuals breed or not does not significantly affect survival by itself (figure 2), but sex does significantly affect survival ($p=0.0005$ ***). Females were found to have a significantly lower survival than males (figure 3). The starting age (age of the birds when put into the experiment) was accounted for in the model and was found to also significantly affect survival (0.0008 ***).

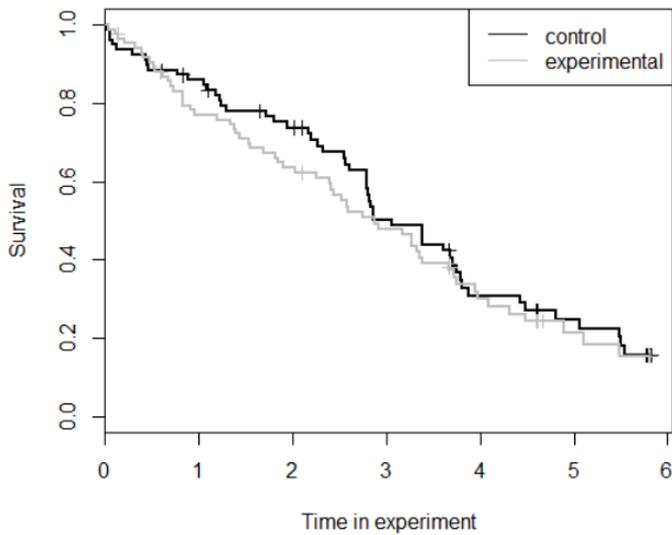


Figure 2. Survival difference of breeding and non-breeding birds. Survival proportion is seen on the y-axis, and the time variable as years the birds spent in the experiment on the x-axis. The latter of which has been corrected for in the model by including the age the individuals had when put into the experiment. The lines in a plot indicate censor points (N=162).

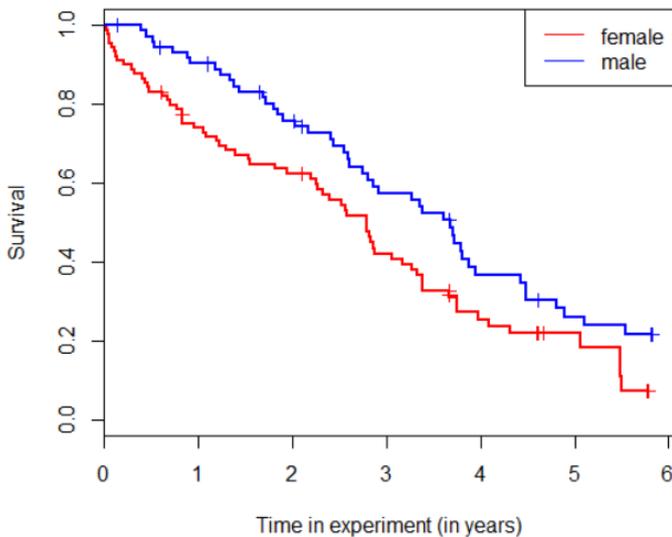


Figure 3. Survival difference of male and female birds. Survival proportion is seen on the y-axis, and the time variable as years the birds spent in the experiment on the x-axis. The latter of which has been corrected for in the model by including the age the individuals had when put into the experiment. The lines in a plot indicate censor points (N=162).

The development of the birds was found to not significantly affect survival, but a trend was found ($p=0.08939$, A1). This analysis was conducted for both sexes combined. In a separate analysis that split the sexes we found that in females the development does significantly affect survival ($p=0.00442$ **). This difference is however only between the no developmental manipulation category and the combined small and large broods (see figure 4). There is no significant difference on survival between the small and large broods. There was no significant survival difference found on the males between the different developmental categories (A2).

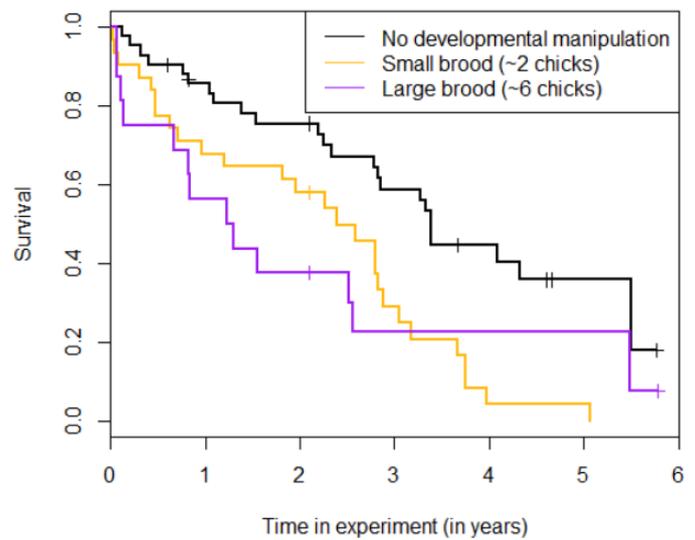


Figure 4. Survival difference of female birds with different developmental categories. Survival proportion is seen on the y-axis, and the time variable as years the birds spent in the experiment on the x-axis. The latter of which has been corrected for in the model by including the age the individuals had when put into the experiment. The lines in a plot indicate censor points (N=89).

Data was furthermore subsetting to view survival differences between breeding and non-breeding individuals. For both breeding and non-breeding individuals, we again found that sex significantly affects survival ($p=0.0013$ ** and $p=0.0153$ * respectively). For both these groups, females have a significantly lower survival than males. We also found that the development significantly affects survival, but only for breeding individuals ($p=0.02654$ *) and not non-breeding individuals (A3). Individuals from small and large broods have a significantly lower survival than individuals without a developmental manipulation (see figure 5). As before, we found no significant survival difference between the small and large broods.

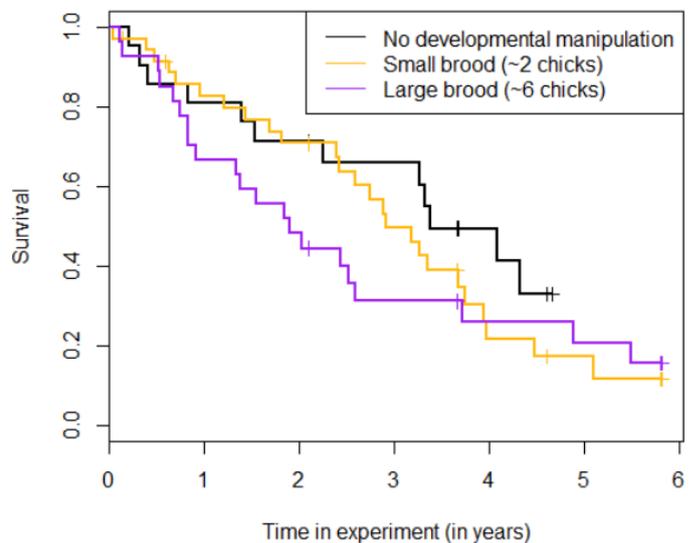


Figure 5. Survival difference of breeding birds with different developmental categories. Survival proportion is seen on the y-axis, and the time variable as years the birds spent in the experiment on the x-axis. The latter of which has been corrected for in the model by including the age the individuals had when put into the experiment. The lines in a plot indicate censor points (N=84).

Despite our findings that breeding females have a significantly lower survival than (breeding) males, we found no significant survival difference between breeding and non-breeding females (A4).

3.2: Reproduction Study results

We used the mass and structural size of chicks as fitness parameters for the reproductive output of the parents. The absolute amount of laid eggs, hatched eggs, and chicks per parental developmental and foraging treatment can be seen in tables 1 and 2 split for females and males respectively. From the perspective of the chicks, we found that the mass of 15 day old chicks was significantly determined by the interaction between the development of the father and the parent's foraging treatment ($p=0.0451$ *). The interaction indicates a difference between the effects of the foraging treatment dependant on the father's development. However despite that, a Tukey post-hoc analysis indicated that the combined father development and foraging treatment do not significantly differ (figure 6). The development of the mother and the clutch size were also tested, but found to not significantly affect the mass of 15 day old chicks.

Table 1. Absolute amount of laid eggs, hatched eggs, chicks that reached day 15, and chicks that reached day 15 per maternal developmental and foraging treatment.

Development treatment	Foraging treatment	Egg amount	Hatched amount	Chicks day 15	Chicks day 30
easy	easy	136	71	57	27
hard	easy	143	76	64	30
easy	hard	121	60	53	34
hard	hard	52	31	19	11

Table 2. Absolute amount of laid eggs, hatched eggs, chicks that reached day 15, and chicks that reached day 15 per paternal developmental and foraging treatment.

Development treatment	Foraging treatment	Egg amount	Hatched amount	Chicks day 15	Chicks day 30
easy	easy	137	83	75	44
hard	easy	106	49	37	18
easy	hard	95	50	40	23
hard	hard	93	50	36	19

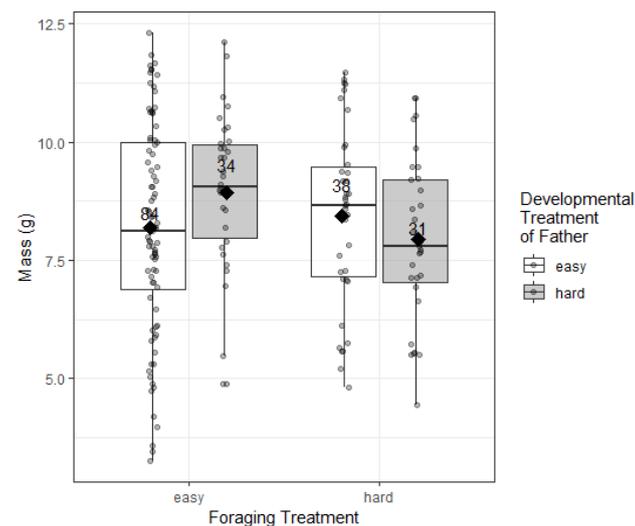


Figure 6. Effect of father development and foraging treatment on the mass of 15 day old offspring. The mass (g) can be seen on the y-axis. The development of the father can be seen coloured: white for easy development and grey for hard development. The foraging treatments (seen on the x-axis) are divided left and right, easy and hard respectively (N=187).

A similar discovery was made for the structural size of the 15 day old chick. We found a significant interaction between the development of

the father and the foraging treatment ($p=0.0263$ *). Much like the mass of 15 day old chicks, their structural size was also decreased when the development of the father was hard and the foraging treatment of the parents was also hard (figure 7). A Tukey post-hoc analysis indicated that the structural size of day 15 chicks was significantly lower when their father had a hard-hard treatment (development and foraging respectively) than when their father had an easy-hard treatment combination ($p=0.0403$ *). Furthermore, we found a significant interaction between the development of the mother and the clutch size ($p=0.0296$ *). The interaction indicates an effect of clutch size dependant on the mother's development. There's a negative effect of clutch size on structural size of chicks on easy development mothers, but not on hard development mothers (figure 8).

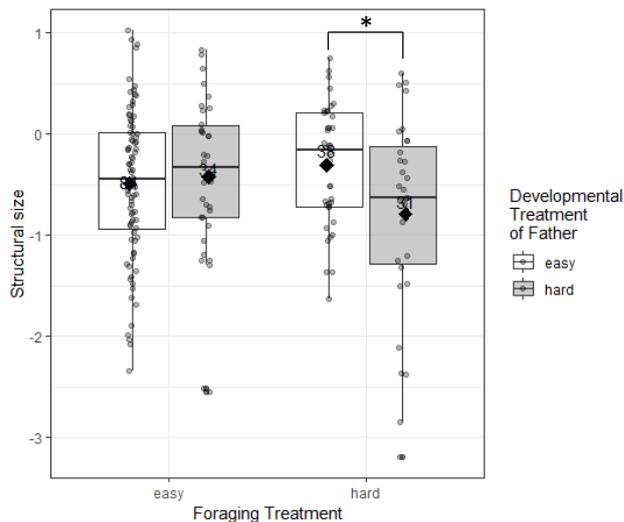


Figure 7. Effect of father development and foraging treatment on the structural size of 15 day old offspring. The mass (g) can be seen on the y-axis. The development of the father can be seen coloured: white for easy development and grey for hard development. The foraging treatments (seen on the x-axis) are divided left and right, easy and hard respectively (N=187).

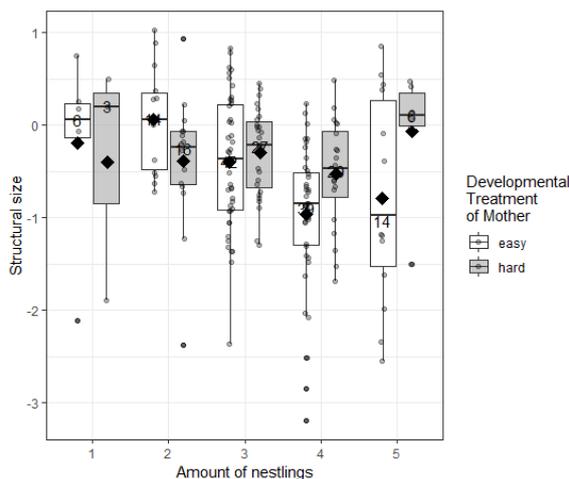


Figure 8. Effect of mother development and amount of nestlings on the structural size of 15 day old offspring. Structural size is on the y-axis. The development of the father can be seen coloured: white for easy development and grey for hard development. The amount of nestlings can be seen on the x-axis (N=187).

For both day 30 structural size and mass, there was no significant effect found of the parental development, foraging treatment, or clutch size (figures 9 - 12).

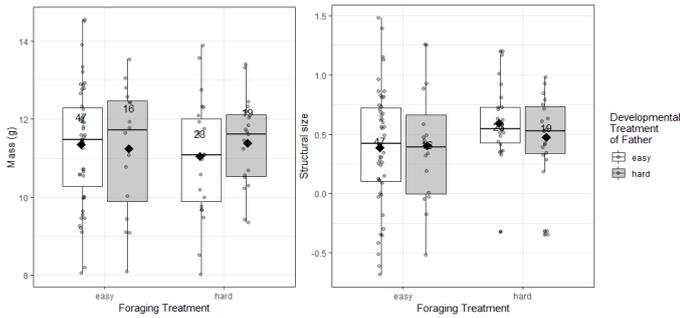


Figure 9. Paternal effects on mass (g)

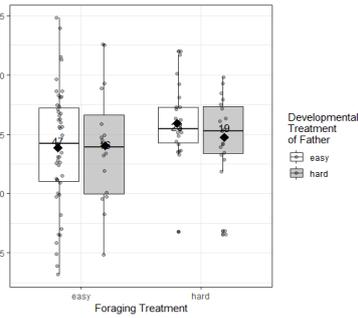


Figure 10. Paternal effects on structural size

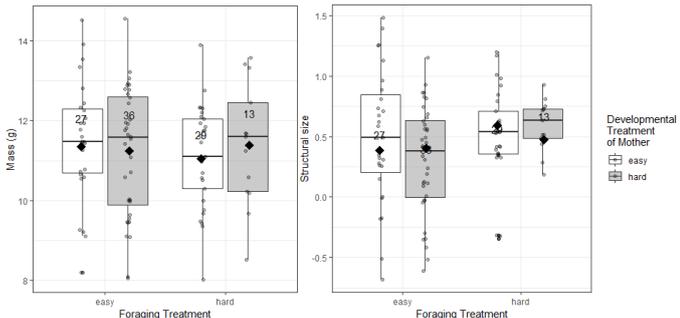


Figure 11. Maternal effects on mass (g)

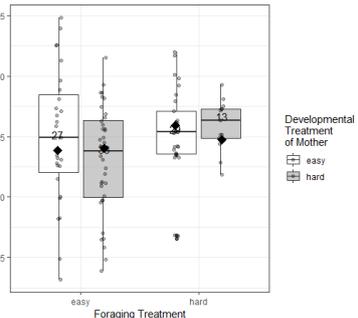


Figure 12. Maternal effects on structural size

These four figures (9-12) display the effect of the paternal/maternal development and foraging treatment on the mass(g)/structural size of 30 day old chicks. The mass(g)/structural size can be seen on the y-axis. The development of the father/mother can be seen coloured: white for easy development, and grey for hard development. The foraging treatments (seen on the x-axis) are divided left and right, easy and hard respectively (N=187).

As a further indication of reproductive output of the parents, we looked at the proportion of chicks that hatched, reached day 15, and reached day 30. From the perspective of both parents, we found no effect of the parent's development or foraging treatment on the proportion of eggs that hatched (A5). For the proportion of chicks that made it to day 15, we found that the father's development had no significant effect (A6). However, we found a significant interaction between the development of the mother and the foraging treatment ($p=0.0235^*$). When a mother has both a hard development and a hard foraging treatment, her proportion of chicks that make it to day 15 is significantly lower than that of mothers with other developments or foraging treatments (figure 13). Apart from these effects however, both parent's development or foraging treatment had no significant effect on the proportion of chicks that made it to day 30 (A7).

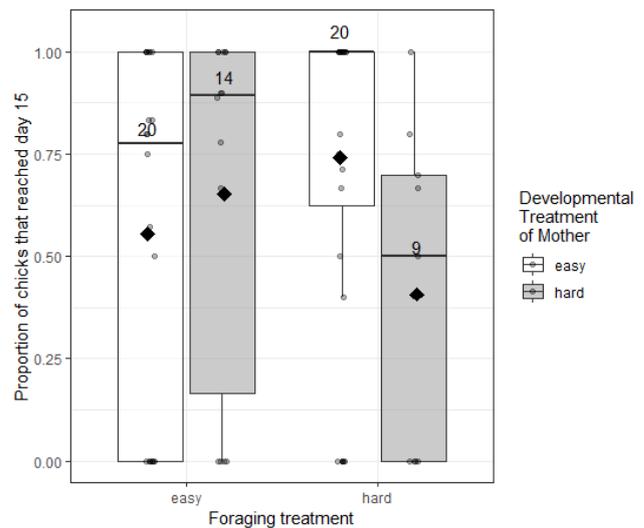


Figure 13. Effect of maternal development and foraging treatment on proportion of chicks that reached day 15. This proportion can be seen on the y-axis. The development of the mother can be seen coloured. white for easy development and grey for hard development. The foraging treatments (seen on the x-axis) are divided left and right, easy and hard respectively (N=63).

Lastly, we tested for selective mortality as a result of the different treatment combinations. We found a significant negative interaction between the development of the father, the foraging treatment, and clutch size ($p=0.0379^*$). This indicates that chicks of fathers with a hard development, hard foraging treatment, and a large clutch size have an increased mortality (table 3).

Table 3. Amount and proportion of chicks alive and dead at day 30 dependant on the father's developmental treatment, foraging treatment, and clutch size

Developmental treatment Father	Foraging Treatment	Clutch size	Total chicks	Dead chicks	Proportion dead chicks
easy	easy	1	3	1	0.33333
hard	easy	1	2	0	0
easy	hard	1	2	0	0
hard	hard	1	2	1	0.5
easy	easy	2	13	4	0.30769
hard	easy	2	6	1	0.16667
easy	hard	2	4	0	0
hard	hard	2	7	3	0.42857
easy	easy	3	18	4	0.22222
hard	easy	3	17	12	0.70588
easy	hard	3	17	4	0.23529
hard	hard	3	17	6	0.35294
easy	easy	4	35	20	0.57143
hard	easy	4	5	1	0.2
easy	hard	4	15	11	0.73333
hard	hard	4	4	4	1
easy	easy	5	15	6	0.4
hard	easy	5	4	3	0.75
hard	hard	5	1	1	1

4. Discussion

4.1: Survival Study

For survival, we found that females have a significantly lower survival than males ($p=0.0005$ ***), and females with a developmental treatment (no matter if easy or hard) have a significantly lower survival than females with no developmental treatment ($p=0.0044$ **). Whether these individuals breed or not does not significantly affect survival, and there are no significant survival differences between easy or hard developmental treatments.

Our results conclude that only females are affected survival-wise. They have lower survival than males and are the only ones who have lower survival when a developmental treatment is present. However, the latter refers to the presence of a developmental treatment, as it did not significantly affect survival whether this treatment was easy or hard, but rather the presence of a developmental treatment affected survival significantly. This could mean that either treatment is simply not favourable for the birds. In other passerines, it's been found that birds often adapt their clutch size to their environmental surroundings (von Haartman, 1957). It could thus be the case that neither a small, nor large brood works well for these birds. After all, it has been found that zebra finches most often lay clutches of four eggs in the wild (Zann, 1996) which is the parameter we chose as having no developmental treatment.

Nevertheless, as previously mentioned in the introduction, Briga *et al.* (2017) found that individuals with a hard development and hard foraging treatment have a lower survival than those of other treatments. That analysis, however, included genetic parentage, whereas the parentage data for this study (for both survival and reproduction studies) is solely based on social parentage. Unfortunately, due to time constraints, adapting genetic parentage onto this study was impossible. While of course social parentage is almost as, if not just as important as genetic parentage, this could mean that certain underlying genetic factors were missed. The zebra finch is after all a species with a high (~15.3%) percentage of extra-pair paternity in captivity (Unpublished data, 2018) despite their monogamous nature, whereas this percentage is much lower in the wild (~3%) (Zann, 1996). Thus, certain genetic variables connected to the developmental treatment might have been overlooked if the developmental treatment of the genetic parentage and social parentage don't overlap.

The two hypotheses of this paper both predict a decrease in survival in lesser quality individuals, which wasn't found here. Previous studies found that individuals with a hard development are of lesser quality and have a decreased survival. Here we find that the simple presence of a developmental treatment decreases survival. This could indicate that any developmental manipulation decreases the quality of an individual, rather than a specific manipulation. This would then be under the assumption that being under the influence of any manipulation decreases expendable energy, or some other limiting resource, otherwise survival would not decrease. These findings might thus not fit well with the pace of life nor the silver spoon hypothesis, as the literature those hypotheses are based on argue that an easy development (small clutch) increases individual quality and hard development (large clutch) decreases individual quality. Although despite that, there could indeed be underlying effects associated with the presence of the manipulation not well measured here that could also decrease this individual quality and thus still work with the hypotheses. After all, if the treatment truly is undesirable for the birds, it could lower their quality significantly to make a difference.

4.2: Reproduction Study

For reproduction, we found that both chick mass and structural size on day 15 was significantly affected by the interaction between the paternal development and foraging treatment ($p=0.04505$ * and $p=0.02633$ * for mass and structural size respectively). For structural size, only easy development and hard foraging differed significantly from hard development and hard foraging ($p=0.0403$ *). However, for mass, none of the treatment combinations differed significantly from each other. Structural size was furthermore significantly affected by the interaction of development of the mother and the clutch size ($p=0.02958$ *), meaning there's a negative effect of clutch size on structural size of chicks on easy development mothers, but not on hard development mothers. For day 30 chicks, however, neither parents' development or foraging treatment significantly affected mass nor structural size. The proportional reproductive output of mothers was significantly affected by the interaction between her developmental treatment and foraging treatment ($p=0.0235$ *). The treatments of the father did not affect this proportion significantly, and neither parents' treatments affected the proportion of chicks that made it to day 30 significantly. Lastly, we found a significant negative interaction between the development of the father, the foraging treatment, and the clutch size on the mortality on the chicks ($p=0.0379$ *), indicating selective mortality.

While our findings indicate a general decrease in reproduction, this decrease is only partial and seemingly temporary. For example, we found a significant negative interaction between the father's development and foraging treatment for both mass of day 15 chicks and their structural size. While this does indicate the importance of the father's role, especially considering that nest contribution by the genetic father is determined by its quality (Sheldon *et al.*, 1997), it also emphasized the fact that we did not find the same interaction or significance for the mother. We did however find a significant interaction between the mother's development and the clutch size affecting the structural size of day 15 chicks. Seemingly, chicks from easy development mothers have lower structural size the higher the clutch size is, as can be seen in figure 7. However, this could also be the result of selective mortality, meaning chicks in such nests simply don't survive unless they're at least a certain structural size large. This turned out to potentially be the case. We found selective mortality on chicks from fathers with a hard development, hard foraging treatment, and an large clutch size. Although the development of the mother is not included in this three-way interaction, the underlying interactions and effects indicate that towards an effect of the development of the mother. However, due to it being an underlying interaction, concluding something from this becomes difficult.

All these findings on the growth of chicks up until 15 days of age appear to disappear however once they reach 30 days of age. We found no significant effect of neither parents' developmental nor foraging treatment on the mass or structural size of 30 day old chicks. This could mean that there is a certain threshold for growth of the chicks that is influenceable by the parents, but after that threshold has been reached, the parents have less influence on the growth of the chicks. This indicates towards a catch-up effect. This is further supported by our findings on the reproductive output of females. While we found that maternal hard development and hard foraging treatment significantly lowers the proportion of chicks that reach day 15, we found no such effect for the proportion of chicks that reach day 30 for both parents.

Thus, it could be the case that the parents only influence the growth and survivability of the chicks early on in life and that this dependency decreases somewhere between being 15 and 30 days of age.

The fact that the effect of the treatment seemingly disappears once chicks are 30 days old could mean the treatments affect the birds less than thought. Zebra finches fledge and leave their birth nest after about 30 days of age (Zann, 1996). Before that time, the birds' wellbeing is entirely determined by their parents, as they are unable to take care of themselves. Thus, the parents' fitness, condition, and developmental and foraging treatment are hypothesised to affect the development of the chicks. Because the birds fledge after 30 days, this means that entire period is the best measure for reproductive success is the effects found on 30 days of age, because the birds depend on their parents. Despite that, we find no effects of the treatment on day 30 proportion of chicks nor of their mass or structural size. Once again, this indicates towards a selective mortality given that the two treatments do significantly affect the chicks growth and mortality on day 15. There is thus perhaps a threshold somewhere between day 15 and day 30 that if the chicks reach that threshold, they will make it to day 30 as well.

4.3: Silver-spoon / Pace of life?

This paper reviews two hypotheses that predict the effect environmental factors have on the trade-off between survival and reproduction: the pace of life hypothesis and the silver spoon hypothesis. The pace of life hypothesis predicts that individuals of lesser quality (e.g. exposed to hard development) make up for their decreased lifespan as a result of their lesser quality by increasing their reproductive success. The silver spoon hypothesis on the other hand argues that individuals must first expend energy into somatic maintenance (survival) in order to be able to reproduce, and thus have a decreased reproductive success.

While our findings do not indicate a general decrease in survival for hard development individuals, there are still partial indicative decreases. Most notably, the presence of a developmental manipulation was found to significantly decrease survival. This could mean that either manipulation is undesirable for the birds, and could thus potentially lower the individuals quality. Of course, individual quality is a rather loose term, but in the context of survivability, it could fit. This view does however not work with the reproduction study, most notably due to a lack of a 'control'. All individuals were subjected to a developmental treatment in the reproduction study, meaning we were unable to test the effects of the presence of said treatment like we were

able to do in the survival study. Thus, while easy and hard development individuals might both be of 'lesser' quality than those without a development, we were unable to test for this, thus making it difficult to draw a proper conclusion on this. Nevertheless, our findings indicate that survival decreased under certain conditions. While it did not generally decrease the way was hypothesized to, decreases were found, rather than increases, which is according to both hypotheses.

Our findings on reproduction complicate matters the most. Potentially due to there being a selective mortality on chicks somewhere between day 15 and day 30, we did not find any effect of the treatments on the growth or mortality of the chicks on day 30. While this does mean our best measure for reproductive success has no significant results, it does still indicate towards some. The treatments were found to negatively affect growth and survivability. Hard treatments were in some cases in interactions with one another and decreasing growth and survival of the chicks, thus also the reproductive output of the parents. While this is not a general reproduction decrease for the hard developmental treatment as hypothesised by the silver spoon hypothesis, it is most certainly not in increase as hypothesised by the pace of life hypothesis. Furthermore, the previously mentioned selective mortality was found at most on chicks from fathers with a hard development, hard foraging, and an increased clutch size. This means those individuals have a decreased reproductive output compared to individuals of other (easier) treatments.

4.4: Conclusion

Despite the results not completely agreeing with our expectations, they still agree most with the silver spoon hypothesis. Both survival and reproduction decreased partially, although not entirely as expected. While this does make conclusion of a hypothesis more difficult, it is still evident that these partial decreases are a better fit to a general decrease, than to a general increase with regards to reproduction, especially given our findings on selective mortality. With our findings we can thus conclude that individuals of lesser quality are under the effect of the silver spoon hypothesis. That being said, the results found here were somewhat lacklustre and less clear than predicted. Moreover, due to the untimely stop of the reproduction study, we were unable to include genetic parentage into our analysis and had little time to study the reproduction effects of the survival study. It would thus be of most interest to continue this study and see whether a more full inclusive analysis also finds that lesser quality individuals are under the effect of the silver spoon hypothesis.

5. Acknowledgments

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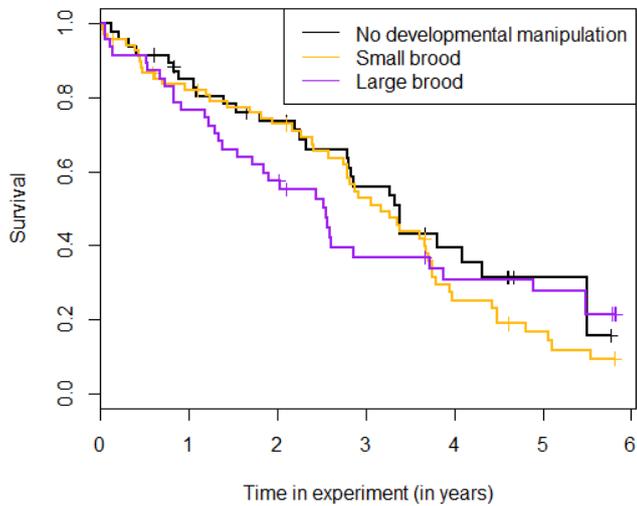
6. References

- Bender, A., & Scheipl, F. (2018). pammtools: Piece-wise exponential Additive Mixed Modeling tools. arXiv preprint arXiv:1806.01042.
- Briga, M. (2016). Growing up and growing old: a longitudinal study on aging in zebra finches. University of Groningen.

- Briga, M., Koetsier, E., Boonekamp, J. J., Jimeno, B., & Verhulst, S. (2017). Food availability affects adult survival trajectories depending on early developmental conditions. *Proc. R. Soc. B*, *284*(1846), 20162287.
- Cairns, D. K. (1988). Seabirds as indicators of marine food supplies. *Biological oceanography*, *5*(4), 261-271.
- Drummond, H., & Ancona, S. (2015). Observational field studies reveal wild birds responding to early-life stresses with resilience, plasticity, and intergenerational effects. *The Auk: Ornithological Advances*, *132*(3), 563-576.
- Gustafsson, L. (1987). Interspecific competition lowers fitness in collared flycatchers *Ficedula albicollis*: an experimental demonstration. *Ecology*, *68*(2), 291-296.
- von Haartman, L. (1957). Adaptation in hole-nesting birds. *Evolution*, 339-347.
- Harshman, L. G., & Zera, A. J. (2007). The cost of reproduction: the devil in the details. *Trends in ecology & evolution*, *22*(2), 80-86.
- Hunt Jr, G. L., Stabeno, P. J., Strom, S., & Napp, J. M. (2008). Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain. *Deep Sea Research Part II: Topical Studies in Oceanography*, *55*(16-17), 1919-1944.
- Ihaka, R., & Gentleman, R. (1996). R: a language for data analysis and graphics. *Journal of computational and graphical statistics*, *5*(3), 299-314.
- Jefferys, W. H., & Berger, J. O. (1992). Ockham's razor and Bayesian analysis. *American Scientist*, *80*(1), 64-72.
- Jimeno, B., Briga, M., Verhulst, S., & Hau, M. (2017). Effects of developmental conditions on glucocorticoid concentrations in adulthood depend on sex and foraging conditions. *Hormones and behavior*, *93*, 175-183.
- Kitaysky, A. S., Piatt, J. F., Hatch, S. A., Kitaiskaia, E. V., Benowitz-Fredericks, Z. M., Shultz, M. T., & Wingfield, J. C. (2010). Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Functional Ecology*, *24*(3), 625-637.
- Koetsier, E., & Verhulst, S. (2011). A simple technique to manipulate foraging costs in seed-eating birds. *Journal of Experimental Biology*, *214*(8), 1225-1229.
- Lack, D. L. (1966). *Population studies of birds*. Clarendon P..
- Neuenschwander, S., Brinkhof, M. W., Kölliker, M., & Richner, H. (2003). Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behavioral Ecology*, *14*(4), 457-462.
- Niemelä, P. T., Dingemanse, N. J., Alioravainen, N., Vainikka, A., & Kortet, R. (2013). Personality pace-of-life hypothesis: testing genetic associations among personality and life history. *Behavioral Ecology*, *24*(4), 935-941.
- Piatt, J. F., Harding, A. M., Shultz, M., Speckman, S. G., Van Pelt, T. I., Drew, G. S., & Kettle, A. B. (2007). Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series*, *352*, 221-234.
- Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4051-4063.
- Ricklefs, R. E. (1993). Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds. In *Current ornithology* (pp. 199-276). Springer, Boston, MA.
- RStudio Team (2015). *RStudio: Integrated Development for R*. RStudio, Inc., Boston, MA URL <http://www.rstudio.com/>.
- Roff, D. A. (2002). *Life history evolution* (No. 576.54 R6).
- Sheldon, B. C., Merilö, J., Qvarnström, A., Gustafsson, L., & Ellegren, H. (1997). Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *264*(1380), 297-302.
- Stamps, J. A. (2006). The silver spoon effect and habitat selection by natal dispersers. *Ecology Letters*, *9*(11), 1179-1185.
- Stearns, S. C. (1992). *The evolution of life histories* (No. 575 S81).
- Zann, R. A. (1996). *The zebra finch: a synthesis of field and laboratory studies* (Vol. 5). Oxford University Press.
- Zera, A. J., & Harshman, L. G. (2001). The physiology of life history trade-offs in animals. *Annual review of Ecology and Systematics*, *32*(1), 95-126.

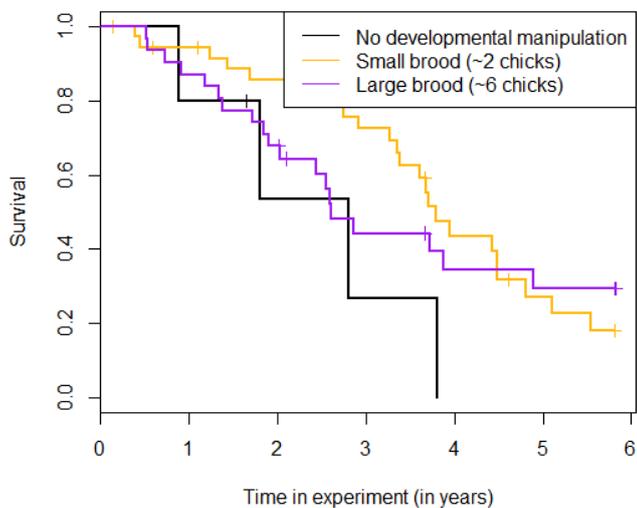
7. Appendix

A1 Effect of developmental treatment on survival for both sexes



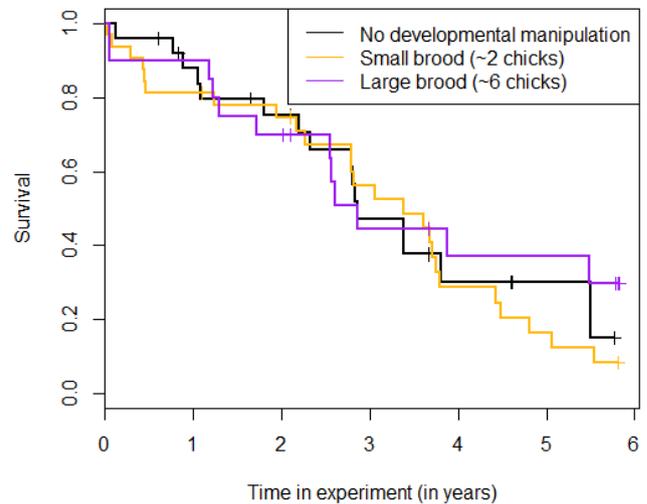
A1. Survival difference of birds with different developmental categories. Survival proportion is seen on the y-axis, and the time variable as years the birds spent in the experiment on the x-axis. The latter of which has been corrected for in the model by including the age the individuals had when put into the experiment (N=162).

A2 Effect of developmental treatment on survival for males



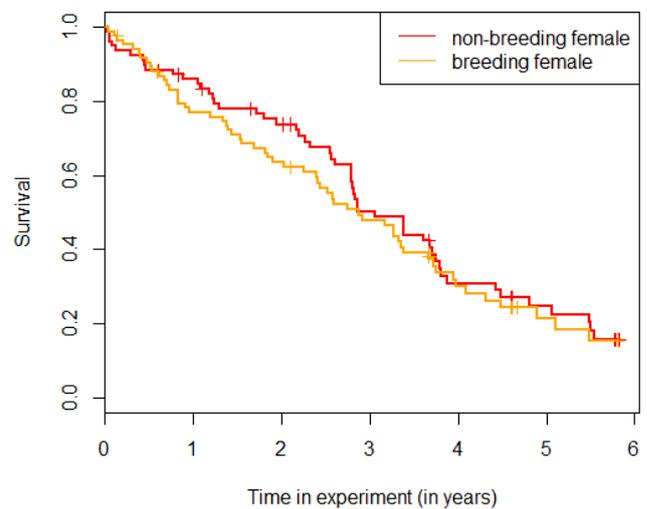
A2. Survival difference of male birds with different developmental categories. Survival proportion is seen on the y-axis, and the time variable as years the birds spent in the experiment on the x-axis. The latter of which has been corrected for in the model by including the age the individuals had when put into the experiment (N=73).

A3 Effect of developmental treatment on survival for non-breeding individuals



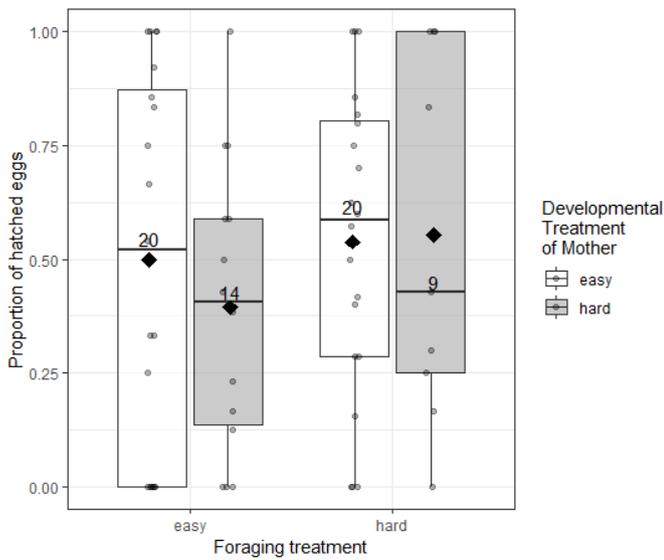
A3. Survival difference of non-breeding birds with different developmental categories. Survival proportion is seen on the y-axis, and the time variable as years the birds spent in the experiment on the x-axis. The latter of which has been corrected for in the model by including the age the individuals had when put into the experiment (N=78).

A4 Survival difference between breeding and non-breeding females



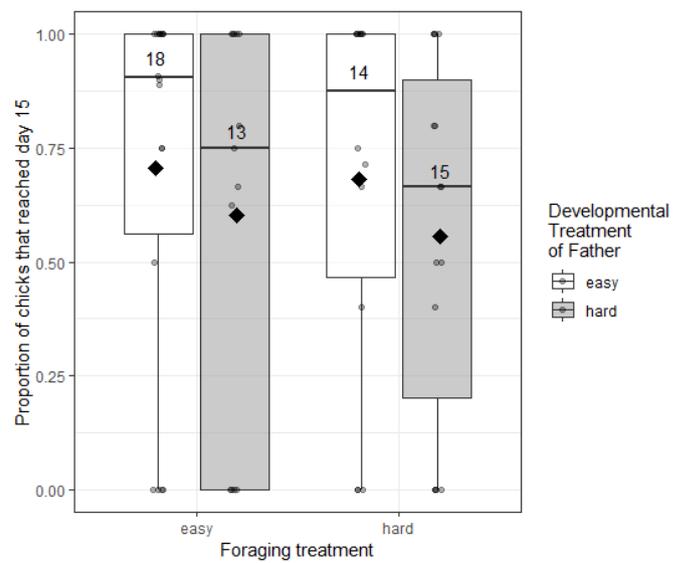
A4. Survival difference of breeding and non-breeding female birds. Survival proportion is seen on the y-axis, and the time variable as years the birds spent in the experiment on the x-axis. The latter of which has been corrected for in the model by including the age the individuals had when put into the experiment (N=89).

A5 Proportion of eggs that hatched

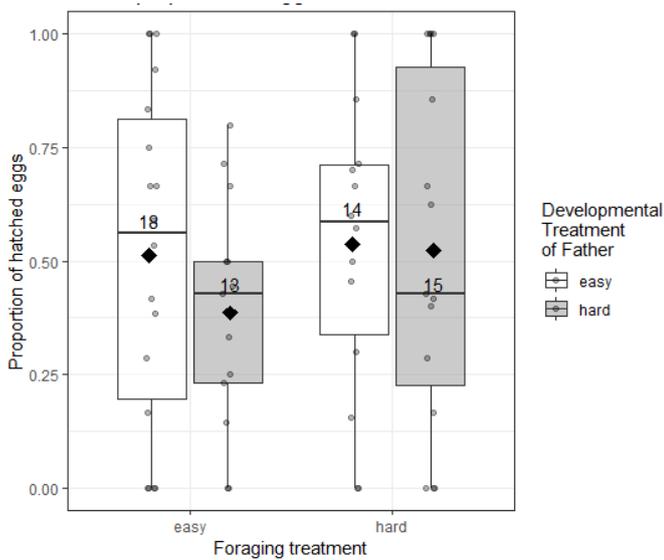


A5.1 Effect of maternal development and foraging treatment on proportion of chicks that hatched. This proportion can be seen on the y-axis. The development of the mother can be seen coloured. white for easy development and grey for hard development. The foraging treatments (seen on the x-axis) are divided left and right, easy and hard respectively (N=63).

A6 Proportion of chicks that reached day 15 affect by father

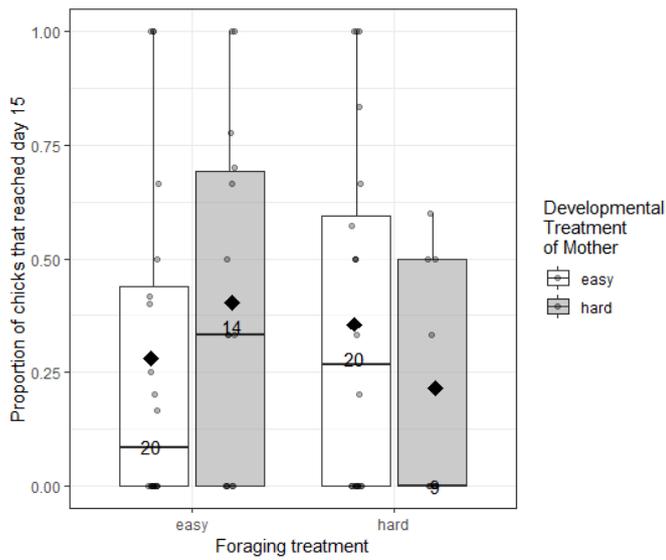


A6. Effect of paternal development and foraging treatment on proportion of chicks that reached day 15. This proportion can be seen on the y-axis. The development of the mother can be seen coloured. white for easy development and grey for hard development. The foraging treatments (seen on the x-axis) are divided left and right, easy and hard respectively (N=60).

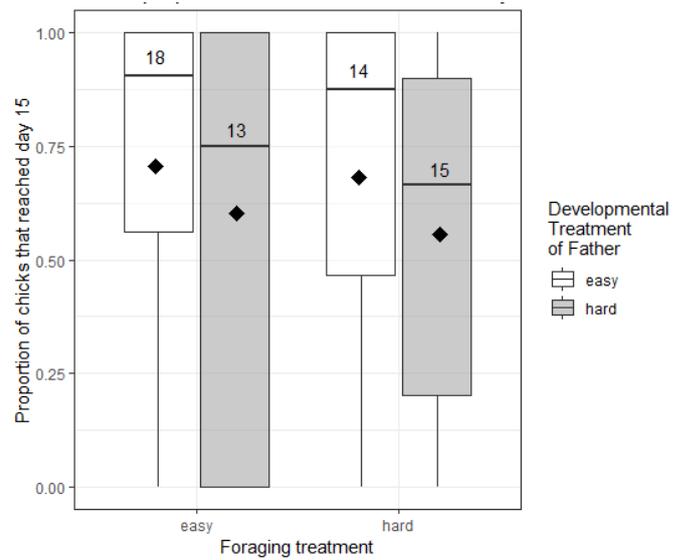


A5.2 Effect of paternal development and foraging treatment on proportion of chicks that hatched. This proportion can be seen on the y-axis. The development of the mother can be seen coloured. white for easy development and grey for hard development. The foraging treatments (seen on the x-axis) are divided left and right, easy and hard respectively (N=60).

A7 Proportion of chicks that reached day 30



A7.1 Effect of maternal development and foraging treatment on proportion of chicks that reached day 30. This proportion can be seen on the y-axis. The development of the mother can be seen coloured. white for easy development and grey for hard development. The foraging treatments (seen on the x-axis) are divided left and right, easy and hard respectively (N=63).



A7.2 Effect of paternal development and foraging treatment on proportion of chicks that reached day 30. This proportion can be seen on the y-axis. The development of the mother can be seen coloured. white for easy development and grey for hard development. The foraging treatments (seen on the x-axis) are divided left and right, easy and hard respectively (N=60).