The effects of hatching asynchrony on growth and mortality patterns in Eurasian Hoopoe *Upupa epops* nestlings

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Growth is a fundamental life history trait in all organisms and is closely related to individual fitness. In altricial birds, growth of many traits is restricted to the short period between hatching and fledging and strongly depends on the amount of food that parents deliver and the extent of hatching asynchrony. However, empirical studies of energy allocation to growth of different body size traits as a function of hatching asynchrony are scarce. We studied growth and mortality of Eurasian Hoopoe *Upupa epops*, a species with a long breeding season and high brood size variance, whose nestlings show pronounced hatching asynchrony, in order to test how hatching asynchrony affects different growth traits in the context of territory quality, season and brood size. The growth of five body traits (body mass, and lengths of tarsus, third primary, bill and longest crest feather) was investigated to understand how it was affected by brood size, hatching date and order, and territory quality. In total, 241 nestlings from 39 nests were measured every 4 days in 2014 in south-western Switzerland. Brood size, hatching date and hatching order had the strongest influence on growth trajectories, although tarsus growth was only marginally affected by these variables. Nestlings that hatched earlier than their siblings were heavier and had longer third primaries, bills and crest feathers compared with later-hatched siblings. In territories of high quality, hatching order differences disappeared for body mass growth, but persisted for lengths of third primary, bill and crest feathers. Brood size was inversely associated with third primary, bill and crest feather lengths, but positively associated with body mass. Nestling mortality was higher in later-hatched nestlings and in broods that were raised in territories of lower quality. Our study shows that in nestlings, energy was allocated differentially between body traits and this allocation interacted with hatching order and territory quality. Rapid mass gain by nestlings was prioritized in order to increase competitive ability. Our results provide support for the brood reduction hypothesis as an explanation of hatching asynchrony in Hoopoes.

Keywords: brood reduction, fledgling condition, nestling growth, nestling mortality, non-linear mixed models.

Growth is a fundamental development in all organisms and has a strong impact on individual fitness (Zach *et al.* 1984, Stearns 1992, Starck &

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Ricklefs 1998). In most birds, growth is very fast, and in altricial species it is mostly restricted to the short period between hatching and fledging. Fast growth is likely to be an adaptation to reduce the exposure time to predators because nestlings of altricial birds cannot escape (Starck & Ricklefs 1998). Body size and energy reserves at fledging

are shaped by growth and often affect subsequent survival. Fledglings in good body condition survive better than those in poorer condition (Naef-Daenzer et al. 2001, Cox et al. 2014, Bouwhuis et al. 2015). Nestling growth is therefore an important determinant of fitness.

Growth of altricial nestlings requires energy that is supplied by the parents, and therefore ultimately depends on food availability and parent quality. The speed of growth is positively related to food intake (Gebhardt-Henrich & Richner 1998, Naef-Daenzer & Keller 1999). Thus, any factor that affects food availability also affects nestling growth, unless parents adjust their feeding behaviour. If the overall food demand for a brood increases or food availability decreases, or both, parents must either increase their effort to deliver food or risk reduced growth or even death of nestlings. By increasing the effort to deliver food, parents may compromise their own survival, as shown experimentally (Masman et al. 1989). Parents thus have to deal with the trade-offs between quality and quantity of nestlings, as well as between current and future reproduction (Drent & Daan 1980).

Variability in nestling growth is related to food availability in the parental territory (Richner 1989), to parental behaviour (Brown 1988) and to competition among nestlings (Neuenschwander et al. 2003). As food availability is often not constant over the entire breeding period, natural selection favours birds that time their broods such that the time of the highest food demand from nestlings coincidences with the food peak (Both & Visser 2001). Growth rates of nestlings often decline over the breeding season, either as a result of seasonally deteriorating foraging conditions or because later broods are initiated by parents with lower provisioning abilities (Morbey & Ydenberg 2000). Parents must distribute food among their nestlings, which compete with each other (Neuenschwander et al. 2003). Competition is expected to be asymmetrical when the nestlings have different ages, which occurs when hatching is asynchronous, because older nestlings can outcompete younger nestlings for food. This can then exacerbate size differences and relative survival prospects of nestlings (Skagen 1987, Vinuela 2000, Rosivall et al. 2005). Indeed, one of the main hypotheses to explain hatching asynchrony is that it is an adaptation to unpredictable food availability (the brood reduction hypothesis; Stenning 1996) that optimizes survival of nestlings. This hypothesis has received empirical support in some studies (Lessells & Avery 1989, Siikamäki 1996, Valkama et al. 2002), but not others (Amundsen & Stokland 1988, Harper et al. 1992, Podlas & Richner 2013).

Studies often quantify nestling growth only as body mass growth. Body mass is an 'omnibus' trait that reflects structural size and energy reserves. However, in nestlings it is expected that energy is allocated differentially among body parts, depending on the environmental stressor (Remes 2007, Gil et al. 2008) such that their fitness is maximized (Schew & Ricklefs 1998, Miller 2010). However, empirical studies are scarce. In particular it is unclear whether and how hatching asynchrony affects energy allocation to different body traits during growth.

Here we studied growth of five body traits (body mass, tarsus, third primary, bill, crest feather) and mortality of Eurasian Hoopoe Upupa epops nestlings. We chose this species because Hoopoes show high variance in brood size, pronounced asynchronous hatching and have a long breeding period (Glutz von Blotzheim & Bauer 1980, Martin-Vivaldi et al. 1999). Hoopoe territory quality can be characterized by the frequency of territory occupancy (Tschumi et al. 2014, Guillod et al. 2016). Our main goal was to assess whether growth of different body traits is affected by territory quality, seasonality and brood size in the same way, whether hatching asynchrony changes these relationships and how hatching asynchrony modulates energy allocation during nestling growth. Based on previous studies we predicted that nestling growth will slow later in the season, will vary inversely with territory quality and brood size and will be lower for later-hatched nestlings. The brood reduction hypothesis assumes that growth of late-hatched nestlings is impaired and nestling mortality increased under harsh environmental conditions, whereas early-hatched nestlings are less or not affected. Therefore, we predicted the existence of interactions between hatching order and hatching date (seasonality), brood size and territory quality in their effects on nestling growth and a negative relationship between nestling mortality and territory quality. Because Hoopoes have developed an efficient defence against mammalian nest predators, which consists of the production of a foul-smelling fluid that is ejected with faeces against the predator (Martin-Vivaldi et al. 1999), nest predation is

generally low and nestlings are therefore unlikely to be under strong pressure to leave the nest as early as possible. We therefore expected an even allocation of the energy to different body traits and therefore the same impacting factors for all of them.

METHODS

Study species

The Hoopoe is a migratory, insectivorous farmland bird that inhabits semi-open habitats such as fruit tree plantations, orchards and vineyards. Hoopoes prefer foraging in habitats consisting of a small-scaled mosaic of patches with vegetation and bare ground (Schaub *et al.* 2010, Tagmann-Ioset *et al.* 2012), where they mainly feed on large invertebrates by scavenging the ground with their uniquely shaped bills. In the study area, Mole-crickets *Gryllotalpa gryllotalpa* make up a high proportion of the prey biomass delivered to chicks (Fournier & Arlettaz 2001, Guillod *et al.* 2016, Ryser *et al.* 2016). Territories in which parents provide more Mole-crickets are occupied more often, have a higher probability of producing a second clutch, and raise more and heavier chicks (Hoffmann *et al.* 2015, Guillod *et al.* 2016), and are therefore of higher quality (Tschumi *et al.* 2014).

Hoopoes from central Europe migrate to the Sahelian belt for the non-breeding season (Bächler *et al.* 2010) and return to the breeding grounds by the end of March (van Wijk *et al.* 2016). They breed in natural or artificial cavities and raise up to two, rarely three, broods annually (Hoffmann *et al.* 2015). Partners may change for the second brood, but both parents always contribute to raising a clutch. A clutch may contain up to 13 eggs (modal clutch size = 8), which are incubated by the female for about 17 days. Incubation often starts after the second or third egg is laid and Hoopoe chicks therefore hatch asynchronously (Martin-Vivaldi *et al.* 1999). After hatching, the nestlings remain in the breeding cavity for 25–28 days. During the first 10 days, the nestlings are brooded by the female and the male delivers food for both the nestlings and the female. Later, both parents provide food for the nestlings. Males tend to feed the larger nestlings, whereas females distribute the collected food evenly among nestlings (Ryser *et al.* 2016).

Study location

This study was carried out from April to July 2014 in the plain of the upper Rhône valley between Sierre and Vernayaz (canton Valais, south-western Switzerland, 46°14′N, 7°22′E). The valley is mainly used for intensive farming with many fruit plantations and vineyards.

Seven hundred Hoopoe nestboxes have been installed since 2002 in the fruit tree plantations with the primary goal of enhancing the initially small population (Arlettaz *et al.* 2010). In the study year, 96 successful broods were recorded in the surveyed nestboxes.

Data collection and chick measurements

All nestboxes in the study area were checked every 2 weeks from mid-April to the end of July to detect broods. We aimed to include a sample of about 40 broods for the current study. These broods were selected as a stratified random sample from all available broods based on the occupancy frequency of the territories. Among territories that were occupied in 2014 we selected 10 broods each at random from territories that had been occupied since 2002 for, respectively 1–3 years, 4–7 years and 8–11 years. Ten further broods were selected randomly with respect to territory occupancy.

The selected broods were visited every 3rd day to gather information about clutch and brood size, hatching date and number of fledglings. The frequent nestbox checks also allowed accurate age determination of nestlings. To reduce the risk of brood abandonment due to the frequent visits at the nests, we only started to measure nestlings when the oldest was 7 days old. All nestlings were measured every 4 days at the same time of the day. The last day of measurement was close to fledging of the oldest nestling (day 28). Thus, for most nestlings, measurements from six different days were recorded. The age of the nestlings on measurement days differed due to asynchronous hatching.

We recorded the following measurements for each nestling: age (in days), body mass (to the nearest of 0.1 g using an electronic balance), tarsus length (to the nearest 0.1 mm using callipers), length of the third primary feather (using millimetre paper and later a standard ruler to the nearest 0.5 mm), bill length (from the distal end of the

nostril to the tip of the bill using millimetre paper) and length of the longest of the erected crest feathers (to the nearest 0.5 mm using millimetre paper). To distinguish nestlings, we painted claws with nail polish with a unique code. At the age of 15 days, all nestlings were ringed with a standard uniquely numbered metal ring. We determined the hatching order for each nestling based on the hatching day. Nestlings hatching on the same day were ranked equally. For example, if a brood contained five nestlings, of which two hatched on day 1, one on day 2, and two on day 4, the recorded hatching order ranks were 1, 1, 2, 3, 3, respectively.

To compare the size of the measured traits when nestlings fledged with that of adults, we used morphological data of adult birds sampled in the study population since 2002. Because crest feather length was measured differently in adults and nestlings, we did not compare this trait between age classes.

Statistical analysis

Nestling growth data were analysed using non-linear mixed models fitted either with the nlme package of R (Pinheiro *et al.* 2013) or with Bayesian methods in JAGS (Plummer 2003). Due to the non-linear nature of growth trajectories, many growth models use a form of logistic function. Following Ricklefs (1967), 1968) and Sofaer *et al.* (2013) we used a logistic function with three parameters:

$$w_t = \frac{A}{1 + e^{K(I-t)}}$$

where w_t is the measurement of a trait at nestling age t (days), A is the asymptote, I the inflection point and K the growth rate constant.

Because the nestling measurements were not independent of each other, we included two uncorrelated random effects. The nestling random effect accounts for the repeated measures of the same nestling. The nest random effect accounts for the fact that siblings share the same nest (environment) and parents (genetics).

To test the impact of territory occupancy, brood size, hatching date and hatching order on nestling growth measures, we included these variables 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. We decided to always use the same linear models on all three target parameters simultaneously to avoid a too large set of candidate models. The candidate set of 23 models included all possible combinations of the considered four covariates as well as interactions between hatching order and territory occupancy, brood size and hatching date. They were fitted with package nlme in R and ranked according to their Akaike information criterion (AIC).

To visualize effect sizes we predicted growth trajectories using different values of the covariates. The computation of the precision of the growth trajectories is difficult using maximum likelihood, but straightforward by Bayesian analysis. Therefore, we 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 & Schaub 2012). Code for all models (nlme, JAGS) is provided in Supporting Information Appendix S1.

Nestling mortality in relation to hatching order and territory quality was analysed with a generalized linear mixed model with a binomial error distribution in R using the package glmer (Bates *et al.* 2015). The binary response variable had a value of zero if the nestling died before fledging and a value of one if the nestling fledged. Nest identity was included as a random factor in all models to account for the non-independence of nestlings from the same nest. The five fitted models considered all combinations of the fixed effects hatching order and territory quality, and the interaction between the two. The best model was chosen using AIC.

RESULTS

Nestling mortality

A total of 241 Hoopoe nestlings from 39 broods hatched; 180 (74.7%) survived until fledging and 61 (25.3%) died before fledging. Thirty-seven (69.8%) of the latter from 11 broods died within the first week after hatching. From 37 of 39 broods at least one nestling fledged. Nestling mortality was affected additively by hatching order and territory quality (Table 1). Mortality increased the later a nestling hatched with respect to its

Table 1. Model selection results for the impact of hatching order and territory quality on Hoopoe nestling mortality, obtained from generalized linear mixed models. All models included nest identity as a random effect. The difference in the Akaike information criterion between the current and the best model (ΔAIC) is shown, together with the model deviance and the number of estimated parameters (np).

Model	np	Deviance	ΔAIC
Intercept only	2	257.12	78.86
Hatching order	3	181.00	4.74
Territory occupancy	3	252.28	76.02
Hatching order + Territory occupancy	4	174.26	0.00
Hatching order * Territory occupancy[a]	5	173.00	0.74

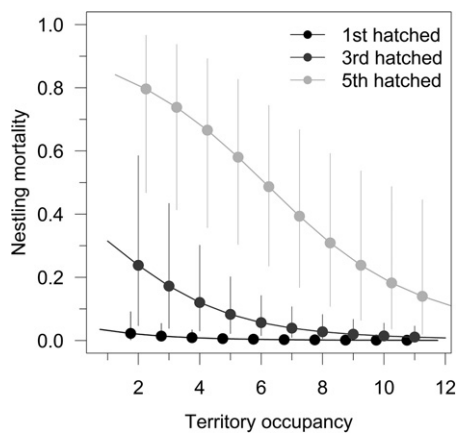[a]Fitting of both main effect and interaction terms.

Figure 1. Predicted mortality of Hoopoe nestlings in relation to territory occupancy (i.e. the number of years a territory was occupied from 2002 to 2014 by a Hoopoe) and hatching order of nestlings. Mortality is defined as the probability that a hatching does not fledge. The vertical lines indicate the 95% confidence interval of the predictions.

siblings (slope = 1.46, sd = 0.27) and declined with increasing territory quality (slope = −0.41, sd = 0.17; Fig. 1).

Variability of impacting variables

For the analysis of nestling growth we included measurements of all nestlings regardless of whether they finally fledged. The first brood hatched on 21 April, the last on 13 July. In all, 178 nestlings (73.9%) from 26 broods hatched in May, 52 (21.6%) from 10 broods in June and 11 (4.5%) from three broods in July. The average brood size (i.e. the number of hatchlings per brood) was 6.18 (sd = 1.79) nestlings with a maximum of nine nestlings (three broods) and a minimum of one

nestling (one brood). The maximum number of nestlings from the same brood that fledged was nine and the maximum number of dead nestlings within a successful brood was four. Broods that hatched in June or July had a lower average brood size of 4.85 (sd = 1.95) nestlings than broods that hatched earlier (6.85, sd = 1.29), with a maximum of eight and a minimum of one. Nestlings typically hatched asynchronously (Supporting Information Appendix S1, Fig. S1), usually 1 day apart, resulting in a pronounced visual difference of development between early- and late-hatched nestlings within the brood. In some broods two nestlings hatched on the same day. From a total of 39 broods, 17 had been chosen from territories with a high occupation rate, and had an average brood size of 6.35 (sd = 1.87) nestlings, 13 had been chosen from territories with a medium occupation rate and had 6.23 (sd = 1.92) nestlings, and nine had been chosen from territories with a low occupation rate and had 5.78 (sd = 1.56) nestlings.

Basic nestling growth

The total number of measurements varied among traits, because some traits could not be measured when the nestlings were too young (body mass: $n = 1135$ from 241 nestlings; tarsus length: $n = 1133$ from 241 nestlings; third primary: $n = 1018$ from 208 nestlings; bill length: $n = 1132$ from 241 nestlings; crest feather length: $n = 1016$ from 208 nestlings). The dataset contained measurements of nestlings that were between 1 and 28 days old. These measurements are shown in Figure 2a–e and Table 2 provides the parameter estimates of the non-linear models, without any covariates, for each trait.

By the day of the last measurement, only growth of body mass and tarsus length had been completed. The growth trajectory of body mass (Fig. 2a) had a sigmoid shape with a high growth rate during the first 8 days. The predicted growth curve did not match closely the data of old nestlings. Hoopoe nestlings reached a body mass peak about 20 days after hatching, and thereafter body mass declined slightly until the nestlings fledged. Such a curve cannot be fitted with the type of model that we used. By the age of 28 days, the predicted body mass was 69.6 g (sd = 10.3), and thus fledglings were on average lighter than adults (adult males: 76.6 g, sd = 8.1, $n = 1081$; adult females: 73.1 g, sd = 9.5, $n = 1277$).
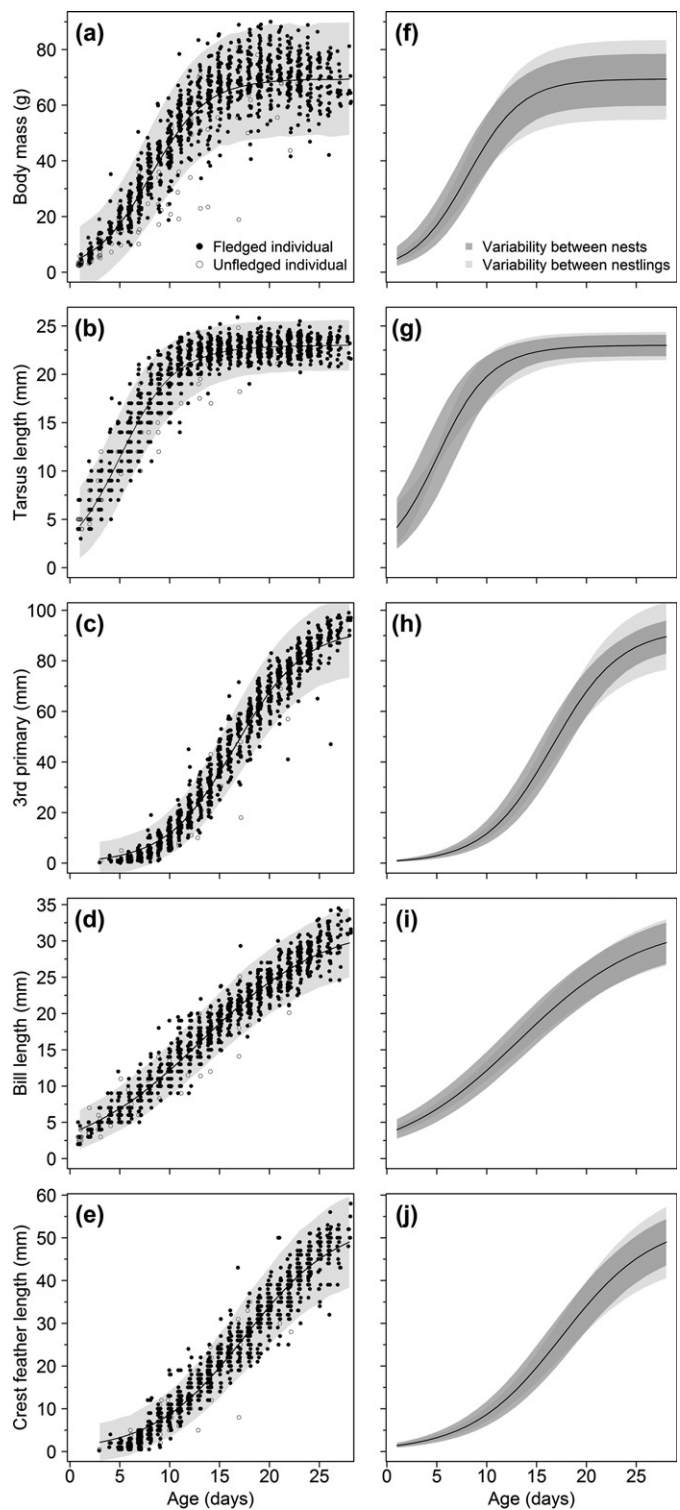
Figure 2. (a–e) Body trait measurements and fitted growth curves using a model without covariates (Table 2). Closed dots refer to individuals that fledged, open dots to those that did not fledge. The grey area indicates the 95% credible intervals. (f–j) The same fitted growth curves for five body traits based on a model without covariates (Table 1). The grey areas indicate the variability between nests and between nestlings within nests (95% credible intervals).

Table 2. Posterior means and 95% credible intervals (in parentheses) of the coefficients of a non-linear growth model without covariates for five body traits of Hoopoe nestlings. The units are g for body mass and mm for the four other traits.

Trait	Asymptote (*A*)	Inflection point (*I*)	Growth rate (*K*)
Body mass	69.50 (67.52, 71.41)	8.08 (7.81, 8.35)	0.367 (0.349, 0.386)
Tarsus length	23.00 (22.77, 23.22)	5.06 (4.77, 5.37)	0.377 (0.359, 0.397)
Third primary	92.59 (90.77, 94.42)	16.58 (16.34, 16.83)	0.295 (0.288, 0.302)
Bill length	32.49 (31.70, 33.26)	13.20 (12.79, 13.60)	0.161 (0.156, 0.167)
Crest feather length	53.84 (52.16, 55.47)	17.53 (17.16, 17.92)	0.219 (0.213, 0.226)

Tarsi grew fast between day 1 and day 10; afterwards their growth levelled off and by the age of about 23 days it was completed (Fig. 2b). The predicted tarsus length at fledging age was 23.0 mm (sd = 1.3), very similar to that of adults (adult males: 23.5 mm, sd = 2.5, *n* = 846; adult females: 22.2 mm, sd = 2.9, *n* = 970).

The bill grew almost linearly until day 28 (Fig. 2c). It reached an average length of 29.7 mm (sd = 2.5) when the nestlings fledged. The average bill length of adult males was 50.3 mm (sd = 6.0, *n* = 938) and of adult females 44.8 mm (sd = 6.2, *n* = 1060). Thus nestlings had reached only about 60% of their final bill length at fledging.

The growth curves of the lengths of the third primary and of the longest crest feather (Fig. 2d,e) were quite similar with distinctive sigmoid shapes. Third primaries had a higher growth rate than crest feathers. At the age of 28 days, the length of the third primaries reached on average 89.6 mm (sd = 8.2), which is about 80% of their final length (third primary length of adult males: 113.9 mm, sd = 3.4, *n* = 488; adult females: 108.3 mm, sd = 3.5, *n* = 563). At the age of 28 days, crest feathers of nestlings reached an average length of 48.8 mm (sd = 5.4). The crest feather certainly continues growing after fledging, because crest feathers of adults are longer (males: 76.6 mm, sd = 8.1, *n* = 944; females: 73.1 mm, sd = 9.5, *n* = 1053, although the measurement technique was different than for nestlings).

Factors associated with nestling growth

Model selection revealed that body mass growth was associated with the interaction of hatching order with territory quality, while no other interaction term received support from the data (Table 3). The most parsimonious model of body mass growth also included brood size and hatching date. Growth of the third primary, bill and crest feather were all associated with brood size,

hatching order and hatching date (Table 3). The AIC difference between best and second-best fitting models was > 2.5 for all three traits, indicating that model selection was robust. The best model for tarsus length contained only brood size and hatching order. Models that were close runners-up (ΔAIC < 2) additionally contained hatching date, brood size or both of these covariates. This suggests that brood size is the main consistent correlate of tarsus growth.

As predicted, body mass increase was independent of hatching order in territories of high quality, whereas late-hatched nestlings grew less quickly than early-hatched nestlings in low-quality territories (Fig. 3). The predicted body mass difference at day 28 between a first and a fifth hatched nestling was 8.8 g (sd = 13.6) in a low-quality territory but only 0.7 g (sd = 13.4) in a high-quality territory. In accordance with our predictions we found that growth of the different body traits was negatively associated with advancing season, with larger broods and with hatching order. The effect of these factors was most marked in the last days before fledging, and less marked at younger ages (Fig. 4), other than for tarsus, where effect sizes, although small, were also apparent at younger ages (Fig. 4b,g,l). Brood size was inversely associated with bill, crest feather and third primary lengths (Fig. 4c,d,e), but positively associated with body mass (Fig. 4a). Hatching order (Fig. 4h,i,j) and hatching date (Fig. 4k–o) were inversely associated with body size traits such that earlier-hatched nestlings were larger and heavier than later-hatched nestlings.

Variability between nests and nestlings

The mixed models allowed estimation of whether variance in growth tended to be larger between nests or between chicks within nests. Generally, the variability between nestlings tended to be larger than the variability between nests, but the

Table 3. Model selection results for the impact of territory occupancy (O), brood size (BS), hatching date (HD), hatching order (HO) and interactions (*) of hatching order with the other covariates on the growth of five body traits in Hoopoe nestlings. The crosses in the table indicate whether a specific covariate has been included in the model. The non-linear model contained the same structure on all the growth parameters (see text). Given is the difference in the Akaike information criterion between the current and the best model (ΔAIC), the deviance (Dev) and the number of estimated parameters (np). The best model is indicated by 0.00 in bold in the ΔAIC column.

| Models | | | | | | | | Body mass | | Tarsus length | | 3rd primary | | Bill length | | Crest feather length | |
O	BS	HD	HO	HO*O	HO*BS	HO*HD	np	ΔAIC	Dev	ΔAIC	Dev	ΔAIC	Dev	ΔAIC	Dev	ΔAIC	Dev
×	×	×	×	×	×	×	31	8.02	7488.3	12.30	3548.6	9.86	5508.3	15.28	3873.5	8.33	4796.4
×	×	×	×	×	×		28	5.66	7492.0	15.01	3557.3	7.41	5511.8	13.29	3877.5	6.38	4800.5
×	×	×	×	×		×	28	2.51	7488.8	9.41	3551.7	6.91	5511.3	9.92	3874.1	9.10	4803.2
×	×	×	×		×	×	28	10.24	7496.5	9.55	3551.9	6.06	5510.5	10.04	3874.2	2.91	4797.0
×	×	×	×	×			25	**0.00**	7492.3	9.97	3558.3	6.64	5517.1	7.76	3877.9	7.03	4807.1
×	×	×	×		×		25	12.83	7505.1	12.83	3561.1	3.80	5514.2	8.42	3878.6	3.28	4803.4
×	×	×	×			×	25	5.93	7498.2	7.55	3555.9	2.66	5513.1	5.25	3875.4	4.08	4804.2
×	×	×	×				22	12.76	7511.1	6.89	3561.2	4.24	5520.7	3.57	3879.8	5.97	4812.1
×	×		×				19	30.17	7534.5	5.95	3566.3	20.74	5543.2	15.10	3897.3	24.49	4836.6
×	×	×					19	19.94	7524.2	7.32	3567.6	52.38	5574.8	55.88	3938.1	20.73	4823.8
×		×	×				19	32.13	7536.4	13.80	3574.1	92.28	5614.7	24.86	3907.0	60.30	4872.4
	×	×	×				19	10.46	7514.8	1.09	3561.4	**0.00**	5522.4	**0.00**	3882.2	**0.00**	4812.1
×	×						16	37.59	7547.9	7.31	3573.6	76.51	5604.9	75.38	3963.6	35.95	4854.1
	×		×				16	56.38	7566.7	12.28	3578.6	106.04	5634.5	30.26	3918.4	60.31	4878.4
×		×					16	37.88	7548.2	18.17	3584.5	112.25	5640.7	81.84	3970.0	61.86	4880.0
		×	×				16	28.83	7539.1	**0.00**	3566.3	17.44	5545.9	14.70	3902.9	19.22	4837.3
×			×				16	17.22	7527.5	1.44	3567.7	49.88	5578.3	51.94	3940.1	15.51	4833.6
	×	×					16	32.24	7542.5	8.14	3574.4	89.93	5618.3	20.43	3908.6	56.34	4874.5
×							13	62.77	7579.1	16.63	3588.9	126.12	5660.5	91.05	3985.2	62.26	4886.4
	×						13	35.92	7552.2	1.43	3573.7	73.89	5608.3	77.12	3971.3	31.11	4855.2
		×					13	58.67	7575.0	6.38	3578.7	100.96	5635.4	29.39	3923.6	55.39	4879.5
			×				13	37.28	7553.6	12.39	3584.7	111.39	5645.7	76.23	3970.4	58.31	4882.4
							10	64.34	7586.6	10.65	3589.0	121.17	5661.6	87.52	3987.7	57.54	4887.7
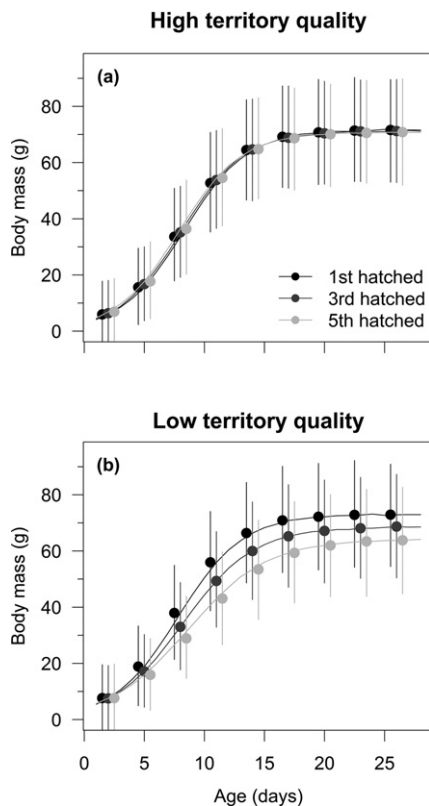
Figure 3. Predicted development of body mass in Hoopoes with respect to territory quality and hatching order. The dots show the posterior means and the vertical lines indicate the 95% credible intervals. The predictions refer to a nestling that hatched on the mean hatching date (23 May) and in a brood with six nestlings. (a) High territory quality refers to territories that were occupied each year since 2002, and (b) low quality to territories that were occupied in a single year only.

difference was marginal (Fig. 2f–j). This trend was strongest for body mass and the length of the third primary.

DISCUSSION

Mortality of Hoopoe nestlings increased the later they hatched compared with their siblings and the lower the quality of the territory in which they were raised. Later-hatched nestlings grew more slowly than their earlier-hatched siblings, yet in territories of high quality, hatching order had no impact on body mass growth. This indicates preferential investment in body mass growth, which can be explained by competition among nestlings. Our findings support the brood reduction hypothesis as an explanation of hatching asynchrony in Hoopoes.

The growth pattern of Hoopoe nestlings was similar to the growth pattern of other altricial birds (Ricklefs 1968, 1973, 1979, Tjörve & Tjörve 2010). By the time Hoopoes fledge, growth of body mass and tarsus were completed, whereas third primary, bill and crest feathers had not reached their final length. The growth of the latter traits was therefore more linear during the nestling period than was the case for the first two. Body mass did not reach an asymptote at time of fledging; rather, nestlings were at their heaviest at an age of about 20 days and tended to decline in mass slightly thereafter. Such a shape is typical for many bird species (Ricklefs 1968) and is probably a consequence of differential investment, as investment in bill and feather growth becomes higher later in nestling development.

Factors associated with nestling growth

The growth of bill and feather lengths of Hoopoe nestlings was affected by brood size as predicted, as these traits grew less fast in nestlings from large broods and achieved a smaller size at fledging than in nestlings from small broods. All body traits with the exception of tarsus length were also associated with hatching date, with early-hatched broods achieving faster growth and larger size at fledging. Hatching order was associated with growth of structural body traits (tarsus, bill, feathers) in the expected way, namely that late-hatched nestlings (low ranked in the hierarchy) grew less quickly than early-hatched nestlings. These relationships were unaffected by territory quality. In contrast, the effect of hatching asynchrony on body mass growth was modulated by territory quality: in territories of high quality, all nestlings achieved similar fledging body mass regardless of hatching order, whereas in low-quality territories, later-hatched nestlings increased body mass less fast, resulting in a lower fledging body mass than in early-hatched siblings.

The only body trait that was barely affected by extrinsic factors and only at early ages was tarsus length. Moreover, in other studies the length of fully grown tarsi of Hoopoe nestlings has been found not to be associated with the biomass of Mole-crickets provisioned by parents (Guillod *et al.* 2016). Although habitat quality and the amount of available food can affect tarsus growth (Richner 1989, Searcy *et al.* 2004), cross-fostered brood experiments showed evidence for a high
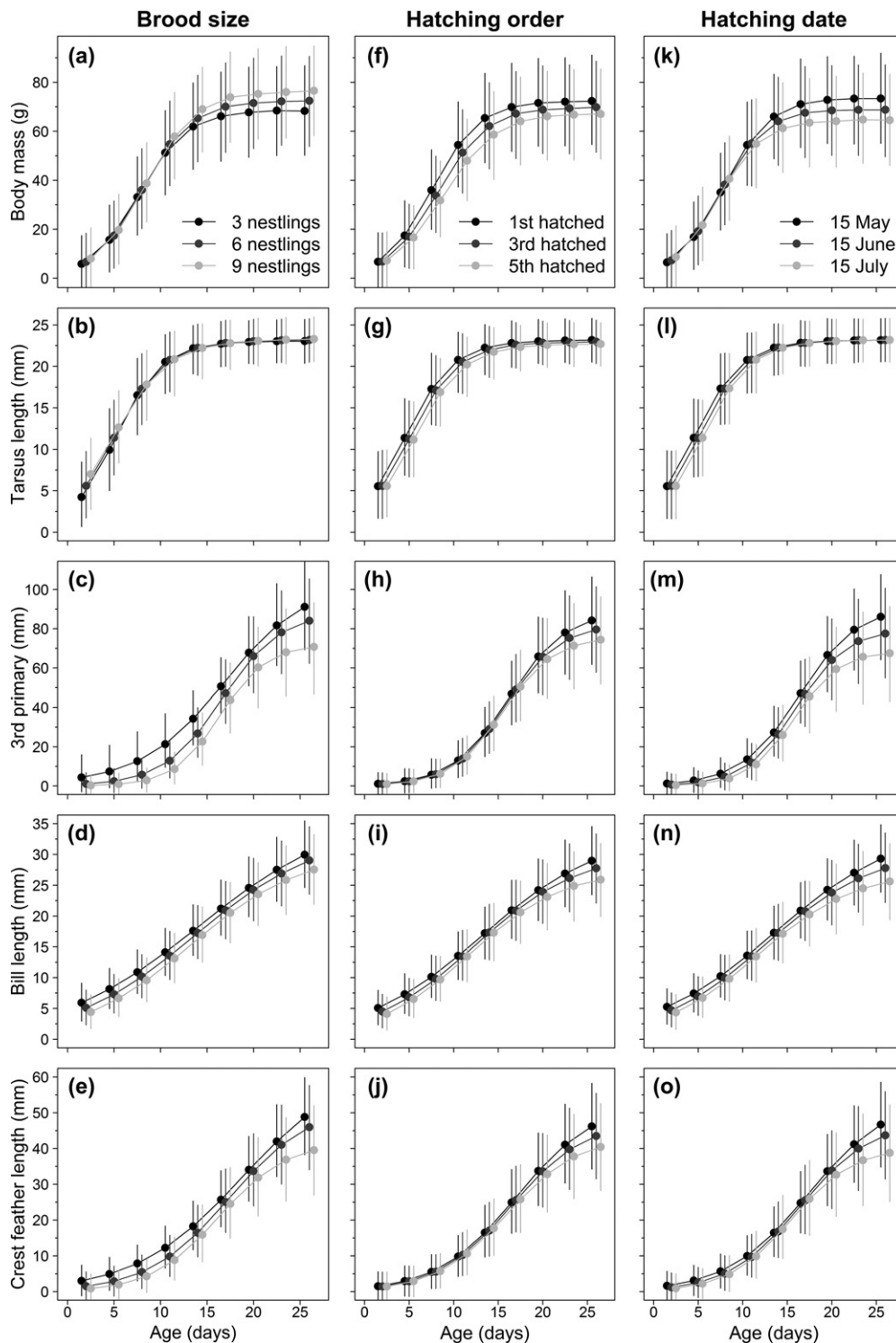
Figure 4. Predicted development of five body traits in Hoopoes with respect to brood size, hatching order and hatching date. The dots show the posterior means and the vertical lines indicate the 95% credible intervals. The predictions refer to a nestling that hatched on the mean hatching date (23 May) and was the first-hatched (panels a–e), to the mean hatching date (23 May) and a brood size of six nestlings (panels f–j) and to a brood size of six nestlings and the first-hatched nestling (panels k–o). All predictions of body mass refer to medium territory quality (territories that were occupied half of the years).

heritability of tarsus length (Alatalo & Lundberg 1986, Smith 1993). According to Alatalo and Lundberg (1986), parent–offspring resemblance is not affected by the nest environment but might be larger between parents and offspring because of the shared genetic background. Tarsus length seems therefore more dependent on genetic than on environmental factors, which explains the weak influence of brood size, hatching order and hatching date on the tarsus growth of Hoopoe nestlings.

Nestlings from early-hatched broods were heavier and larger when they fledged compared with nestlings from late broods. Female Hoopoes that initiated broods early in the breeding season are likely to be of high quality (Hoffmann *et al.* 2015), indicating that differential intrinsic quality might be the reason for the impact of season on nestling growth, although seasonally declining food availability cannot be ruled out (Morbey & Ydenberg 2000). Because the time available before migration is shorter for late fledglings than for early ones and the former possibly have to grow more after fledging, this could come at a significant cost. It may explain the pronounced lower return rate of late-hatched Hoopoe fledglings compared with early-hatched fledglings (Hoffmann *et al.* 2015). Other studies also have found that the body mass of fledglings has a positive effect on post-fledging survival (Naef-Daenzer *et al.* 2001, Bouwhuis *et al.* 2015). The timing of the brood typically also affects clutch size and finally reproductive success, which are greater in early than in late broods (Lack 1968, Hochachka 1990, Siikamäki 1998). Taken together, it is beneficial for Hoopoes to begin their the first brood as early as possible because early broods produce more fledglings of higher quality and this increases the probability of raising second broods (Hoffmann *et al.* 2015).

Brood size had different associations with the growth of different body traits. A larger brood size was associated with larger body mass at fledging, but with reduced lengths of bill, crest feather and third primary. While some studies have found that increasing brood size reduced the growth of nestlings (von Haartman 1953, Klomp 1970, Roulin *et al.* 1999), increased competition among siblings has been associated with increased growth rates in other studies (Ricklefs 1979, 1982, Werschkul & Jackson 1979). Competition can enhance selection to increase growth rates (Werschkul & Jackson 1979). In contrast to body mass, a larger brood size was inversely associated with the growth of the other body traits, thus suggesting that the available energy resources for body growth were allocated differentially to the traits. Hoopoe nestlings seem to invest more in body mass growth when brood size, and thus competition, increases and this might come at the cost of reduced growth of bill, third primary and crest feathers.

Asynchronous hatching generally results in a size hierarchy among nestlings with the consequence that later-hatched nestlings in the brood suffer more from food shortages than those hatching earlier (Slagsvold 1986), resulting in differential mortality and nestling growth patterns (Starck & Ricklefs 1998). Accordingly, we found higher nestling mortality in later-hatched nestlings and that the growth of surviving nestlings depended on their hatching order. Lengths of bill, third primary and crest feathers of Hoopoe nestlings that hatched earlier grew generally faster and achieved a larger size than later-hatched siblings of the same brood. Speed of body mass growth was reduced in late-hatched nestlings when the brood was raised in a territory of low quality, but this difference disappeared if the brood was raised in a territory of high quality. Given that the growth of feathers and bill was affected by hatching order regardless of territory quality, our findings suggest that in lower-ranked nestlings, energy was allocated in the first place to body mass growth. Larger Hoopoe nestlings are generally fed more often by their parents than are small nestlings (Ryser *et al.* 2016). Hence, body mass has an effect on the competitive performance of the nestlings, suggesting that it is beneficial for nestlings to be as heavy as possible with respect to their siblings. The growth of nestlings depends not only on their competitive abilities, but also on the feeding behaviour of the parents, which is sex-specific in Hoopoes (Ryser *et al.* 2016). Males feed nestlings less often, but with larger prey items than females. Males generally do not enter the nesting cavity when nestlings are fed and thus the competitive stronger nestlings that have access to the entrance receive more food from males (Ryser *et al.* 2016). In contrast, females typically enter the nest cavity and allocate their food more evenly among nestlings, even showing a tendency to preferentially provision food to hungry and small nestlings (Ryser *et al.* 2016). Yet in territories of low quality, males deliver fewer large prey items (Guillod *et al.* 2016), with the consequence that large nestlings are never fully fed and dominate any feeding event, which

in turn results in impaired growth and increased mortality of small nestlings.

Our study showed that energy available was allocated in nestlings differentially between body traits and that this allocation changed with hatching order and territory quality in an interacting way. Competition among nestlings is the likely reason for differential energy allocation. The main benefits of improved competitive abilities are reduced mortality at the nestling and presumably at the post-fledging stages. Our study highlights the need to measure multiple body traits when studying associations between nestling growth and hatching asynchrony.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Hoopoe nestlings from two broods.

Appendix S1. R and JAGS code of the nestling growth models.