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Growth of European Hoopoes (*Upupa epops*): An investigation of factors affecting nestling growth

Master Thesis

angestrebter akademischer Grad:

„Master of Science (MSc) in Wildlife Ecology and Wildlife Management“

an der Universität für Bodenkultur

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Wien, Mai 2015

Abstract

Growth is fundamental life history trait in all organisms and closely related with individual fitness. In altricial birds growth is restricted to the short period between hatching and fledging and mostly depends on food availability and frequent feeding by the parents. Different studies of birds have already emphasized within and between species how variation in growth rates underlies ecological conditions such as food availability or sibling competition.

One major goal of this study was to describe the growth of five body traits (body mass, tarsus, 3rd primary, bill, crest) of European Hoopoe (*Upupa epops*) nestlings and to investigate the impact of various factors on these traits.

From beginning of May 2014 until end of July 2014 these five body traits were measured every four days from a total of 236 Hoopoe nestlings from 39 nests in the plain of the upper Rhône valley in the canton Valais, south-western Switzerland and subsequently the data was analysed by applying non-linear mixed models.

Model selection determined number of siblings, hatching date and the rank of the nestlings within a brood as the factors with the strongest influence on the growth trajectories. In addition, no difference of growth variability between nestlings or between nests was found. Another goal of this study was to find suitable parameters for an accurate age determination of Hoopoe nestlings, whereby the body traits bill and 3rd primary appeared to be suitable.

This is, to my knowledge, the first study that has investigated the growth of Hoopoe nestlings thoroughly and with the use of nonlinear mixed models. However, since the influence of weather and sex, which are likely to be additional prominent factors, was not investigated within the framework of this study, further studies should ascertain the impact of these factors.

Keywords

Nestling growth, Growth trajectories, Nonlinear mixed models, Hatching asynchrony, Upupa epops

Zusammenfassung

Wachstum ist einer der wichtigsten physiologischen Abläufe im Leben von Organismen mit dem Ziel eine maximale individuelle Fitness zu erlangen. Bei Vogelarten, die wie der Wiedehopf (*Upupa epops*) Nesthocker sind, ist das Wachstum auf eine kurze Zeitspanne zwischen dem Schlupf und dem Flüge werden beschränkt und richtet sich nach dem Nahrungsangebot und der Fütterungshäufigkeit durch die Eltern. Das Hauptziel dieser Studie war die Beschreibung von jeweils fünf Wachstumsparametern (Gewicht, Tarsus, 3. Handschwinge, Schnabel, Haube) von Nestlingen des Wiedehopfs und in weiterer Folge die Untersuchung verschiedener Einflussfaktoren auf den Wachstumsverlauf dieser Parameter.

Von Anfang Mai 2014 bis Ende Juli 2014 wurden diese fünf Wachstumsparameter alle 4 Tage von insgesamt 236 Wiedehopf Nestlingen aus 39 Brutten in der Ebene des oberen Rhodentals im Kanton Wallis im Südwesten der Schweiz gemessen und anschließend mit nichtlinearen gemischten Modellen ausgewertet.

Die Anzahl der Geschwister, das Brutdatum und der Rang der Nestlinge innerhalb der Brut wurden dabei anhand der Modelselektion bei allen Wachstumsparametern als die Faktoren mit dem stärksten Einfluss ermittelt. Zusätzlich wurde kein Unterschied der Varianz beim Wachstum zwischen Nestlingen und zwischen Nester festgestellt. Ein weiteres Ziel dieser Studie war es geeignete Parameter für eine genaue Altersbestimmung zu finden. Die Schnabellänge und die Länge der dritten Handschwinge haben sich dabei als geeignet herausgestellt.

Nach meinem Wissenstand ist dies die erste Studie die das Wachstum von Wiedehopfnestlingen eingängig und mit Hilfe von nichtlinearen gemischten Modellen untersucht hat. Da allerdings Faktoren wie zB. das Wetter und das Geschlecht, die möglicherweise auch einen Einfluss haben könnten, im Rahmen dieser Studie nicht berücksichtigt wurden, sollten weiterführende Studien diese Faktoren in ihre Untersuchungen miteinbeziehen.

Schlagwörter

Nestlingswachstum, Wachstumskurven, nichtlineare gemischte Modelle, Asynchroner Schlupf, Upupa epops

Introduction

Growth is a fundamental development in all organisms (Roff 1992; Zach et al. 1984; Starck & Ricklefs 1998). As a consequence, growth has to be organised in a way that individual fitness is maximised and therefore it is one of the most studied life history traits in avian physiology. In most birds, growth is very fast and in altricial species restricted to the short period between hatching and fledging. A fast growth is likely an adaptation to reduce the exposure time to predators, as nestlings of altricial birds cannot escape (Starck & Ricklefs 1998). Growth can also affect post-fledging survival, fledglings with good body condition have higher survival compared to fledglings in bad body condition (Naef-Daenzer et al. 2001).

Growth requires energy that is supplied by the parents, and therefore ultimately depends on food availability and parent quality. Fast growth is possible if parents deliver enough food (Starck & Ricklefs 1998). Thus, food availability is a key factor affecting nestling growth and any factor that affects food availability has an impact on nestling growth (Geiser et al. 2008). Nestlings of a brood compete for food among each other. If the overall food demands of the nestling increase (e.g. high number of siblings), parents can either increase their effort to deliver food, or alternatively maintain their effort, risking reduced growth of their nestlings or even their death. By increasing the effort to deliver food adults may compromise their survival, as shown in an experimental study (Masman et al. 1989). Thus, parents have to make a number of smart decisions when they raise young to maximize their fitness (Drent & Daan 1980).

The delivered food has to be distributed among the nestlings. The growth of the nestlings can be negatively affected by the number of nestlings (Neuenschwander et al. 2003) because less energy is available for each nestling. However, since birds adjust clutch size according to the quality of the territory and of their own, effects are often only visible when the number of nestlings is changed experimentally (Neuenschwander et al. 2003; Roulin et al. 1999; Slagsvold 1986).

Competition is expected to be asymmetrical when the nestlings have different ages, which occurs when hatching is asynchronous. Because older nestlings are larger they can outcompete younger nestlings for food. Therefore growth of younger nestlings can be reduced compared to that of their older brothers and sisters and their size at fledging smaller (Vinuela 2000).

Food availability is often not constant during the complete breeding period, but has a peak (at least in temperate environments). Birds try to time their brood in

such a way that the time of the highest food demand coincides with the food peak. Birds that start breeding later in the season adapt their clutch size which is decreasing seasonally (Öberg et al. 2014). If they do that in a good way, the same amount of food should be available to the nestlings as in early broods, and consequently nestling growth should not be different.

Food availability is also a feature of territory quality. Thus, nestlings that are raised in territories of high quality are expected to benefit from good food availability ensuring fast growth. As birds are likely to adapt clutch size also to food availability (Drent & Daan 1980) therefore no effect of territory quality on nestling growth may be apparent.

Hatching asynchrony is a strategy to cope with variable food availability. In the best case, all nestlings can grow to the normal size and fledge, but in the worst case, the older nestlings outcompete the younger ones for food and consequently only the older nestlings grow normally and fledge. A prominent factor affecting food availability is the weather. In particular in insectivorous species bad weather reduces the supply of insects and increases the energetic demands of the nestling which results in impaired nestling growth (Walther et al. 2002; Geiser et al. 2008; Arlettaz et al. 2010).

Finally, nestling growth is often characterized by body mass growth only. Yet, other body traits, such as tarsus, bill and feather lengths also characterize growth and they may be affected by different factors than body mass. For example, when food resources become limited, organisms may on the one side reduce their overall growth or on the other side balance their investment in different organs (Schew & Ricklefs 1998). This kind of adaptive development plasticity was also shown with spotless starlings (*Sturnus unicolor*), where sibling's competition was artificially enlarged and at the end of nestlings period experimental chicks developed wider gapes (Gil et al. 2008).

Here I studied growth of nestlings of the European Hoopoe *Upupa epops*. To the best of my knowledge nestling growth in Hoopoes never been studied thoroughly. Bussmann (1950) conducted a study about Hoopoe nesting growth in 1950, where nestlings of only 2 broods were measured. The cavity breeding Hoopoe has a large variation in the number of nestlings, hatching is often asynchronous and the breeding period is long. Moreover, territory quality can be characterized by the frequency of territory occupancy (Tschumi et al. 2014) and different components of breeding success depend on weather, suggesting short term variation of food availability (Arlettaz et al. 2010). This set-up is ideal to study the impact of different factors on a variety of nestling growth measures. Specifically I described the growth

of five traits (body mass, tarsus, 3rd primary, bill, crest) and investigated which of those traits is fully grown when the nestlings fledge. Then I studied the impact of hatching date, territory quality, number of siblings and hatching rank on these traits. I was interested to understand which of the factors were the most important to affect nestling growth and whether the same factors were important in all traits. Furthermore, I studied the variability of nestling growth, both between nestlings of the same nest and among nests. Finally, I aimed to derive a reliable method that allows aging nestlings based on body measurements. Here it was important to assess which body measure is the most suited.

Material & Methods

Study species

The European Hoopoe is a migratory, non-passerine and insectivorous farmland bird, which likes to inhabit semi-open habitats such as fruit tree plantations, orchards and vineyards. It mainly feeds on large invertebrates such as mole crickets (*Gryllotalpa gryllotalpa*) by scavenging the ground with its unique shaped bill (Svensson et al. 2009; Fournier & Arlettaz 2001). Mole crickets also make up a large amount of the prey biomass parents deliver to their chicks (Fournier & Arlettaz 2001). Hoopoes prefer foraging in habitats consisting of a small scaled mosaic of patches with vegetation and bare grounds (Schaub et al. 2010, Tagmann-loset et al. 2010). Habitats containing significant patches of grass and bare ground are therefore crucial features for foraging species to thrive. Such habitats are rare in grassland dominated farming, but can be common in intensively farmed special cultures (vineyards, fruit tree plantations).

In the 1960s Hoopoe populations were common in the Swiss lowlands but can nowadays only be found in certain areas and are mainly restricted to the cantons Valais, Grison and Ticino (Mühlethaler & Schaad 2010). In Switzerland the Hoopoe is classified as an endangered species (Keller et al. 2010). Due to conservation projects in Switzerland some populations especially the one in Central Valais have recovered since the year 2000 (Mühlethaler & Schaad 2010; Arlettaz et al. 2010, BioScience Studie).

The decline of the Hoopoe populations in central Europe has multiple reasons. One of the major reasons is the intensification of farming practices (Schaub et al. 2010). The use of insecticides to maximize harvest decreased food supply and

the loss of breeding cavities led to a decline of the habitat quality (Fournier & Arlettaz 2001).

Under good weather conditions with sufficient food resources and if breeding starts early in the season, Hoopoes may raise up to two annual broods. Hoopoe females not always choose the same partner for second broods, but both parents always contribute to raise a clutch (Hoffmann et al. 2015).

Hoopoes arrive on the study area in Central Valais by the end of March and the first clutches are usually initiated by the end of April (van Wijk & Schaub 2014). Hoopoe broods can contain up to 13 eggs, which are incubated by the female for about 15 days. Incubation often starts before the last egg is laid and as a result Hoopoe chicks hatch asynchronously (Martín-Vivaldi et al. 1999). After hatching, the nestlings are raised for another 25-28 days. During the first ten days the nestlings are brooded by the female and the male delivers food for both, the chicks and the female. Later, both parents provide food for the chicks.

Study location

This study was carried out from mid April 2014 until end of July 2014 in the plain of the upper Rhône valley between Sierre and Vernayaz (canton Valais, south-western Switzerland, 46°140N, 7°220E). The valley is mainly used for intensive farming with many fruit plantations and vineyards.

Since about year 2000, 700 Hoopoe nest boxes were installed in the fruit tree plantations with the primary goal to enhance the small population (Arlettaz et al. 2010). The easy access to the birds in these plantations additionally allows an extensive monitoring of this population to the benefit of several studies in the past.



Fig 1. The upper Rhône valley in the Canton Valais/Switzerland

Data collection and chick measurements

All nest boxes of the whole the study area were checked every 10 days from the middle of April 2014 to the end of July 2014 to gather information about broods (clutch size, hatching success, phenology, etc.) and location of occupied nest boxes. About 100 broods occur in the study area annually, but only a sample of them was included in the nestling growth study. The goal was to get measurements of nestling growth from a minimum of 30 broods. These 30 broods were not selected completely at random, but based on the occupancy frequency of the territories from previous years. Territory occupancy is an adequate measurement of territory quality (Tschumi et al. 2014), and thus a stratified random sample of broods was considered to ensure a pronounced gradient of territory quality. Among territories that were occupied in 2014 we selected 10 territories at random which had been occupied in the past 1-3 years, 4-7 years and 8-11 years. Additionally, 10 nest boxes were selected completely randomly from second broods with focus on the same female only. To facilitate fieldwork, only nest boxes with good access were chosen.

The selected nest boxes were checked every third day to gain information about clutch size, hatching date and number of nestlings. For an accurate description of the nestling's growth it was very important that the age of the nestlings was known exactly. Hence, the broods were monitored tightly to assess the exact hatching date of the targeted broods.

In order to avoid brood abandonment due to the frequent visits at the nests, we only started measurements when the oldest nestling was 7 days old. All chicks were measured every 4 days at the same time of the day, where the last day of measurement was close to the fledging age (day 27). Thus, for most nestlings and broods, the measurements were taken at 6 days.

The following measurements were recorded from each nestling: Age (in days), body mass (to the nearest of 0.1 grams using an electronic balance- Domo DO9096W, Appendix Fig. A3), tarsus length (to the nearest of 0.1 mm using a calliper, Appendix Fig. A4) (Sutherland et al. 2004), length of 3rd primary feather (using millimetre paper and later a standard ruler to the nearest of 0.5 mm, Appendix Fig. A5), bill (from the outer end of the nose hole to the tip of the bill) and length of the longest of the erected crest feathers (Appendix Fig. A6). The latter two traits were measured using millimetre paper. To distinguish the siblings, claws were painted with nail polish with a unique code. The identical claws of the right and the left foot were painted to ensure individual identification in the case the colour was worn. At the age

of 15 days, all nestlings were marked with a ring (Appendix Fig. A7). The hatching order (rank) was determined for each nestling based on the hatching day. Nestlings that hatched at the same day got the same rank. For example, if a brood contained 5 nestlings, of which two hatched at day 1, one at day 2 and two at day 4, the recorded ranks were 1, 1, 2, 3, 3.

In order to compare growth parameters of nestlings with parameters of adults, measurements of adult birds, which had been sampled since 2002, were used. All body traits were measured the same way except crest length. Instead of measuring the longest erected crest feather as done in this study, the laid down crest of adults was measured with a calliper.

Statistical analysis

All data were analysed using nonlinear mixed models fitted with the nlme package of R (Pinheiro et al. 2007) based on the descriptions and suggestions written in Sofaer et al. (2013). Due to the nonlinear nature of growth trajectories many growth models use a kind of logistic function. Data on nestling growth are usually repeated measurements on the same individual and nestlings share the same nest. Therefore, nonlinear mixed effects models appear to be ideal for fitting avian growth curves and are widely used (Lindstrom & Bates 1990; Sofaer et al. 2013).

Growth curves were modelled with a logistic function with three parameters: the asymptote (A), the inflection point (I), and the growth rate constant (K) (Sofaer et al. 2013; Starck & Ricklefs 1998) :

$$W_t = \frac{A}{1 + e^{(k(1-t))}} \quad \text{where } w_t = \text{measurement at } t \text{ and } t = \text{nestling age (days)}.$$

Since the measurements were not independent from each other, I included two random effects. The nestling random effect accounts for the repeated measures of the same nestling. The nest random effect accounts for the fact that some nestlings share the same environment (nest) and parents (genetics). The inclusion of these random effects also allowed the estimation of the amount of variations between nests and between individuals within the nest and ensured appropriate standard errors which is important for model selection (Sofaer et al. 2013).

Additionally, I chose the model whose random effects were not correlated neither on the nest nor on the nestling level. This was decided based on a preliminary analyses where I noticed that correlations hardly have an impact on the effects I was interested.

The impacting variables were included in the non-linear mixed model as covariates. These could affect the three target parameters of the growth model (A, K, I) independently of each other. Yet, I decided to have always the same model on the three target parameters. This was done to avoid having a too large set of candidate models.

The candidate set of models included all possible combinations of the considered four covariates, i.e. 16 models for each measured trait. The models were ranked according to the Akaike's information criterion (AIC). All these analyses were conducted by using the statistical software R accessed by RStudio (Version 0.98.1062 – © 2009-2013 RStudio, Inc.).

To visualize the effects sizes I predicted growth trajectories using different levels of the impacting factors. The computation of the precision of the growth trajectories is difficult using maximum likelihood, but straightforward in the Bayesian mode of analysis. Therefore, I refitted the best model for each trait using JAGS (Plummer 2003), which performs a Bayesian analysis using Markov Chain Monte Carlo simulations. The precision of the growth trajectories can then be simply obtained from the posterior samples (Kéry 2010).

Results

A total of 236 Hoopoe nestlings from 39 nests were measured within 3 months. 183 (77.5%) nestlings survived until fledging, while 53 (22.5%) died before fledging. 37 (15.7%) of the latter from 11 broods died within the first week after hatching. A further 8 nestlings from 2 different broods were predated and the remaining individuals died for unknown reasons. 37 out of 39 broods were successful, which means that at least 1 nestling fledged.

For the statistical analysis I included all measurements of nestlings regardless of whether they finally fledged. This was done because I wanted to study the full variability of nestling growth instead of only successfully fledged individuals.

Description of independent variables

Brood phenology

The first measured brood hatched on April 21st, which was the earliest brood in the study area. 154 (65.3%) nestlings of 23 clutches hatched in May. 62 (26.3%) chicks out of 11 broods hatched in June and 20 chicks (8.4 %) of 5 broods hatched in July, whereby the last measured brood hatched on the 18th of July.

Brood size

The average brood size for all first broods was 6.18 (± 1.7) nestlings with a maximum of 9 chicks (3 broods) and a minimum of 5 chicks (4 broods). The maximum number of chicks from the same brood that fledged was 9 chicks and the maximum chick loss within a successful clutch was 4 chicks. Broods that hatched later in the season (June/July) had an average brood size of 4.35 (± 1.83) nestlings, with a maximum of 7 chicks and a minimum of 1 chick.

Nestling rank

All 39 clutches hatched asynchronously (Appendix, Fig. A1 and A2) where most of the times the chicks hatched one day apart. In some clutches 2 chicks hatched on the same day (independent of their rank), but there was always a big (visual) difference of development between early-hatched chicks and late hatchlings.

Occupancy

From a total number of 39 broods, 13 broods were chosen from nest boxes with a high occupation rate which had an average brood size of 6.75 (± 1.48) chicks in the 2014 season. 9 broods were chosen from nest boxes with a medium occupation rate with 6.67 (± 1.12) chicks per brood and 8 broods were chosen from boxes with a low occupation rate and had 6.75 (± 1.28) chicks per clutch.

Description of basic nestling growth

During the study period a total number of 1140 measurements of body traits were taken. These measurements are shown in Figure 2a-e, with measurements of nestlings that survived until fledging date (black) and measurements of nestlings that died before fledging date (red). The data set contains measurements of nestlings that were between 1 and 28 days old. Table 1 shows the parameter estimates of the non-linear models without any covariates for each trait.

At the day of the last measurement growth of only 2 body traits was completed: body mass and tarsus. The growth trajectory of body mass (Fig. 2a) shows a sigmoid pattern with a high growth rate in the first 8 days. The predicted growth curve does not match closely with the measured points at all ages. Hoopoe nestlings reach a body mass peak around age 20. In the following the body mass declines slightly until the nestlings fledge. Such a curve cannot be fitted with the type of model that I used. By the age of 28 days, the predicted body mass was 71.5 grams (SE: ± 9.62), thus the fledglings were on average slightly lighter than the adults (adult males: 76.6 g ± 8.14 , n = 1081; adult females: 73.1 g ± 9.5 , n = 1277).

Tarsi were fully grown by the age of 23 days (Fig. 2b). The fully grown tarsus length was 23.2 mm (± 1.43), which is very comparable to that of the adults (adult males: 23.5 mm ± 2.5 , n = 846; adult females: 22.2 mm ± 2.9 , n = 970). The logistic growth curve of the tarsus increases steeply between day 1 and day 10 and becomes very shallow afterwards. As a result tarsi achieve a longer period of asymptotic growth than any other investigated body trait.

The growth of the bill was almost linear until day 28 (Fig. 2c). The bill reached an average length of 30.2 mm (± 3.0) when the nestlings fledged (day 28). The average bill length of adult males is 50.3 mm (± 6.0 , n = 938) and of females 44.8 mm (± 6.17 , n = 1060). Thus nestlings reached only about 60% of their final bill length when they fledge.

The growth curves of the length of 3rd primary and of the crest (Fig. 2d and 2e) were quite similar with distinctive sigmoid shapes. 3rd primaries had a higher growth rate constant than crest feathers. At the age of 28 days, the length of the 3rd primaries reached on average 87.1 mm ($\pm$ 10.7), which is about 80% of their final length (3rd primary length of adult males: 113.9 mm ($\pm$ 3.40) n = 488; adult females: 108.3 mm ($\pm$ 3.46), n = 563). At the age of 28 days crest feathers of nestlings reached an average length of 47.3 mm ($\pm$ 6.79, Fig. 2e), which is about 63% of their final length (crest length of adult males: 76.6 mm ($\pm$ 8.14) n = 944; adult females: 73.1 mm ($\pm$ 9.5) n = 1053).

Table 1. Estimated growth parameters ($\pm$ SE in parentheses) of five body traits for Hoopoe nestlings based on a model without covariates. A: asymptote, I: inflation point, K: growth rate constant.

Growth Parameter	A	I	K
Body mass	69.33 (0.89)	8.08 (0.13)	0.37 (0.01)
Tarsus	23.05 (0.11)	5.23 (0.16)	0.38 (0.01)
Bill	32.39 (0.39)	13.01 (0.23)	0.16 (0.00)
3 rd primary	91.67 (0.89)	16.45 (0.14)	0.30 (0.00)
Crest	52.54 (0.84)	17.19 (0.20)	0.23 (0.00)

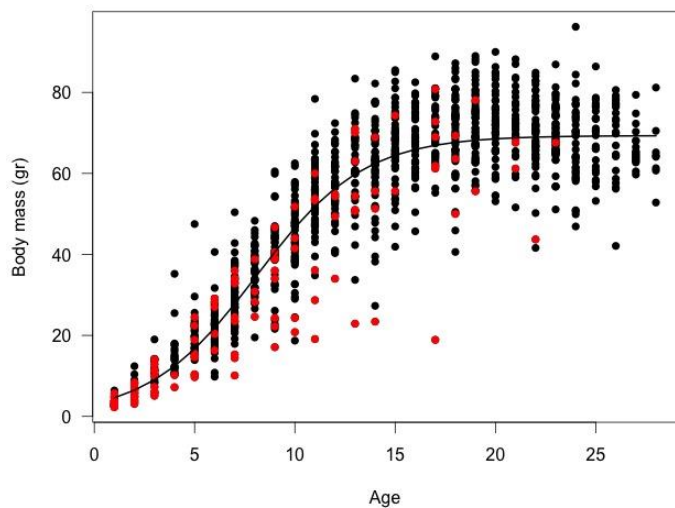


Fig. 2a

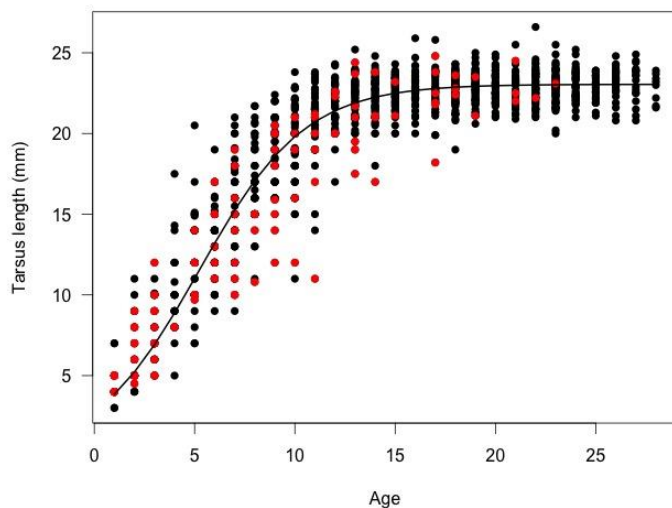


Fig. 2b

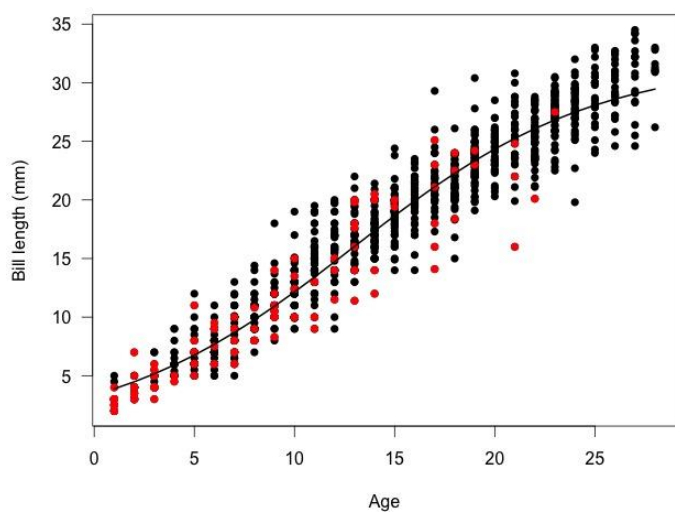


Fig. 2c

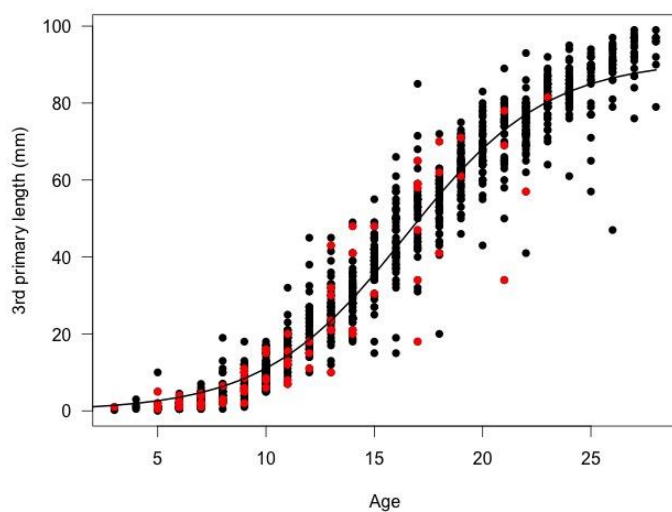


Fig. 2d

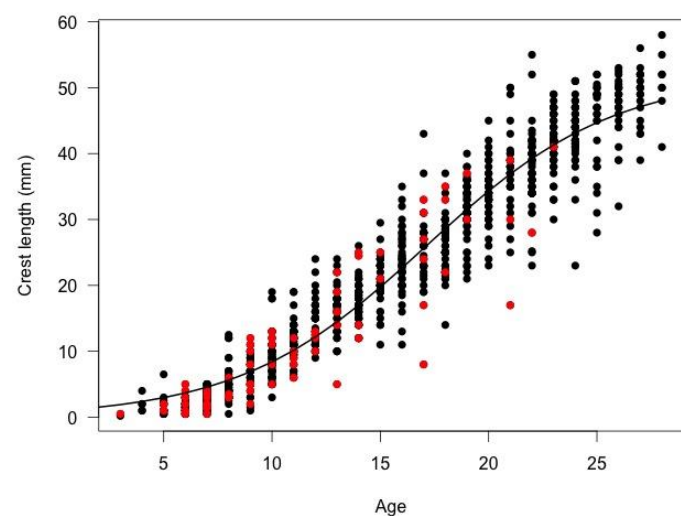


Fig. 2e

Figure 2a-e: Body trait measurements and fitted growth curves using a model without covariates (Table 1). (2a) body mass, (2b) tarsus length, (2c) bill length, (2d) 3rd primary length, (2e) crest length. Black dots refer to individuals that fledged, red dots to those that did not fledge.

Factors impacting nestling growth

Body mass growth

Model selection revealed that the best model includes number of siblings, nestling rank and hatching date (Table 2). Territory occupancy was included in the second best model, but the support by the data was less. All the other models had ΔAIC values > 5 indicating that their support by the data was really weak.

The predicted body mass growth curves show that hatching date had a positive impact on the asymptotic mass. Chicks that hatched earlier in the season reached a higher asymptotic mass and had a later inflection point than chicks that hatched later in the season (Fig. 3a). The number of siblings also had an impact on body mass, where nestlings with more siblings reached a higher asymptotic mass, than individuals with less siblings (Fig. 3b). Moreover, nestlings that hatched earlier than their nest mates also reached a higher asymptotic mass (Fig. 3c).

Table 2. Model selection results for the impact of covariates on body mass growth. The crosses in the table indicate, whether a specific covariate has been included in the model. Given is the difference in the Akaike criterions between the current and the best model (ΔAIC), the model's deviance (DEV) and the number of estimated parameters (K).

Model	Occupancy	Siblings	Rank	Date	ΔAIC	DEV	K
m21.W		x	x	x	0	7739.23	19
m30.W	x	x	x	x	2.65	7735.88	22
m13.W		x		x	5.16	7750.38	16
m22.W	x	x		x	8.02	7747.25	19
m16.W			x	x	12.65	7757.88	16
m19.W	x		x	x	12.92	7752.14	19
m06.W				x	16.44	7767.67	13
m10.W	x			x	17.64	7762.87	16
m12.W		x	x		18.98	7764.21	16
m25.W	x	x	x		20.64	7759.86	19
m03.W		x			23.19	7774.42	13
m07.W	x	x			25.23	7770.46	16
m09.W	x		x		36.11	7781.34	16
m05.W			x		37.69	7788.92	13
m02.W	x				40.68	7791.91	13
m01.W					41.27	7798.49	10

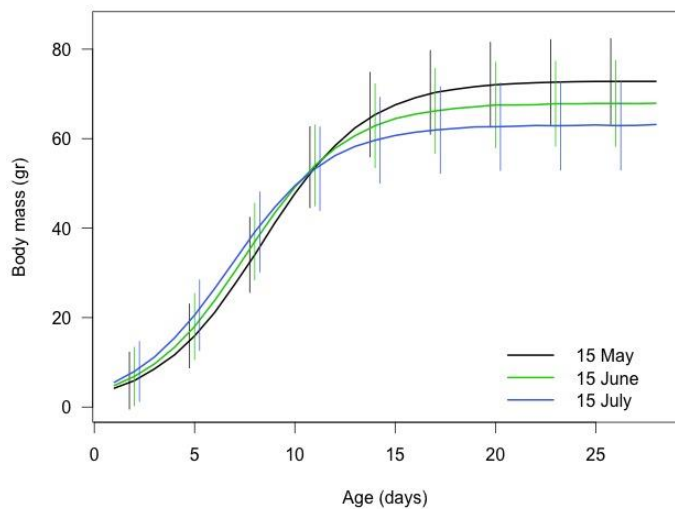


Fig. 3a Growth trajectories of body mass predicted from the best model (Table 2) for different hatching dates. The number of siblings was 6, and the nestling rank 1 (first hatched). The vertical lines show the 80% confidence interval.

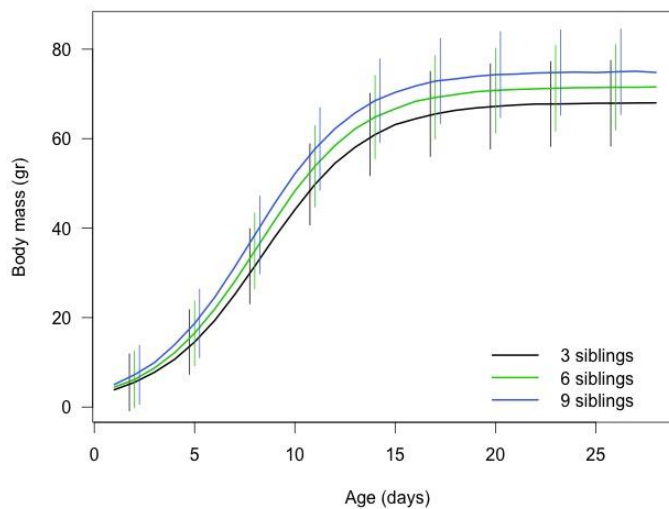


Fig. 3b Growth trajectories of body mass predicted from the best model (Table 2) for different number of siblings. The nestling rank was 1 (first hatched), and the date was 23rd of May (hatching peak). The vertical lines show the 80% confidence interval.

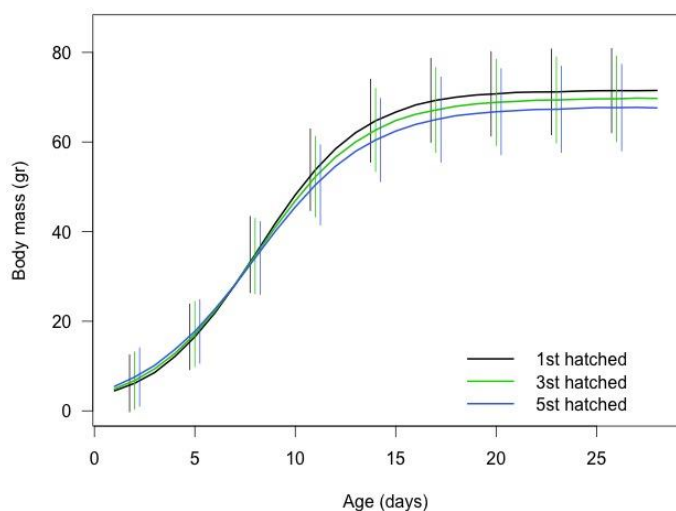


Fig. 3c Growth trajectories of body mass predicted from the best model (Table 2) for different rank of nestling. The number of siblings was 6, and the hatching date was 23rd of May (hatching peak). The vertical lines show the 80% confidence interval.

Tarsus length

Model selection revealed that the best model includes number of siblings, nestling rank and hatching date (Table 3). The second best model included the two covariates siblings and rank, and the third best model siblings and hatching date. Both models had ΔAIC values < 1 indicating that their support by the data was quite strong. In all the top models siblings was included, while there was some uncertainty about the rank and the hatching date. The best model including occupancy had a high ΔAIC score, indicating that occupancy was unimportant for tarsus growth.

The predicted tarsus growth curves for different hatching dates were quite similar, indicating that hatching date had a marginal effect of tarsus growth only (Fig. 4a). Different numbers of siblings affected tarsus growth until they were 12 days old (Fig. 4b). Tarsi of nestlings with more siblings grew faster. After day 12 the tarsus growth and its final length appears to be independent on the number of siblings (Fig. 4b). Furthermore, the predicted growth curves for nestlings with different rank were also very similar suggesting that the rank had a marginal effect only (Fig. 4c). Thus, although model selection indicated effects of siblings, hatching date and rank on tarsus growth, the effect sizes appear to be marginal.

Table 3. Model selection results for the impact of covariates on tarsus growth. The crosses in the table indicate, whether a specific covariate has been included in the model. Given is the difference in the Akaike criterions between the current and the best model (ΔAIC), the model's deviance (DEV) and the number of estimated parameters (K).

Model	Occupancy	Siblings	Rank	Date	ΔAIC	DEV	K
m21.T		x	x	x	0	3758.96	19
m12.T		x	x		0.911	3765.87	16
m13.T		x		x	0.939	3765.90	16
m03.T		x			3.382	3774.34	13
m30.T	x	x	x	x	6.055	3759.01	22
m25.T	x	x	x		6.732	3765.69	19
m22.T	x	x		x	6.938	3765.90	19
m16.T			x	x	7.93	3772.89	16
m07.T	x	x			8.794	3773.75	16
m05.T			x		10.766	3781.72	13
m06.T				x	12.04	3783.00	13
m19.T	x		x	x	13.823	3772.78	19
m01.T					14.905	3791.86	10
m09.T	x		x		16.03	3780.99	16
m10.T	x			x	17.936	3782.89	16
m02.T	x				20.039	3791.00	13

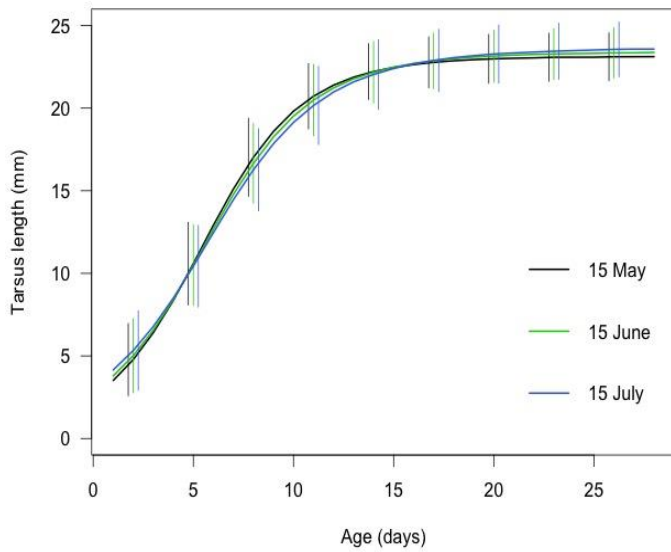


Fig. 4a Growth trajectories of tarsus length predicted from the best model (Table 3) for different hatching dates. The number of siblings was 6, and the nestling rank 1 (first hatched). The vertical lines show the 80% confidence interval.

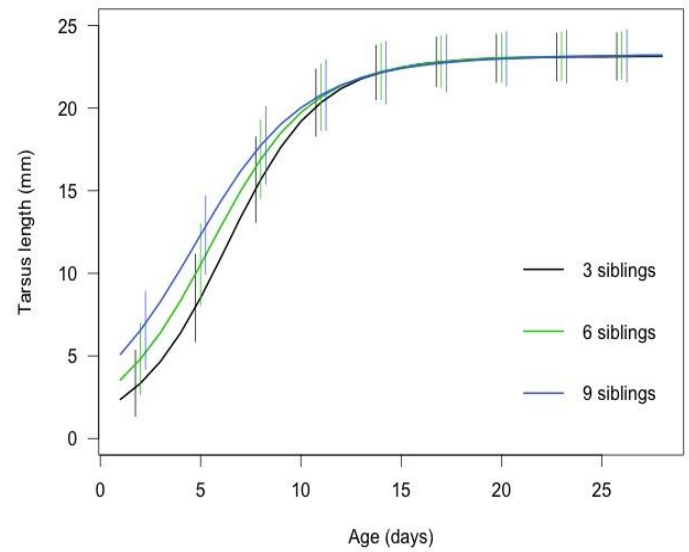


Fig. 4b Growth trajectories of tarsus length predicted from the best model (Table 3) for different number of siblings. The nestling rank was 1 (first hatched), and the date was 23rd of May (hatching peak). The vertical lines show the 80% confidence interval.

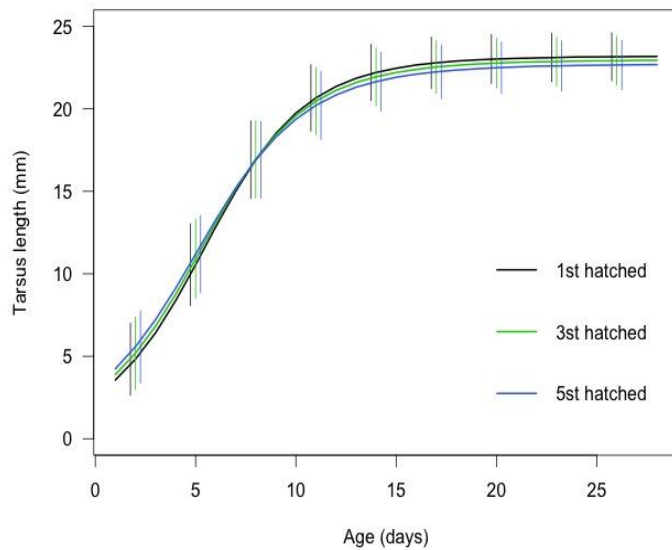


Fig. 4c Growth trajectories of tarsus length predicted from the best model (Table 3) for different rank of nestling. The number of siblings was 6, and the hatching date was 23rd of May (hatching peak). The vertical lines show the 80% confidence interval.

3rd primary length

Model selection revealed that the best model included number of siblings, nestling rank and hatching date (Table 4). The second best model included in addition occupancy, yet the support of that model by the data was clearly less. All the other models had ΔAIC values > 10 indicating that their support by the data was really weak.

The predicted 3rd primary growth curves show that hatching date had a positive impact on the length of the 3rd primary. Chicks that hatched earlier in the season reached longer 3rd primary feathers than chicks that hatched later in the season (Fig. 5a). The number of siblings also had an impact on the 3rd primaries, where nestlings with more siblings reached a shorter 3rd primary feather than individuals with less siblings (Fig. 5b) Moreover, nestlings that hatched earlier than their nest mates also reached longer primaries and had a later inflection point than nestlings which hatched later (Fig. 5c). Overall, mostly the asymptote was affected by the impacting factors.

Table 4. Model selection results for the impact of covariates on 3rd primary growth. The crosses in the table indicate, whether a specific covariate has been included in the model. Given is the difference in the Akaike criterions between the current and the best model (ΔAIC), the model's deviance (DEV) and the number of estimated parameters (K).

Model	Occupancy	Siblings	Rank	Date	ΔAIC	DEV	K
m21.H		x	x	x	0	6078.23	19
m30.H	x	x	x	x	4.436	6076.66	22
m12.H		x	x		11.9	6096.13	16
m25.H	x	x	x		15.696	6093.92	19
m13.H		x		x	31.043	6115.27	16
m22.H	x	x		x	33.477	6111.70	19
m03.H		x			44.709	6134.93	13
m07.H	x	x			48.306	6132.53	16
m16.H			x	x	52.248	6136.47	16
m19.H	x		x	x	54.882	6133.11	19
m05.H			x		57.087	6147.31	13
m09.H	x		x		62.435	6146.66	16
m06.H				x	65.613	6155.84	13
m10.H	x			x	66.11	6150.34	16
m01.H					70.009	6166.23	10
m02.H	x				74.643	6164.87	13

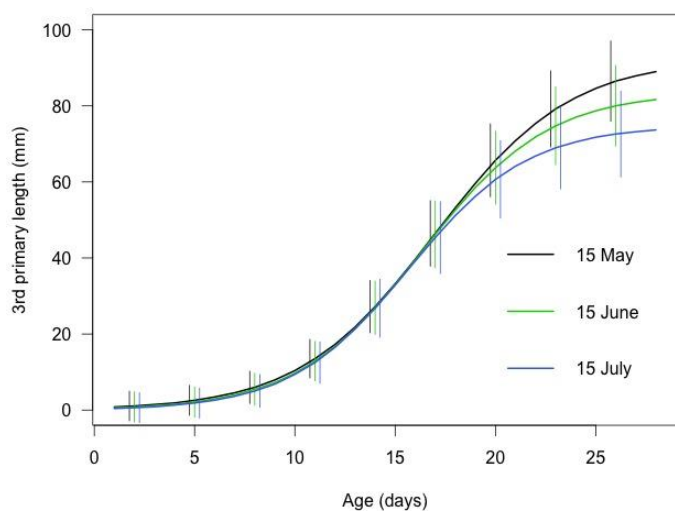


Fig. 5a Growth trajectories of 3rd primary length predicted from the best model (Table 4) for different hatching dates. The number of siblings was 6, and the nestling rank 1 (first hatched). The vertical lines show the 80% confidence interval.

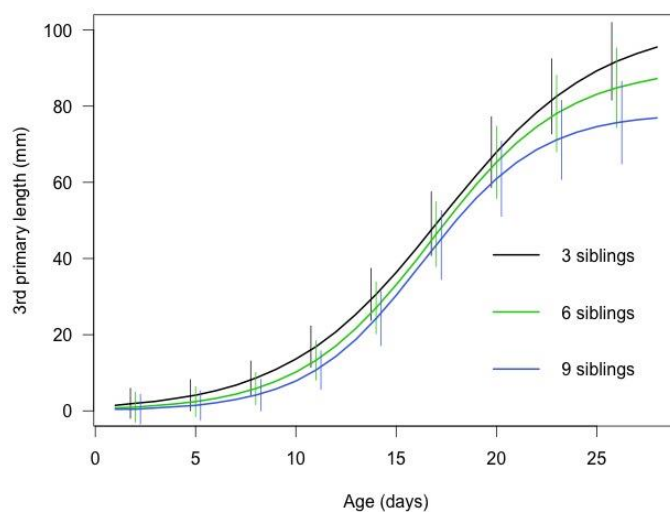


Fig. 5b Growth trajectories of 3rd primary length predicted from the best model (Table 4) for different number of siblings. The nestling rank was 1 (first hatched), and the date was 23rd of May (hatching peak). The vertical lines show the 80% confidence interval.

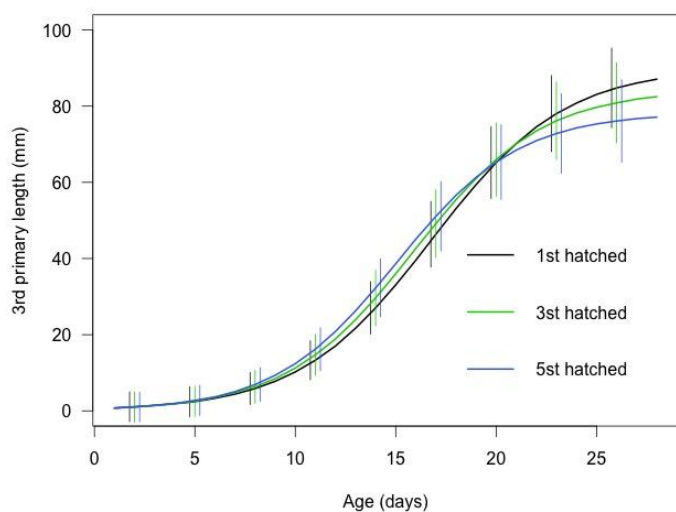


Fig. 5c Growth trajectories of 3rd primary length predicted from the best model (Table 4) for different rank of nestling. The number of siblings was 6, and the hatching date was 23rd of May (hatching peak). The vertical lines show the 80% confidence interval.

Bill length

Model selection revealed that the best model for bill growth includes number of siblings, nestling rank and hatching date (Table 5). The second best model included in addition territory occupancy with a ΔAIC value < 1 indicating that the support by the data was quite strong. The third best model included occupancy, siblings and rank with a ΔAIC value < 3 also indicating that the support was less strong.

The bill grew almost linearly from hatching until day 28. The different impacting factors were relevant at fledging, but not so much in the earlier development phases. Chicks that hatched earlier in the season reached a longer bill and had a later inflection point than chicks that hatched later in the season (Fig. 6a). The number of siblings negatively impacted bill length. Nestlings with fewer siblings had a longer bill, than individuals with more siblings (Fig. 6b). Finally, nestlings that hatched earlier than their nest mates also had a longer bill (Fig. 6c).

Table 5. Model selection results for the impact of covariates on bill growth. The crosses in the table indicate, whether a specific covariate has been included in the model. Given is the difference in the Akaike criterions between the current and the best model (ΔAIC), the model's deviance (DEV) and the number of estimated parameters (K).

Model	Occupancy	Siblings	Rank	Date	ΔAIC	DEV	K
m21.B		x	x	x	0	4196.647	19
m30.B	x	x	x	x	0.11	4190.757	22
m25.B	x	x	x		2.837	4199.484	19
m12.B		x	x		7.096	4209.743	16
m09.B	x		x		16.149	4218.796	16
m16.B			x	x	16.642	4219.289	16
m05.B			x		17.859	4226.506	13
m19.B	x		x	x	18.336	4214.983	19
m13.B		x		x	37.916	4240.563	16
m22.B	x	x		x	38.207	4234.854	19
m07.B	x	x			42.67	4245.317	16
m03.B		x			49.548	4258.195	13
m06.B				x	57.478	4266.125	13
m01.B					60.131	4274.778	10
m10.B	x			x	61.376	4264.023	16
m02.B	x				61.629	4270.276	13

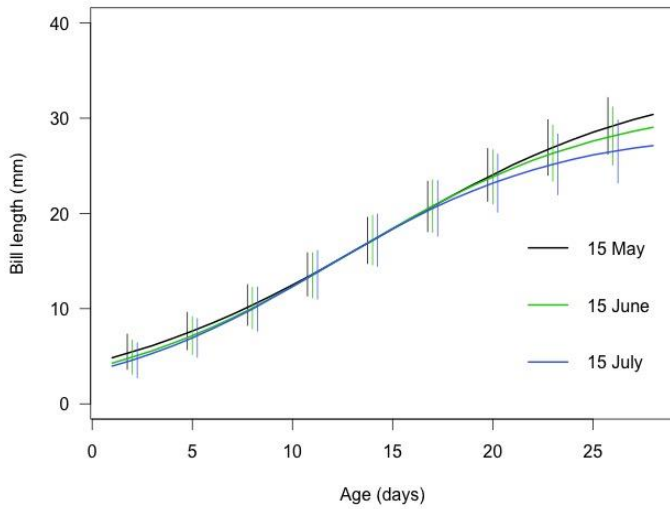


Fig. 6a Growth trajectories of bill length predicted from the best model (Table 5) for different hatching dates. The number of siblings was 6, and the nestling rank 1 (first hatched). The vertical lines show the 80% confidence interval.

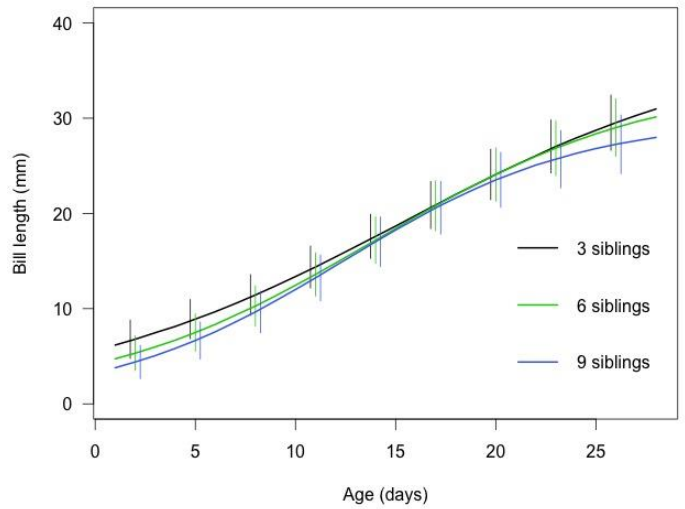


Fig. 6b Growth trajectories of bill length predicted from the best model (Table 5) for different number of siblings. The nestling rank was 1 (first hatched), and the date was 23rd of May (hatching peak). The vertical lines show the 80% confidence interval.

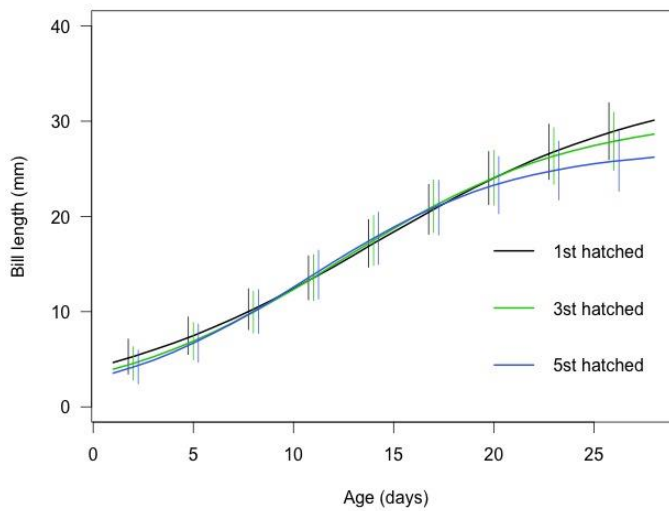


Fig. 6c Growth trajectories of bill length predicted from the best model (Table 5) for different rank of nestling. The number of siblings was 6, and the hatching date was 23rd of May (hatching peak). The vertical lines show the 80% confidence interval.

Crest length

Model selection revealed that the best model included number of siblings, nestling rank and hatching date (Table 6). The second best model included siblings and rank of nestlings. It had a ΔAIC value < 2 indicating that the support by the data was less strong.

The crest length had not reached an asymptote at fledging, thus the crest certainly continued growing after fledging. The predicted crest growth curves show that hatching date had a positive impact on the growth of the crest. Chicks that hatched earlier in the season had longer crest feathers when they fledge and had a later inflection point than chicks that hatched later in the season (Fig. 7a). The number of siblings affected crest length negatively; nestlings with fewer siblings reached a longer crest, than individuals with more siblings (Fig. 7b). The rank of the nestlings had a marginal effect on the crest feather growth only. All growth curves are quite similar but first hatched nestlings tended to reach longer crest feathers at fledging (Fig. 7c).

Table 6. Model selection results for the impact of covariates on crest growth. The crosses in the table indicate, whether a specific covariate has been included in the model. Given is the difference in the Akaike criterions between the current and the best model (ΔAIC), the model's deviance (DEV) and the number of estimated parameters (K).

Model	Occupancy	Siblings	Rank	Date	ΔAIC	DEV	K
m21.C		x	x	x	0	5254.11	19
m13.C		x		x	1.851	5261.96	16
m30.C	x	x	x	x	5.229	5253.38	22
m03.C		x			5.693	5271.93	13
m22.C	x	x		x	6.508	5260.62	19
m12.C		x	x		6.755	5266.86	16
m07.C	x	x			11.164	5271.27	16
m25.C	x	x	x		12.542	5266.65	19
m05.C			x		37.333	5303.44	13
m01.C					40.66	5312.77	10
m16.C			x	x	40.901	5301.01	16
m09.C	x		x		41.201	5301.31	16
m02.C	x				43.669	5309.83	13
m19.C	x		x	x	44.032	5298.14	19
m06.C				x	45.255	5311.36	13
m10.C	x			x	47.447	5307.56	16

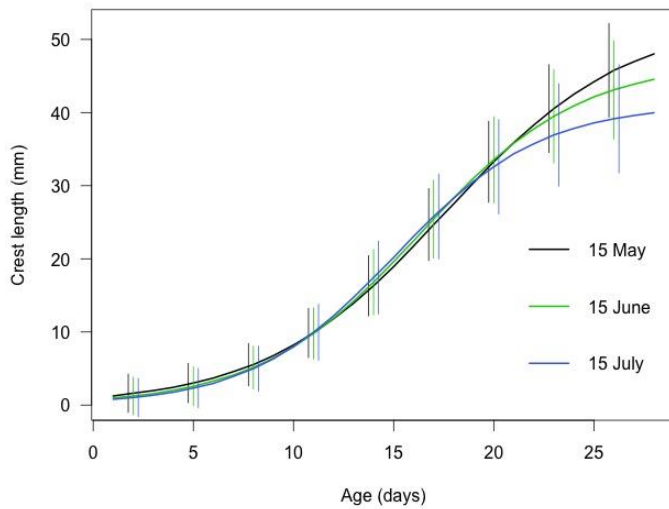


Fig. 7a Growth trajectories of crest length predicted from the best model (Table 6) for different hatching dates. The number of siblings was 6, and the nestling rank 1 (first hatched). The vertical lines show the 80% confidence interval.

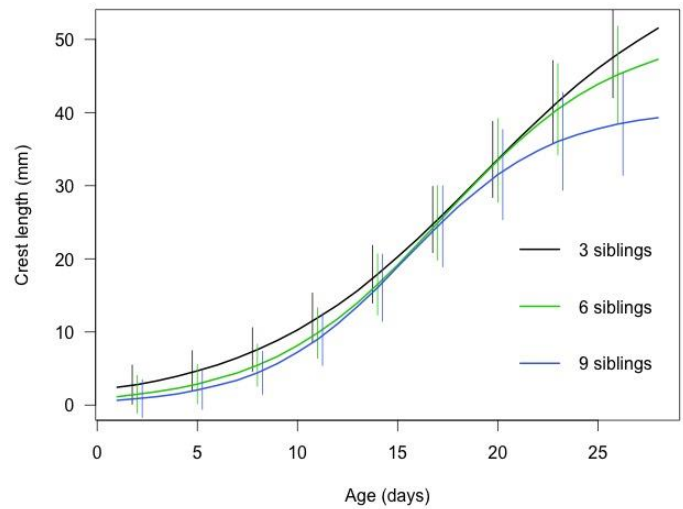


Fig. 7b Growth trajectories of crest length predicted from the best model (Table 6) for different number of siblings. The nestling rank was 1 (first hatched), and the date was 23rd of May (hatching peak). The vertical lines show the 80% confidence interval.

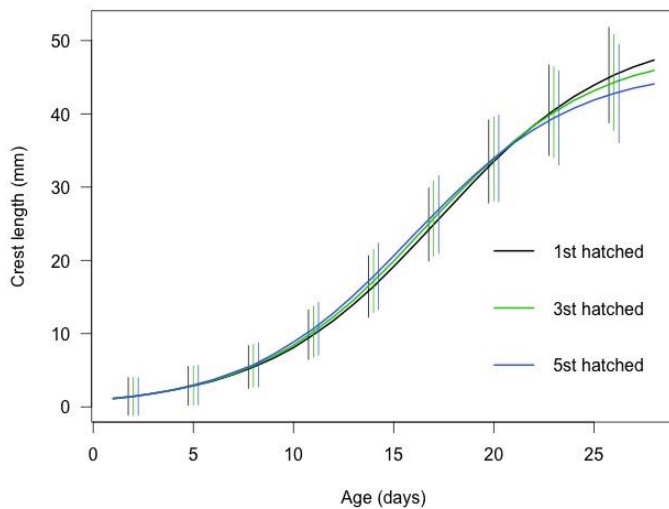


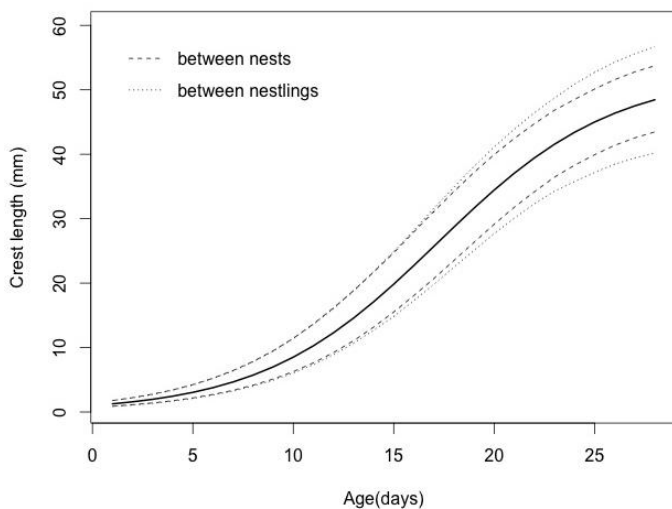
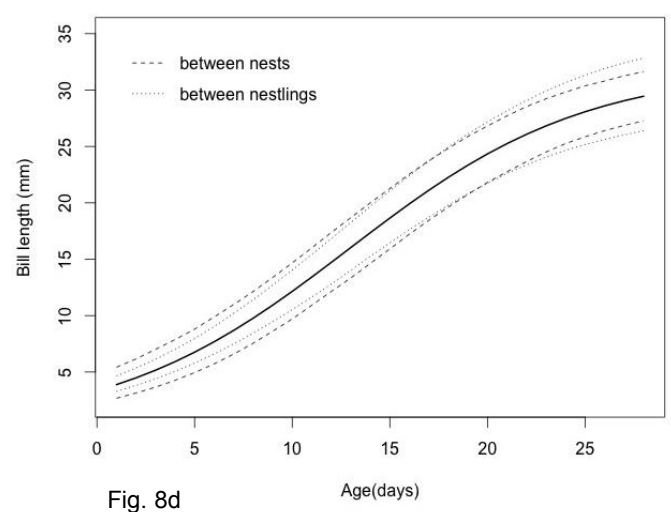
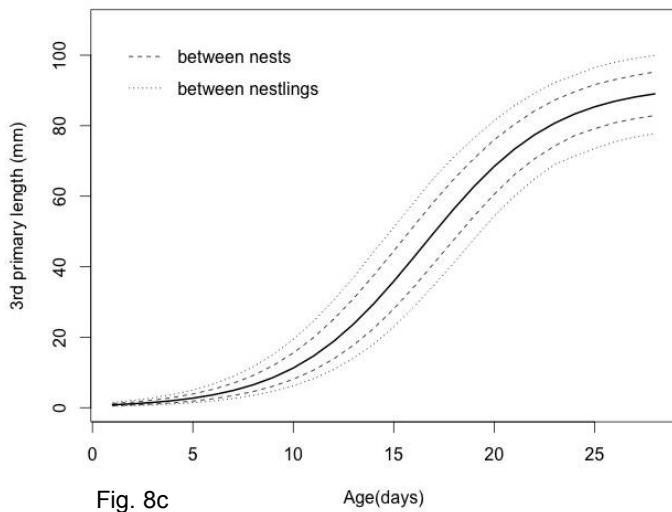
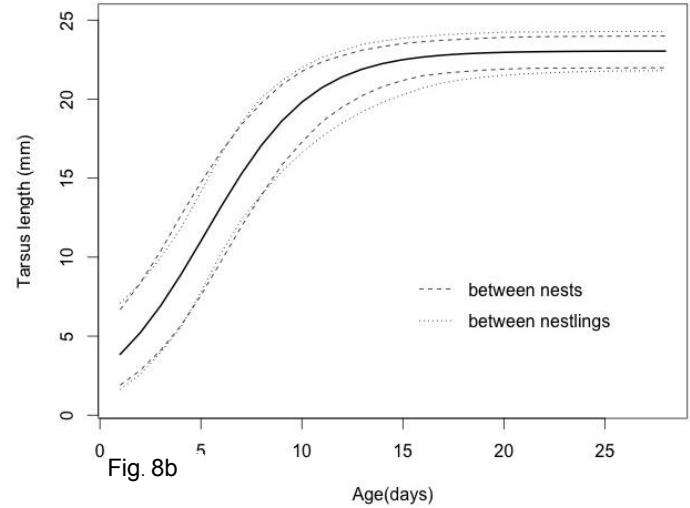
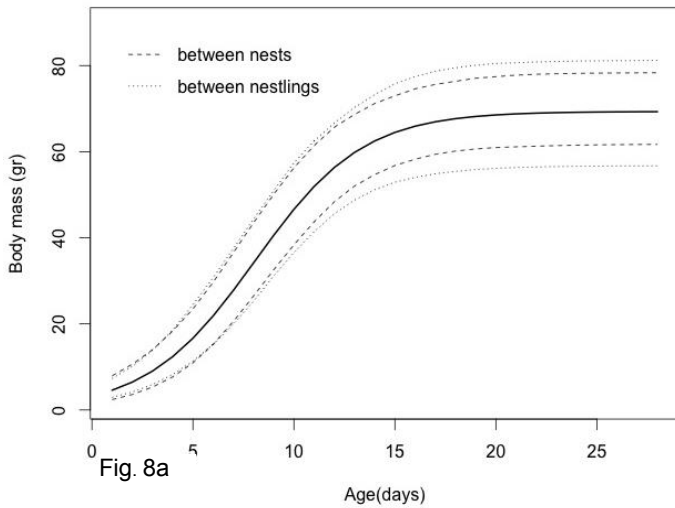
Fig. 7c Growth trajectories of crest length predicted from the best model (Table 6) for different rank of nestling. The number of siblings was 6, and the hatching date was 23rd of May (hatching peak). The vertical lines show the 80% confidence interval.

Table 7. Estimated growth parameters ($\pm$ SE) of five body traits based on the best models (Tables 2-6) with three covariates (No. of Siblings, nestling rank, hatching date)

Parameter type	Estimates	Body mass	Tarsus length	3rd primary	Bill length	Crest length
Asymptote (A)	Intercept	68.509 (2.193)	22.631 (0.301)	115.731 (2.971)	40.324 (1.381)	73.944 (3.776)
	No. of siblings	1.175 (0.309)	0.065 (0.043)	-3.265 (0.410)	-0.765 (0.177)	-3.344 (0.526)
	Nestling rank	-0.725 (0.364)	-0.059 (0.044)	-2.445 (0.442)	-1.430 (0.177)	-0.748 (0.453)
	Hatching date	-0.158 (0.036)	0.011 (0.005)	-0.234 (0.053)	-0.078 (0.023)	-0.172 (0.052)
Inflection point (I)	Intercept	9.540 (0.517)	7.067 (0.533)	17.884 (0.509)	15.475 (0.796)	21.691 (0.917)
	No. of siblings	-0.131 (0.070)	-0.241 (0.063)	-0.088 (0.079)	-0.155 (0.118)	-0.592 (0.134)
	Nestling rank	-0.024 (0.048)	-0.108 (0.043)	-0.371 (0.055)	-0.612 (0.080)	-0.329 (0.095)
	Hatching date	-0.026 (0.006)	0.004 (0.007)	-0.015 (0.007)	-0.028 (0.010)	-0.041 (0.011)
Growth rate constant (K)	Intercept	0.401 (0.052)	0.488 (0.052)	0.238 (0.019)	0.126 (0.015)	0.120 (0.020)
	No. of siblings	0.003 (0.008)	-0.006 (0.008)	0.010 (0.003)	0.001 (0.002)	0.016 (0.003)
	Nestling rank	-0.014 (0.005)	-0.011 (0.005)	0.007 (0.003)	0.011 (0.002)	0.003(0.003)
	Hatching date	0.000 (0.001)	-0.001 (0.001)	0.000 (0.000)	0.000 (0.000)	0.001 (0.000)

Variability between nests and nestlings

The applied mixed models allowed the visualization how strongly growth varied between nestlings of a nest and between nests. Generally, these two measures of variability were similar, yet the variability between nestlings tended to be slightly larger than the variability between nests (Fig. 8a-e). This trend was strongest for body mass and the length of the 3rd primary.



Discussion

I investigated the growth of five body traits (body mass, tarsus, bill, 3rd primary and crest) in Hoopoe nestlings by using nonlinear mixed models. At the time of fledging only tarsus length and body mass reached the level of the adults, while bill, crest and 3rd primary continued growing after fledging. Growth parameters of all five traits were impacted by the hatching date, the number of siblings and the rank of siblings. Territory occupancy (habitat quality) had no effect. Based on these results it appears that lengths of bill and 3rd primary are the best body traits for aging Hoopoe nestlings reliably.

Description of basic nestling growth

The nestling growth of Hoopoes has so far never been investigated in depth. The only exception to my knowledge is Bussmann (1950), who measured nestlings of two broods. The described general pattern of Bussmann (1950) fit well with my findings. By the time of the last measurement growth of only two body traits (body mass, tarsus) was already completed and three body traits (3rd primary, bill, crest) had not reached their adult size. The growth of the latter traits was therefore more linear during the nestling period than the former two. In contrast to tarsus length did body mass not reach an asymptote. Rather, maximal body mass was reached by about day 20, thereafter it tended to decline slightly (Fig. 2a). Such a shape is typical for many bird species (Ricklefs 1968), and is presumably a consequence of differential investment (e.g. a higher investment in feather and structural growth) but little evidence has been provided yet to confirm this hypotheses (Ricklefs 1968). The applied nonlinear growth model is not able to fit such a model and consequently the estimated body mass asymptote does not correspond to the body mass at fledging.

The only body trait that was hardly affected by extrinsic factors and only in a very early age was the tarsus. Since chicks at an early age had a higher amount of water in their tissue (Ricklefs 1979), the exact tarsus length was rather difficult to assess. The growth trajectories of tarsus of Hoopoes were very similar to growth curves of other species (Ricklefs 1979; Tjørve & Tjørve 2010) with a steep increase in the beginning and shallow pattern after the inflection point. Cross-fostered brood experiments with European starlings (*Sturnus vulgaris*) and Pied Flycatcher (*Ficedula hypoleuca*) showed evidence for significant heritability of tarsus length (Smith 1993; Alatalo & Lundberg 1986) and according to Alatalo & Lundberg (1986) parent-

offspring resemblance is not affected by the nest environment, but might be larger between parents and offspring because of the shared environmental background. As tarsus length is therefore more dependent on heritability than on extrinsic factors, this would explain the weak influence of the three prominent factors on the tarsi of Hoopoe nestlings. Additionally, the two constants K and A are also negatively correlated and the recession forces A to be estimated lower than it actually would be (Remes & Martin 2002).

A further goal of this study was to detect specific body traits, which are suitable for reliably aging Hoopoe nestlings. For an accurate age determination growth of body traits should be linear and ideally not very variable. It appears that three body traits fulfill the needed criteria, tarsus, bill and 3rd primary. As mentioned earlier, the tarsus is fully growth already by about day 15, and thus the period of linear growth is restricted between days 1 and 10. Since I opted for traits that allow age of the nestlings at all ages (and particularly at the usual ringing age around day 19), tarsus is not ideal. However, bill length and the length of the 3rd primary fulfill the needs and thus I recommend their use for the aging of the nestlings. The accuracy of the age determination might be improved, if the sex-specific growth trajectories are known and the sex of the nestlings is known.

Factors impacting nestling growth

Model selection of all five body traits revealed three identical factors to have a significant impact on nestling growth: Hatching date, number of siblings and rank of siblings. The frequency of territory occupancy, which is a surrogate of territory quality, had no effect. The impacting factors affected nestling growth parameters in different ways (Table 7). However, at the time of fledging, the predicted size of the traits was similarly affected: nestlings were heavier and the traits longer when they hatched early in the season and the brood was small (Fig. 3, 5, 6 and 7). A noticeable exception was tarsus length whose length at time of fledging hardly differed with these impacting factors (Fig. 4).

The timing of the brood is an important factor that affects many aspects of its outcome. Usually the clutch size is larger in earlier broods resulting in larger annual reproductive success (Lack 1968; Hochachka 1990; Siikamäki 1998). Two main factors are responsible for the seasonal clutch size decline: seasonal variation of the environment and the variation of parental or territory quality (Siikamäki 1998). I do not know which is operating in the Hoopoes, its investigation would require experimental approaches. I found that the nestlings achieved larger size at fledging when they stem from earlier compared to late broods suggesting that fledglings from early broods

need to invest less in growth after fledging compared to fledglings from later broods. Since the time available until migration starts is much less in late fledglings than in early ones and in addition the former have to grow more, this could be a significant cost. This may be a reason for the pronounced lower return rate of late fledglings compared to early fledglings (Hoffmann et al. 2015). In summary, it is very beneficial for Hoopoes to start with the first brood as early as possible, because they produce more fledglings of higher quality and because it allows a second brood (Hoffmann et al. 2015).

The number of siblings had differential impacts on body trait growth. A larger number of siblings enhanced body mass at fledging, while it resulted in reduced length of bill, crest and 3rd primary. Competition among siblings has been associated with growth rates in different studies in the past (Ricklefs 1979; Ricklefs 1982; Werschkul & Jackson 1979) and competition can apply strong selection to increase the rate of growth (Werschkul & Jackson 1979). Even though the opposite has been widely found in other species (von Haartman 1953; Roulin et al. 1999; Klomp H. 1970) the growth of Hoopoe chicks may underlie the theory that competition can increase the rate of growth. Additionally, a higher number of begging chicks can increase the stimulation of the foraging activity of parents which could also be taken into account (von Haartman 1953). In contrast to body mass a higher number of siblings affected the growth of the other body traits negatively. I can only speculate that one of the reasons for this negative correlation could be reduced space for each nestling in clutches with more siblings, leading to a slower growth of these body traits. A study with nestlings of manipulated American kestrel broods also showed a slower development of primary feathers in enlarged broods, but possible reasons are still to be investigated (Gard & Bird 1992). Another reason might be differential growth. If there are many siblings there might be strong selection to increase body size in order to become a stronger competitor, and this might come at the cost of reduced structural growth.

A common strategy to reduce sibling competition is hatching asynchrony which occurs in many altricial bird species meaning that there is a times span (up to several days) between the hatching of the first egg and the emergence of the last chick. One of the consequences of asynchronous hatching is size hierarchy among nestlings and therefore differences in offspring condition (Slagsvold 1986). Hatching asynchrony is among others an adaptation to environmental constraints such as food availability (Stenning 1996) and usually the last hatched chick in the brood suffers most from food shortages (Starck & Ricklefs 1998). I found that the asymptotic growth of all body traits of early hatchings was higher compared to later hatched nest mates. Observations of Martin-Vivaldi (1999) show that size of nestlings correlate with

feeding frequency, as female Hoopoes fed the largest begging chick regardless of smaller simultaneously begging chicks. As a consequence, if the amount of food is not increased, typically the stronger nestlings successfully compete against the weaker individuals and therefore a difference in body condition often become apparent. According to Martin-Vivaldi (1999) Hoopoes can therefore be considered as brood reduction strategists and this pattern of food delivery helps them to reduce clutch sizes by selective starvation of the youngest but the evolutionary significance of hatching asynchrony is yet poorly understood (Wilson & Clark 1981).

Contrary to my expectations, the frequency of territory occupancy was not a prominent factor affecting nestling growth. Territory occupancy reflects territory quality (Tschumi et al. 2014) and thus it can be expected higher growth rates of nestlings raised in territories of higher quality. A possible explanation for why I have not found the expected relationships is the ability of birds to adapt to the environment by adjusting their clutch sizes. Bird should produce clutches that result in a number of nestlings that could be raised, given territory and parental quality (Lack 1947; Martin-Vivaldi et al. 1999). This potential flexibility for adaption to the environment could also be the reason why there was no difference between the variance of nestlings in the same nest and that of nestlings between nests. On the other side, variability within the nest was generally quite large, which is likely caused by the asymmetrical competition due to the asynchronous hatching. Nevertheless, further studies with experimental clutch size manipulations would be needed to be more conclusive about the effect of territory quality on nestling growth.

Besides territory occupancy, the impact of another factor has been tested on nestling growth: the location of the nest boxes in the study area (east or west orientation) but equal to territory occupancy it was not found to be a prominent factor by model selection. Although the eastern part of the area is managed slightly different due to allot settlement rather than intensively managed fruit plantations, the study area is still quite homogenous and therefore this factor did not have an impact on nestling growth.

A factor that affects food availability in insectivorous species is the weather, and as such weather affect reproductive success in Hoopoes (Arlettaz et al. 2010). Varying food availability is likely to impact also nestling growth. Nevertheless, the effect of weather on nestling growth has not been investigated in my study, because of two reasons. Firstly, weather conditions were little variable and generable very favourable for Hoopoes in the year 2014. Therefore it would have been more interesting to investigate nestling growth if I had data stem from different years. Secondly, the parameter weather could not be added to my non-linear mixed models

and the application of completely different models would have been necessary to account for this parameter. Finally, the sex was also not included in my analyses. Since adult males are slightly larger than females, sex might affect nestling growth. If sex did in fact affect nestling growth, not accounting for it would increase the variability, hence sex could be one reason for the large variability. As nestlings were not sexed in this study, sex-specific growth pattern could not be studied.

Conclusion

Hoopoe nestling growth showed similar pattern as found in other birds and was most strongly impacted by three factors. Under the assumption that large and heavy fledglings have highest survival prospects, the most advantageous conditions for Hoopoe nestling is to hatch as early as possible, to have as few siblings as possible and to hatch earlier than the siblings. Indeed a previous study has shown that Hoopoe fledglings survive better when they are from early broods (Hoffmann et al. 2015) and my study highlights a possible mechanism of this result. Early hatched nestlings are not only larger, they also have more time for full development before they start migration as they stay a longer time in the breeding area than late fledglings (van Wijk et al. in prep.).

Acknowledgements

I wish to express my sincere thanks to my supervisor Dr. Michael Schaub from the Swiss ornithological institute for his great commitment during the whole process of writing this master thesis, for his critical and most helpful comments and also for his great support during my fieldwork.

I also want to take this opportunity to thank all people involved in the Hoopoe field season in 2014 and special thanks belong to my boyfriend Wilhelm for his encouragement and for lending a sympathetic ear for all my matters at any time.

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Appendix



Fig. A1 Chicks of different age of the same brood caused by asynchronous hatching, 1 day old (right) up to 7 days old (left)



Fig. A2 Chicks of different age of the same brood caused by asynchronous hatching, 7 day old (right) up to 13 days old (left)



Fig. A3 Body mass measurement by using an electronic balance



Fig. A4 Measurement of tarsus length by using a calliper



Fig. A5 Measurement of 3rd primary with a standard ruler



Fig. A6 Measurement of the crest with millimetre paper



Fig. A7 15 days old chick after ringing

```
#####
# R-Script for Hoopoe nestling growth model
# cf. Sofaer et al. (2013), J. Avian Biol. 44: 469-478
#
#####
#
# M. Schaub
# B. Hildebrandt
#
#####

# Read the data

attach(dataset)
require(nlme)

# Define a logistic function.
OnePop = function(Age, Asym, xmid, K){ Asym/(1 + exp((xmid - Age)*K))
}

# Calculate the derivatives of the function
DerivOnePop = deriv(body(OnePop)[[2]], namevec = c("Asym", "xmid", "K"),
function.arg = OnePop)

# Starting values; these can be estimates from nls (i.e. a model without
random effects), or from previous studies
startOnePop = c(Asym = 70, xmid = 8.1, K = .35)

#gnlsControl()

OnePop_NoRE_gnls = nls(Body mass ~ Asym/(1 + exp((xmid - Age)*K)), start =
startOnePop)

summary(OnePop_NoRE_gnls)

# Syntax for models with Nest and Nestling random effects on all parameters

k1 <- which(is.na(dataset$Age))
k2 <- which(is.na(dataset$Body mass))

nest_id = dataset$BoxNo[-k2]
nestling_id = dataset$Ring[-k2]

# Mache neue Variable Nestling_ID, so dass es für die Auswertung passt

nestling_id_new <- numeric(length(nestling_id))

nest_no <- unique(nest_id)

for (j in 1:length(nest_no)){
  id <- which(nest_id == nest_no[j])
  nestling_no <- unique(nestling_id[id])
  for (i in 1:length(nestling_no)){
    y <- which(nestling_id[id] == nestling_no[i])
    nestling_id_new[(min(id)-1+y)] <- i
  }
}

startOnePop = c(Asym = 69, xmid = 8, K = .37)

# nlmeControl()

# Random Effekt Nest

#1
OnePop_i_Nest = nlme(Body mass ~ DerivOnePop( Age, Asym, xmid, K), fixed =
Asym + xmid + K ~ 1, random = Asym + xmid + K ~ 1 | nest_id, start =
startOnePop)
```

```

summary(OnePop_i_Nest)

# Random Effekt Nestling

#2
OnePop_i_Nestling = nlme(Body mass ~ DerivOnePop( Age, Asym, xmid, K), fixed
= Asym + xmid + K ~ 1, random = Asym + xmid + K ~ 1 | nestling_id, start =
startOnePop)

summary(OnePop_i_Nestling)

# Random Effekt Nest und Nestling

#3
OnePop_i_NestNestling = nlme(Body mass ~ DerivOnePop( Age, Asym, xmid, K),
fixed = Asym + xmid + K ~ 1,
random = Asym + xmid + K ~ 1 | nest_id/nestling_id_new, start = startOnePop)

Summary(OnePop_i_NestNestling)

GroupedNestNestling = groupedData(Body mass ~ Age | nest_id/nestling_id)

# Mod 0

m0.w = nlme(Body mass ~ DerivOnePop(Age , Asym, xmid, K), data =
GroupedNestNestling, fixed = Asym + xmid + K ~ 1, random = list(nest_id =
pdDiag(Asym + xmid + K ~ 1), nestling_id = pdDiag(Asym + xmid + K ~ 1)),
start = startOnePop)

summary(m0.w)

#####

# Models with fixed covariates

#####

#for 0 Covariable

OnePopCov0 = function(Age, Asym.int, xmid.int, K.int){
(Asym.int)/(1 + exp(((xmid.int) - Age)*(K.int)))
}

# Calculate the derivatives of the function
DerivOnePopCov0 = deriv(body(OnePopCov0)[[2]], namevec = c("Asym.int",
"xmid.int", "K.int"), function.arg = OnePopCov0)

startOnePop = c(Asym.int = 70, xmid.int = 8, K.int = .35)

# we chose the model with random effects not correlated neither on nest level
nor on nestling level and no influence of the covariable on beta value ( beta
value assumed 0)

y <- dataset$Body mass[-k2]

m1.w = nlme(y ~ DerivOnePopCov0(Age, Asym.int, xmid.int, K.int), data =
GroupedNestNestling, fixed = Asym.int + xmid.int + K.int ~ 1,
random = list(nest_id =pdDiag(Asym.int + xmid.int + K.int ~ 1), nestling_id =
pdDiag(Asym.int + xmid.int + K.int ~ 1)), start = startOnePop)

summary (m1.w)

```

```

# for 1 Covariable

OnePopCov1 = function(Age, Asym.int, Asym.betal, xmid.int, xmid.betal, K.int,
K.betal, covariable1){
  (Asym.int + Asym.betal*covariable1)/(1 +
exp(((xmid.int+xmid.betal*covariable1) - Age)*(K.int+K.betal*covariable1)))
}

# Calculate the derivatives of the function
DerivOnePopCov1 = deriv(body(OnePopCov1)[[2]], namevec = c("Asym.int",
"Asym.betal", "xmid.int",
"xmid.betal", "K.int", "K.betal"), function.arg = OnePopCov1)

startOnePop1 = c(Asym.int = 70, Asym.betal = 0, xmid.int = 8, xmid.betal = 0,
K.int = .35, K.betal = 0)

# we chose the model with the random effects not correlated neither on nest
level nor on nestling level and no #influence of the covariable on beta value
( beta value assumed 0)

# for 2 covariables

OnePopCov2 = function(Age, Asym.int, Asym.betal, Asym.beta2, xmid.int,
xmid.betal, xmid.beta2, K.int, K.betal, K.beta2, covariable1, covariable2){
  (Asym.int + Asym.betal*covariable1 + Asym.beta2*covariable2)/(1 +
exp(((xmid.int+xmid.betal*covariable1+xmid.beta2*covariable2) - Age)*
(K.int+K.betal*covariable1+K.beta2*covariable2)))
}

# Calculate the derivatives of the function

DerivOnePopCov2 = deriv(body(OnePopCov2)[[2]], namevec = c("Asym.int",
"Asym.betal", "Asym.beta2", "xmid.int",
"xmid.betal", "xmid.beta2", "K.int", "K.betal", "K.beta2"), function.arg =
OnePopCov2)

startOnePop2 = c(Asym.int = 70, Asym.betal = 0, Asym.beta2 = 0, xmid.int = 8,
xmid.betal = 0, xmid.beta2 = 0, K.int = .35, K.betal = 0, K.beta2 = 0)

# we chose the model with random effects correlated neither on nest level nor
on nestling level and no influence
#of the covariable on beta value (beta value assumed 0)

m7.w2OS = nlme(y ~ DerivOnePopCov2(Age, Asym.int, Asym.betal, Asym.beta2,
xmid.int, xmid.betal, xmid.beta2,
K.int, K.betal, K.beta2, covariable1 = Occupancy, covariable2 = Siblings),
data =
GroupedNestNestling, fixed = Asym.int + Asym.betal + Asym.beta2 + xmid.int +
xmid.betal + xmid.beta2 + K.int +
K.betal + K.beta2 ~ 1, random = list(nest_id =pdDiag(Asym.int + xmid.int +
K.int ~ 1), nestling_id =
pdDiag(Asym.int + xmid.int + K.int ~ 1)), start = startOnePop2)

summary (m7.w2OS)

# for 3 covariables

OnePopCov3 = function(Age, Asym.int, Asym.betal, Asym.beta2, Asym.beta3,
xmid.int, xmid.betal, xmid.beta2, xmid.beta3, K.int, K.betal,
K.beta2, K.beta3, covariable1, covariable2, covariable3){ (Asym.int +
Asym.betal*covariable1 + Asym.beta2*covariable2 + Asym.beta3*covariable3)/

```

```

(1 + exp(((xmid.int+xmid.betal*covariable1+xmid.beta2*covariable2 +
xmid.beta3*covariable3) - Age)*(K.int + K.betal*covariable1 +
K.beta2*covariable2 + K.beta3*covariable3)))
}

# Calculate the derivatives of the function

DerivOnePopCov3 = deriv(body(OnePopCov3)[[2]], namevec = c("Asym.int",
"Asym.betal", "Asym.beta2","Asym.beta3", "xmid.int",
"xmid.betal", "xmid.beta2","xmid.beta3", "K.int", "K.betal","K.beta2",
"K.beta3"), function.arg = OnePopCov3)

startOnePop3 = c(Asym.int = 70, Asym.betal = 0, Asym.beta2 = 0, Asym.beta3 =
0, xmid.int = 8, xmid.betal = 0,
xmid.beta2 = 0, xmid.beta3 = 0, K.int = .35, K.betal = 0, K.beta2 = 0,
K.beta3 = 0)

m17.w3OSB = nlme(y ~ DerivOnePopCov3(Age, Asym.int, Asym.betal, Asym.beta2,
Asym.beta3, xmid.int, xmid.betal, xmid.beta2,
xmid.beta3, K.int, K.betal, K.beta2, K.beta3, covariable1 = Occupancy,
covariable2 = Siblings, covariable3 = Bro), data =
GroupedNestNestling, fixed = Asym.int + Asym.betal + Asym.beta2 + Asym.beta3
+ xmid.int + xmid.betal + xmid.beta2 + xmid.beta3
+ K.int + K.betal + K.beta2 + K.beta3 ~ 1, random = list(nest_id
= pdDiag(Asym.int + xmid.int + K.int ~ 1), nestling_id =
pdDiag(Asym.int + xmid.int + K.int ~ 1)), start = startOnePop3)

summary (m17.w3OSB)

#for 4 covariables

OnePopCov4 = function(Age, Asym.int, Asym.betal, Asym.beta2, Asym.beta3,
Asym.beta4, xmid.int, xmid.betal, xmid.beta2, xmid.beta3, xmid.beta4, K.int,
K.betal,
K.beta2, K.beta3, K.beta4, covariable1, covariable2, covariable3,
covariable4){ (Asym.int + Asym.betal*covariable1 + Asym.beta2*covariable2 +
Asym.beta3*covariable3 +
Asym.beta4*covariable4)/(1 + exp(((xmid.int+ xmid.betal*covariable1+
xmid.beta2*covariable2 + xmid.beta3*covariable3 +
xmid.beta4*covariable4) - Age)*(K.int + K.betal*covariable1 +
K.beta2*covariable2 + K.beta3*covariable3 + K.beta4*covariable4)))
}

# Calculate the derivatives of the function

DerivOnePopCov4 = deriv(body(OnePopCov4)[[2]], namevec = c("Asym.int",
"Asym.betal", "Asym.beta2","Asym.beta3","Asym.beta4", "xmid.int",
"xmid.betal", "xmid.beta2","xmid.beta3", "xmid.beta4","K.int",
"K.betal","K.beta2", "K.beta3","K.beta4"), function.arg = OnePopCov4)

startOnePop4 = c(Asym.int = 70, Asym.betal = 0, Asym.beta2 = 0, Asym.beta3 =
0, Asym.beta4 = 0, xmid.int = 8, xmid.betal = 0, xmid.beta2 = 0, xmid.beta3 =
0, xmid.beta4 = 0, K.int = .35, K.betal = 0, K.beta2 = 0, K.beta3 = 0,
K.beta4 = 0)

m27.w4OSBR = nlme(y ~ DerivOnePopCov4(Age, Asym.int, Asym.betal, Asym.beta2,
Asym.beta3, Asym.beta4, xmid.int, xmid.betal, xmid.beta2,
xmid.beta3, xmid.beta4, K.int, K.betal, K.beta2, K.beta3, K.beta4,
covariable1 = Occupancy, covariable2 = Siblings, covariable3 = Bro,
covariable4 = Rid), data =
GroupedNestNestling, fixed = Asym.int + Asym.betal + Asym.beta2 + Asym.beta3
+ Asym.beta4 + xmid.int + xmid.betal + xmid.beta2 + xmid.beta3 + xmid.beta4 +

```

```

K.int + K.beta1 + K.beta2 + K.beta3 + K.beta4 ~ 1, random = list(nest_id
=pdDiag(Asym.int + xmid.int + K.int ~ 1), nestling_id =
pdDiag(Asym.int + xmid.int + K.int ~ 1)), start = startOnePop4)

summary (m27.w4OSBR)

#for 5 covariables

OnePopCov5 = function(Age, Asym.int, Asym.beta1, Asym.beta2, Asym.beta3,
Asym.beta4,Asym.beta5, xmid.int, xmid.beta1, xmid.beta2, xmid.beta3,
xmid.beta4,xmid.beta5, K.int, K.beta1,
K.beta2, K.beta3, K.beta4,K.beta5, covariable1, covariable2, covariable3,
covariable4, covariable5){ (Asym.int + Asym.beta1*covariable1 +
Asym.beta2*covariable2 + Asym.beta3*covariable3 +
Asym.beta4*covariable4 + Asym.beta5*covariable5)/(1 + exp(((xmid.int+
xmid.beta1*covariable1+ xmid.beta2*covariable2 + xmid.beta3*covariable3 +
xmid.beta4*covariable4 + xmid.beta5*covariable5) - Age)*(K.int +
K.beta1*covariable1 + K.beta2*covariable2 + K.beta3*covariable3 +
K.beta4*covariable4 + K.beta5*covariable5)))
}

# Calculate the derivatives of the function

DerivOnePopCov5 = deriv(body(OnePopCov5)[[2]], namevec = c("Asym.int",
"Asym.beta1", "Asym.beta2","Asym.beta3","Asym.beta4","Asym.beta5","xmid.int",
"xmid.beta1", "xmid.beta2","xmid.beta3", "xmid.beta4", "xmid.beta5","K.int",
"K.beta1","K.beta2","K.beta3","K.beta4","K.beta5"), function.arg =
OnePopCov5)

startOnePop5 = c(Asym.int = 70, Asym.beta1 = 0, Asym.beta2 = 0, Asym.beta3 =
0, Asym.beta4 = 0, Asym.beta5 = 0, xmid.int = 8, xmid.beta1 = 0,
xmid.beta2 = 0, xmid.beta3 = 0, xmid.beta4 = 0, xmid.beta5 = 0, K.int = .35,
K.beta1 = 0, K.beta2 = 0, K.beta3 = 0, K.beta4 = 0, K.beta5 = 0)

m32.w5OSBRH = nlme(y ~ DerivOnePopCov5(Age, Asym.int, Asym.beta1, Asym.beta2,
Asym.beta3, Asym.beta4, Asym.beta5, xmid.int, xmid.beta1, xmid.beta2,
xmid.beta3, xmid.beta4,xmid.beta5, K.int, K.beta1, K.beta2, K.beta3, K.beta4,
K.beta5, covariable1 = Bro, covariable2 = Siblings, covariable3 = Occupancy,
covariable4 = Rid,
covariable5 = Date), data = GroupedNestNestling, fixed = Asym.int +
Asym.beta1 + Asym.beta2 + Asym.beta3 + Asym.beta4 + Asym.beta5 + xmid.int +
xmid.beta1 + xmid.beta2 + xmid.beta3 + xmid.beta4 + xmid.beta5+
K.int + K.beta1 + K.beta2 + K.beta3 + K.beta4 + K.beta5 ~ 1, random =
list(nest_id =pdDiag(Asym.int + xmid.int + K.int ~ 1),
nestling_id = pdDiag(Asym.int + xmid.int + K.int ~ 1)), start = startOnePop5)

summary (m32.w5OSBRH)

#####

# Plot

growth.plot <- function(asym = c(70, 68), xmid = c(8,7.5), K = c(0.35, 0.4),
D = 28) {
  if (length(asym)==1) {
    y <- numeric
    for (t in 1:D){
      y[t] <- asym / (1+exp(K*(xmid-t)))
    }
    plot(x=1:D, y=y, type = "l", xlab = "Age")
  }
  if (length(asym)>1) {
    y <- matrix(NA, nrow = length(asym), ncol = D)
    for (j in 1:length(asym)){
      for (t in 1:D){

```

```

        y[j,t] <- asym[j] / (1+exp(K[j]*(xmid[j]-t)))
    }
}
plot(x=1:D, y = y[1,], type = "l", xlab = "Age (days)", ylim = range(y),
ylab=" Bill (mm)")
for (i in 2:length(asym)){
    lines(x=1:D, y = y[i,], col = i, lwd= "1.5")
}
}
}

#####

# für Body mass

sib <- c(5,5,5)
rank <- c(1,3,6)
date <- c(23,23,23)

growth.plot(asym=c(mod$coef$fix[1]+mod$coef$fix[2]*sib[1]+mod$coef$fix[3]*
rank[1]+mod$coef$fix[4]*date[1],mod$coef$fix[1]+mod$coef$fix[2]*sib[2]+
mod$coef$fix[3]*rank[2]+mod$coef$fix[4]*date[2],mod$coef$fix[1]+mod$coef$fix[
2]*sib[3]+mod$coef$fix[3]*rank[3]+mod$coef$fix[4]*date[3]),xmid=c(mod$coef$fi
x[5]+mod$coef$fix[6]*sib[1]+mod$coef$fix[7]*rank[1]+mod$coef$fix[8]*date[1],m
od$coef$fix[5]+mod$coef$fix[6]*sib[2]+mod$coef$fix[7]*rank[2]+
mod$coef$fix[8]*date[2],mod$coef$fix[5]+mod$coef$fix[6]*sib[3]+mod$coef$fix[7
]*rank[3]+mod$coef$fix[8]*date[3]),K=c(mod$coef$fix[9]+mod$coef$fix[10]*sib[1
]+mod$coef$fix[11]*rank[1]+mod$coef$fix[12]*date[1],mod$coef$fix[9]+mod$coef$
fix[10]*sib[2]+mod$coef$fix[11]*rank[2]+mod$coef$fix[12]*date[2],mod$coef$fix
[9]+mod$coef$fix[10]*sib[3]+mod$coef$fix[11]*rank[3]+mod$coef$fix[12]*date[3]
))

legend(x=15, y=40, legend=c("15th May", "15th June", "15th July"), lty=
c(1,1,1), col = c("black", "red", "green"), bty="n",lwd = "1.5")
legend(x=15, y=40, legend=c("3 Siblings", "6 Siblings", "9 Siblings"), lty=
c(1,1,1), col = c("black", "red", "green"), bty="n",lwd = "1.5")
legend(x=15, y=40, legend=c("1st hatched", "3rd hatched", "6th hatched"),
lty= c(1,1,1), col = c("black", "red", "green"), bty="n", lwd = "1.5")

#####

# Darstellung der Variabilität zwischen den Nestern und zwischen den
Nestlingen (innerhalb der Nester), hier für Body mass

growth.plot.var <- function(asym.Nest, xmid.Nest, K.nest, asym.Nestling,
xmid.Nestling, K.nestling, D = 28) {
    qv <- function(x) quantile(x, c(0.025, 0.975))
    y.Nest <- matrix(NA, nrow = length(asym.Nest), ncol = D)
    for (j in 1:length(asym.Nest)){
        for (t in 1:D){
            y.Nest[j,t] <- asym.Nest[j] / (1+exp(K.Nest[j]*(xmid.Nest[j]-t)))
        }
    }
    cri.Nest <- apply(y.Nest[2:nrow(y.Nest)],2,qv)
    y.Nestling <- matrix(NA, nrow = length(asym.Nestling), ncol = D)
    for (j in 1:length(asym.Nestling)){
        for (t in 1:D){
            y.Nestling[j,t] <- asym.Nestling[j] /
(1+exp(K.Nestling[j]*(xmid.Nestling[j]-t)))
        }
    }
    cri.Nestling <- apply(y.Nestling[2:nrow(y.Nestling)],2,qv)

    plot(x=1:D, y = y.Nestling[1,], type = "l", xlab = "Age(days)", ylim =
range(cbind(y.Nest, y.Nestling)), ylab="Body mass(gr)", lwd = 2)
    lines(x=1:D, y = cri.Nest[1,], lty = 2)

```

```

lines(x=1:D, y = cri.Nest[2,], lty = 2)
lines(x=1:D, y = cri.Nestling[1,], lty = 3)
lines(x=1:D, y = cri.Nestling[2,], lty = 3)
legend(x=1, y = max(cbind(y.Nest, y.Nestling)), legend = c("between nests",
"between nestlings"), lty = c(2,3), bty = "n")
}

m1.w = nlme(Body mass ~ DerivOnePop(Age , Asym, xmid, K), data =
GroupedNestNestling, fixed = Asym + xmid + K ~ 1, random = list(nest_id =
pdDiag(Asym + xmid + K ~ 1), nestling_id = pdDiag(Asym + xmid + K ~ 1)),
start = startOnePop)

summary(m1.w)

Std_Nest <- c(4.292065, 0.6118075, 0.0321028)
Std_Nestling <- c(6.260035, 0.6132903, 2.535051e-05)

sim <- 1000

asym.Nest <- rnorm(sim, m1.w$coef$fixed[1], Std_Nest[1])
asym.Nest <- c(m1.w$coef$fixed[1], asym.Nest)

xmid.Nest <- rnorm(sim, m1.w$coef$fixed[2], Std_Nest[2])
xmid.Nest <- c(m1.w$coef$fixed[2], xmid.Nest)

K.Nest <- rnorm(sim, m1.w$coef$fixed[3], Std_Nest[3])
K.Nest <- c(m1.w$coef$fixed[3], K.Nest)

asym.Nestling <- rnorm(sim, m1.w$coef$fixed[1], Std_Nestling[1])
asym.Nestling <- c(m1.w$coef$fixed[1], asym.Nestling)

xmid.Nestling <- rnorm(sim, m1.w$coef$fixed[2], Std_Nestling[2])
xmid.Nestling <- c(m1.w$coef$fixed[2], xmid.Nestling)

K.Nestling <- rnorm(sim, m1.w$coef$fixed[3], Std_Nestling[3])
K.Nestling <- c(m1.w$coef$fixed[3], K.Nestling)

growth.plot.var(asym.Nest, xmid.Nest, K.Nest, asym.Nestling, xmid.Nestling,
K.Nestling, 28)

```