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Effects of weather conditions, time of breeding, brood size and hatching order on Eurasian bittern nestling growth in a food-rich fishpond habitat

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The development of nestlings depends on both biological and weather factors. However, their combined effect differs among bird species. In this study, the impacts of three temperature variables, precipitation, wind speed, timing of breeding, brood size and hatching order on the growth of Eurasian bittern *Botaurus stellaris* chicks were analysed. Measurements of 183 nestlings from 57 nests were made at fishpond complexes in eastern Poland. Relative growth rates (RGR) were calculated on the basis of tarsus length and body mass. Generalised linear mixed models showed that brood size, hatching order and precipitation were the most important factors. Nestlings in broods of two and three grew faster than those from broods of four and five. In the largest broods, the fifth-hatched chicks had lower growth rates; this also applied to the oldest chicks in all brood-size categories. Nestlings from late-season nests showed enhanced mass and tarsus growth, while heavier precipitation and strong winds depressed growth rates. The study emphasises that even among bitterns breeding in food-rich habitats like fishponds, the chicks in largest broods run the risk of lower growth rates.

Introduction

The growth of nestlings is the result of a compromise between selective factors and internal constraints (Starck & Ricklefs 1998, West *et al*. 2001). Among different environmental factors, weather conditions are important owing to their multifaceted (direct or indirect) effect on growth rates and may have serious consequences for bird reproduction (Konarzewski & Taylor 1989, McCarty & Winkler 1999, Remeš & Martin 2002). Nestling development is especially dependent on temperature and precipitation (Beintema & Visser 1989a, Bradbury *et al*. 2003, Kosicki & Indykiewicz 2011), and prolonged adverse conditions may lead to chilling, thereby directly decreasing chick survival (Beintema & Visser 1989b). Young chicks are particularly exposed to severe weather because of their higher thermosensitivity (Angilletta *et al*. 2010). After nestlings begin to thermoregulate on their own, unfavourable conditions increase energy demands for thermoregulation, reducing the availability of resources for development (Schew & Ricklefs 1998). Moreover, adverse weather negatively affects food supply and reduces feeding time for parents, leading to lower provisioning rates (Beintema & Visser 1989b, McCarty & Winkler 1999, Bradbury *et al*. 2003).

Biological traits like breeding timing and sibling competition are associated with the influence of weather parameters on nestling development (Werschkul & Jackson 1979, Remeš & Martin 2002, Ritz *at al*. 2005, Gill *et al*. 2008). Timing of breeding is especially important for migratory birds nesting in high latitudes (Perrins 1970). However, an early breeding date is a feature of the quality of adults that can provide good parental care, and chicks hatched early are believed to grow faster than later hatching ones (Nisbet *et al*. 1998, Ritz *at al*. 2005). Differences in growth rate are also promoted by sibling competition, which is a mechanism whereby brood size can be adjusted to the level the parents can cope with during unfavourable weather (Siikamäki 1996).

The relationship between nestling growth and weather factors in combination with biological traits has most often been studied in typical altricial passerine birds with biparental care of the young (Remeš & Martin 2002, Martin *et al*. 2011). Much less attention has been paid to species in which only one of the sexes rears the nestlings. In the current study, we investigated the influence of weather conditions and biological factors on the growth of Eurasian bittern *Botaurus stellaris* (hereafter bittern) chicks. Of high conservation concern, this species is seriously endangered throughout Europe (White *et al*. 2006). The breeding range covers the entire Eurasia and North Africa and, consequently, a wide variety of microclimates and habitats (Kushlan & Hafner 2000, Puglisi & Bretagnolle 2005, Poulin *et al*. 2005, Polak *et al*. 2008). In comparison with populations from western Europe, bittern populations studied in eastern Poland are dense, stable and in good condition (Polak & Kasprzykowski 2010). This is mainly a consequence of bird-friendly fish management and a high proportion of emergent vegetation cover, which appears to be a particularly suitable habitat (Polak *et al*. 2008). Also, the large proportion of birds in the population found to be employing a clumped nesting strategy confirms that the food resources in fishpond complexes are rich (Kasprzykowski & Polak 2013).

The bittern's mating system is unique among ardeids, and provisioning by the female only may have an important influence on the growth and development of the young (Puglisi & Bretagnolle 2005). Females raising their broods on their own are influenced by food resource distribution (Adamo *et al*. 2004, White *et al*. 2006) and are compelled to decide how to organise the rhythm of feeding by choosing a suitable area and time of day for foraging. In such a situation the long absence of the female during severe weather could influence the fitness and survival of chicks. However, the impact of weather on the bittern's biological parameters has received little attention. In a previous study, we found that rainfall caused females to lay smaller eggs, and that heavy rain and strong winds were correlated with greater chick mortality (Polak & Kasprzykowski 2013). Our hypothesis in the present study is that weather factors influence growth rates. We expected that periods of adverse weather would negatively affect the growth of bittern chicks, very likely by the indirect effect of reducing the availability of delivered food rather than by direct exposure. Apart from weather conditions, we expected that biological factors like breeding timing, hatching order and the number of nestlings would govern nestling growth and consequently increase the mortality of late-hatched chicks (*see* Gilbert *et al*. 2005). In comparison with other breeding ecosystems, fishponds offer rich food resources that could mitigate negative environmental factors. Therefore, we also anticipated that biological factors would have a greater impact on the growth rate of bittern nestlings than meteorological parameters.

Material and methods

Study area

The study was conducted in at fishpond complexes (50°55´–52°11´N, 21°58´–22°54´E) in the open agricultural landscape of eastern Poland. The various complexes (15–203 ha; total area 975 ha) supported vegetation dominated by reed (*Phragmites australis*), lesser bulrush (*Typha angustifolia*), bulrush (*Scirpus lacustris*) and sedges (*Carex* spp.). Most were stocked with common carp (*Cyprinus carpio*), which made up 95%–100% of the biomass of all the fish being farmed. Other species farmed included pike (*Esox lucius*), wels catfish (*Silurus glanis*), tench (*Tinca tinca*) and grass carp (*Ctenopharyngodon idella*). All study sites were managed extensively in the same way with occasional reed cutting. These environmental conditions give rise to large densities of the Eurasian bittern breeding population: 1.1 and 12.5 indiv./100 ha for males, and between 1.1 and 20.0 indiv./100 ha for females (Polak & Kasprzykowski 2009).

Field procedures

The methodology for monitoring and assessing local population of breeding bitterns was taken from Poulin and Lefebvre (2003). Potential nest sites were surveyed from 2003 to 2009 throughout the breeding season, starting from the end of April. On the first visits, the precise locations of the territorial males' booming sites were defined. Nests were located during regular walks through the emergent vegetation. The positions of all nests found were recorded on a 1:5000 scale sketch map of the area, and the coordinates of all the nests were determined by GPS. Each nest was discovered either in the egg laying or the egg incubation phase. To determine the hatching date more precisely, a "water test" was carried out to assess the floating behaviour of the eggs (Demongin *et al*. 2007). The hatching date of some nestlings was determined by direct observation. For other nestlings in the same brood this parameter was defined by assuming that the interval between the laying of consecutive eggs was two days (Demongin *et al*. 2007). Nest visits were carried out in such a way as to minimise disturbance to the birds. During the first inspection the nestlings were marked with coloured rings, later to be replaced with metal rings. During each inspection, the numbers of nestlings were noted and the following biometric measurements taken: tarsus length according to Piersma (1984) and body mass. These two parameters appear to be best suited for describing the growth of bittern nestlings. Body mass appears to be affected more by environmental factors. In addition, the rapid growth of the tarsi is the upshot of an anti-predator strategy in nestlings that enables them to leave the nest relatively early in life simply by walking off through the reeds (Demongin *et al*. 2007). Callipers were used for measuring tarsi lengths (± 0.1 mm) and a Pesola spring balance for weighing the nestlings (± 1 g). We investigated 57 nests with an average of 4.3 nestlings. Some 366 measurements of growth variables were made on 183 nestlings. To avoid pseudoreplication, only one estimate of nestling growth was included in the analysis. Measurements were done in the first two weeks of chick life, when biometric characters have a linear growth curve (Demongin *et al*. 2007). The time interval between consecutive nest inspections was from 4 to 6 days, with the first measurement taken when the mean age of nestlings was from 5 to 7 days and the second when they were 10–14 days old.

Meteorological data were obtained from Radawiec (51°13´N, 22°23´E) and Siedlce (52°25´N, 22°26´E), sites of the two meteorological stations situated closest to the pond complexes (Polak & Kasprzykowski 2013). Five weather parameters were calculated for each growth period of nestlings: mean temperature (°C), mean daily temperature range (°C), mean daily minimum temperature (°C), total precipitation (mm) and mean wind speed (km h^{-1}).

Statistical analyses

In accordance with Brody (1945) and You *et al*. (2009), we calculated the Relative Growth Rate (RGR) for each individual nestling as:

$$\mathrm{RGR} = [(\ln W_t - \ln W_0)/t] \times 100\ (\%),$$

where W_0 and W_t are the respective biometric measurements taken at the beginning and the end of the growth period t. In this way, daily increments in tarsus length and body mass, expressed as percentages of initial values, were obtained.

We focused our analysis on five possible predictors of RGR of bittern nestlings. These were: (1) brood size, estimated as the number of live nestlings in the nest; (2) hatching order of the nestlings within the brood (labelled a, b, ..., e); (3) laying date of the first egg in the clutch, standardised for between-year variation by setting it to 0 for the first egg laid in the study population in the season; (4) precipitation during the time window between two consecutive measurements of the nestling (hereafter rain); and (5) mean wind speed during the same time. As regards the weather variables, we originally analysed five of the parameters listed above, averaged over the period of measured nestling growth. Variation in these variables was summarised by principal component scores obtained from PCA, in order to obtain predictors free from multicollinearity problems. Here, PC1 reflected mostly the contrast between wind (loading 0.51) and mean temperature (–0.59), while PC2 measured mostly precipitation (–0.71). However, in subsequent analyses, models with wind entered in place of PC1 and rain instead of PC2 provided a better fit than models using the PCA scores. Therefore, we decided to use simple wind and rain averages in our models, which was acceptable, given they were not correlated in our data set ($r = -0.08$, df = 181, $p > 0.27$).

We analysed the possible effect of five predictors on the growth rate of tarsus and body mass of bittern nestlings using an information-theoretic approach (Burnham & Anderson 2002). Multiple competing models were assessed regarding their fit to the data using AIC as the leading criterion. To compare the relative importance of multiple predictor variables, we used summed Akaike weights across all the analysed models where the focal predictor occurs. Generalised linear mixed models (GLMM) were employed to analyse the relationship between the daily relative growth rates of two response variables (tarsus length and body mass) and our focal predictors, using identity link and Gaussian error. The five main predictors were considered fixed factors, while nest identity and year were further introduced as random factors to account for within-subject consistency in response. Following Zuur *et al.* (2009) we identified the optimal structure of the random component of our candidate models, using a comparison of models with the same beyond-optimal structure of fixed effects while differing in their random effects. For mass increments, the model with nest identity nested within year performed better (AIC = 812.18) than the model with no random component (AIC = 848.44) or a random component including nest only (AIC = 816.72). The same held true for tarsus growth rates (AIC = 624.47, 651.53 and 627.82, respectively). Thus, in our further analyses, we assumed that random effects (intercepts) in the candidate GLMM included nest (brood) identity nested within year. All models were fitted in the R environment with the *lme4* package (R Core Team 2013).

We had initially intended to start from a global model which, for the fixed component, included our five focal covariates as the main factors plus all their two-way interactions. However, this model had > 40 parameters to estimate and was impossible to fit as GLMM. Even when we retained only biologically plausible interactions, the resulting model still had over 20 parameters to estimate with 183 data points. Nevertheless, the ratio of the total sample size to the number of fixed effect levels being tested should exceed at least 10 (or even 20) to obtain reliable results (Harrell 2001, Bolker *et al.* 2009). The two interactions that were worth retaining, given the aims of our analysis, i.e. brood size × hatching order and brood size × rain, also turned out to be problematic. The hatching order and brood size factors were partially confounded (as nestlings "e" can occur only in broods of five, etc.), which meant that the mixed model could not be fitted. It was possible to fit interaction brood size × rain but the estimates yielded were rather unreliable, most probably due to the lack of observations of small broods exposed to heavy rain in our data. Therefore, following Bolker *et al.* (2009), we eventually decided to reduce the model complexity and run the final analysis using only additive parameters in the fixed component of GLMM. Our global model for the relative growth rate of tarsus or mass was thus: RGR ~ brood.size + laying.date + hatch.order + rain + wind + (1|year/nest). We calculated AIC_c and other relevant statistics for all possible subsets of the global model, i.e. 32 models (including the null model and the global model) using the *MuMIn* package. Pseudo-R^2 for the GLMM was calculated following Nakagawa and Schielzeth (2013) as implemented in the *MuMIn* package. The *lsmeans* package was used to extract least-squares means and 95% confidence limits for all categorical effects.

Results

Mass increments averaged 6.45% per day, with extensive variation between individual nestlings (IQR: 4.67–8.12). Modelling factors influencing variation in the daily mass gain revealed that brood size, hatching order and rain had an importance exceeding 0.90, while laying date and wind were less important (Table 1). The 95% confidence model set included only five models (Table 2). The best model for daily mass gain included all five predictors and was 1.7 times better than the second competing model, which lacked wind among the predictors. The strong effect of brood size on the rate of mass gain was non-linear. Nestlings in broods of two and three grew faster than those from broods of four, and almost 1.5 times faster than from broods of five (Fig. 1). Hatching order also affected mass gain, mostly because the last-hatched nestlings in broods of five grew much slower than their siblings. In the other three smaller brood size categories, there were no signs of last-chick disadvantage, however. Also second-hatched nestlings grew fastest in all categories of brood size (*see* Fig. 1). Unexpectedly, oldest nestlings had visually lower growth rates, even lower than the fourth chick in larger broods. Despite partial confounding of hatching order and brood size (*see* "Statistical analysis"), inspection of the raw data confirmed that brood size and hatching order affected mass gain in an additive rather than an interactive manner. Finally, both heavy rain and strong wind negatively influenced mass increments, although the effect of rain was better supported by the data (Table 3). Laying date had a positive effect on nestling growth, with birds gaining mass faster in late clutches. The best model explained 64% of the variation in the relative mass gain rate, including 36% explained

Table 1. Relative importance of predictor variables for models of RGR of mass and tarsus increments. For each response variable, importance (summed Akaike weight of all models containing the focal predictor; Burnham & Anderson 2002) was calculated across the entire set of 32 competing models analysed.

Variable	Mass	Tarsus
Brood size	0.998	0.909
Hatching order	0.989	0.993
Rain	0.937	0.991
Laying date	0.689	0.608
Wind	0.599	0.715

Table 2. Results of five models for RGR of mass and six models for RGR of tarsus constituting the 95% confidence set selection. Degrees of freedom (df), model log-likelihood (LL), corrected AIC criterion (AIC$_c$), the difference between AIC$_c$ of the focal model and the best model in the data set (ΔAIC$_c$) and weight for the model (AIC$_c$wt) are shown.

Model (fixed effects)	df	LL	AIC$_c$	ΔAIC$_c$	AIC$_c$wt
RGR Mass					
Intercept + brood.size + laying.date + hatch.order + rain + wind	14	–363.111	756.7	0.00	0.400
Intercept + brood.size + laying.date + hatch.order + rain	13	–364.817	757.8	1.07	0.235
Intercept + brood.size + hatch.order + rain + wind	13	–365.223	758.6	1.88	0.156
Intercept + brood.size + hatch.order + rain	12	–366.532	758.9	2.18	0.135
Intercept + brood.size + laying.date + hatch.order + wind	13	–367.021	762.2	5.47	0.026
RGR Tarsus					
Intercept + brood.size + laying.date + hatch.order + rain + wind	14	–253.444	537.4	0.00	0.410
Intercept + brood.size + hatch.order + rain + wind	13	–255.267	538.7	1.30	0.214
Intercept + brood.size + laying.date + hatch.order + rain	13	–255.669	539.5	2.10	0.143
Intercept + brood.size + hatch.order + rain	12	–256.953	539.7	2.35	0.127
Intercept + hatch.order + rain + wind	10	–260.383	542.0	4.66	0.040
Intercept + laying.date + hatch.order + rain + wind	11	–259.266	542.1	4.69	0.039

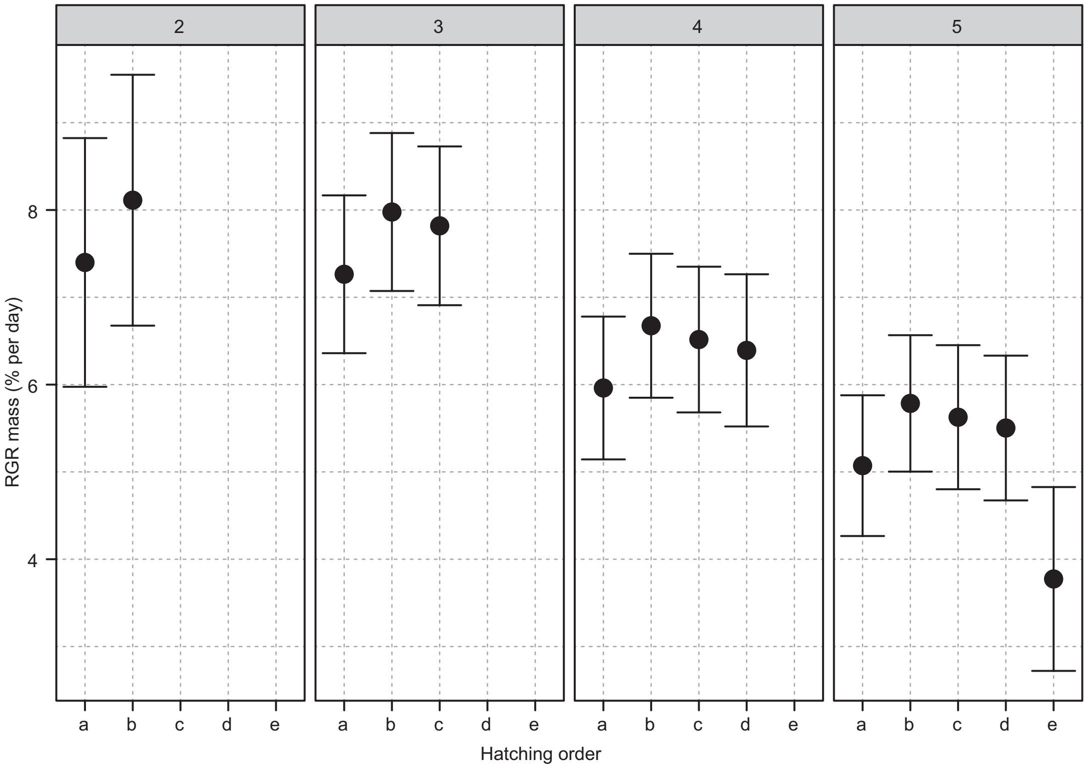

Fig. 1. Variation in RGR of mass in bittern nestlings in relation to brood size (panels) and hatching order. Modelled means ± 95% confidence limits from the best model selected are shown. Values extracted using the *lsmeans* package.

Table 3. Estimates of model coefficients for the best GLMM models of RGR for mass and tarsus increments. For fixed effects, standard errors and associated values of test statistics *Z* are shown, while *p* values are not used in GLMMs fitted with *lme4* (*see* Long 2012). For random effects the values given are variance estimates and their standard deviations.

	RGR Mass			RGR Tarsus		
	Estimate	SE	*Z*	Estimate	SE	*Z*
Fixed effects						
(Intercept)	10.094	1.141	8.844	5.412	0.624	8.674
Brood size 3	–0.135	0.791	–0.171	0.217	0.396	0.549
Brood size 4	–1.438	0.779	–1.844	–0.509	0.389	–1.310
Brood size 5	–2.327	0.779	–2.984	–0.756	0.389	–1.945
Laying date	0.064	0.029	2.181	0.029	0.015	1.937
Hatch order b	0.713	0.299	2.385	0.379	0.172	2.207
Hatch order c	0.555	0.319	1.739	0.223	0.183	1.217
Hatch order d	0.431	0.362	1.192	0.142	0.208	0.681
Hatch order e	–1.298	0.533	–2.433	–0.869	0.304	–2.854
Rain	–0.043	0.014	–2.971	–0.027	0.007	–3.674
Wind	–0.205	0.110	–1.861	–0.133	0.060	–2.210
Random effects						
Nest: Year	1.537	1.239		0.253	0.503	
Year	0.154	0.393		0.159	0.399	
Residual	2.122	1.457		0.708	0.842	

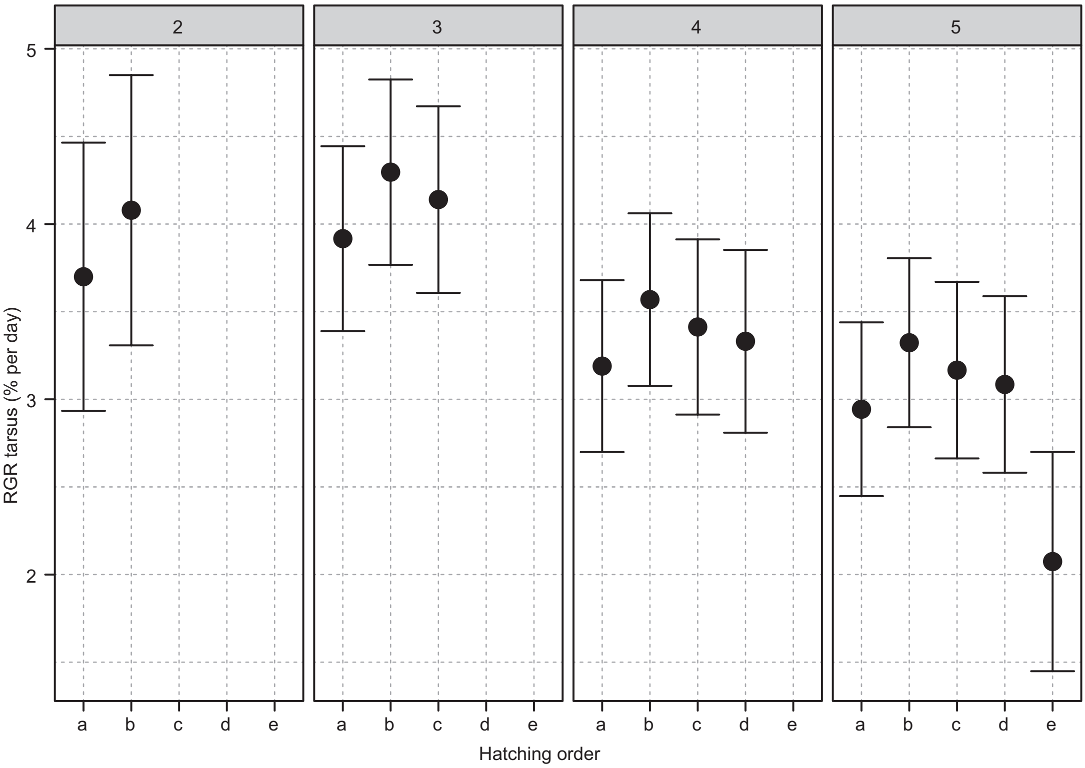

Fig. 2. Variation in RGR of tarsus in bittern nestlings in relation to brood size (panels) and hatching order. Modelled means ± 95% confidence limits from the best model selected are shown. Values extracted using the *lsmeans* package.

by fixed effects only, as estimated by pseudo-R^2 statistics for GLMM.

Variation in the rate of tarsus growth found among bittern nestlings was also extensive, with the daily average of 3.57% (IQR: 2.56–4.59). Results of model selection for tarsus growth paralleled those for mass gain. Among five fixed predictors analysed across 32 candidate models, there was strong evidence for the effects of laying order, brood size and rain (all with importance > 0.90), and moderate evidence for the effects of wind and laying date (Table 1). The six top models formed a 95% confidence set (Table 2), with the best model having almost twice the support of the second model (evidence ratio 1.92). As with mass gain, the global model appeared to be the best model for tarsus growth based on AIC_c criteria. Patterns of variation in tarsus growth with brood size and hatching order were very similar to those found in mass gain. Nestlings in broods of two and three showed faster tarsus growth than those in broods of four and five (Fig. 2). Last-hatched birds in broods of five showed retarded growth, with daily rates being almost two times smaller than in broods of two. However, other nestlings in the same broods grew almost as fast as their counterparts in broods of four. Lower tarsus growth rates were noted for oldest nestlings in comparison with second, third and fourth siblings. Increased precipitation and strong wind depressed tarsus growth, while nestlings from late-season clutches generally showed enhanced growth rates (Table 3). Pseudo-R^2 statistics revealed that the top GLMM model for tarsus growth rate, selected from the set of 32 competing models, explained 58% of the variation between nestlings (including 34% explained by fixed effects).

Discussion

The growth rates of body mass and tarsus length of bittern nestlings changed in a very similar way. Of all the modelling factors, those most affecting mass and tarsus gain were biological: brood size and hatching order. We found that the effect of brood size on growth rate was non-linear, and that body increments achieved a higher level in broods consisting of two and three nestlings and a lower level in larger broods. It seems that large broods are relatively hard to rear by single females, which are under greater pressure of food limitation in comparison to monogamous species, as they need to collect food without male help. Especially in the first week of the chicks' lives, food provision is limited because the female still has to warm her brood and does not leave the immediate surroundings of the nest (White *et al*. 2006, Gilbert *et al*. 2007). After ten days, however, the chicks are capable of huddling up to one another to keep warm, and the female starts to undertake longer foraging flights to richer food sources (Mallord *et al*. 2000). However, further studies of measuring the food provisioning rate of bittern females are required to support this hypothesis.

Generally, the influence of nestling numbers on growth rates could be explained by the importance of food limitation and to a lesser extent by sibling competition. Negative interactions among nestlings leading to fighting behaviour are often observed in other heron species (Fujioka 1985, Mock *et al*. 1987). An extreme example could be found in grey heron *Ardea cinerea* colonies, where the most important factor affecting losses is siblicide (Jakubas 2004). However, negative interactions between bittern nestlings seem to occur mostly in nests with five nestlings, where only the fifth chick's growth rate is clearly lower. The effect of competition is further enhanced by asynchronous hatching: bittern chicks usually hatch at one- or two-day intervals (Puglisi & Bretagnolle 2005). Consequently, partial losses are mainly due to nestling starvation; the primary reason for higher mortality among the youngest chicks in the largest broods is their failure to compete successfully with their older siblings for food (Polak & Kasprzykowski 2010). In a British population of the bittern, most of the chicks that hatched late in the pecking order did not fledge (Gilbert *et al*. 2007).

Our study showed that second nestlings grew faster together with third and fourth chicks, according to hatching order. Fifth-hatched nestlings in broods of five, because of their much lower growth rates, were at a clear disadvantage. Slow growth of the youngest offspring was observed in species with hatching asynchrony where size and age hierarchy within the brood occur (Amundsen & Stokland 1988, Mock & Parker 1997, Moreno-Rueda *et al*. 2007). The last-hatched chicks could be treated as surplus offspring serving as insurance against the accidental loss of nestlings prior to independence (Forbes 1990). But how to explain the unexpectedly slower growth rates of the oldest chicks in all brood size categories? This difference in chick development could be due to variation in egg quality. Females might differentially allocate resources across the laying order within clutches and by this mechanism engineer competition amongst offspring (Schwabl 1996, MacCluskie *et al*. 1997, Griffith & Gilby 2013). Kozlowski and Ricklefs (2010) showed that first-laid eggs in asynchronous cockatiel *Nymphicus hollandicus* clutches contained less yolk and had lower concentrations of testosterone than eggs midway through the laying sequence. Generally, androgens led to an increase in growth and begging intensity in the first half of chick development (Buchanan *et al*. 2007, Muriel *et al*. 2013). Thus, the slower development of first-hatching nestlings, which seems to occur commonly in the bittern population studied here, might reduce the effects of hatching asynchrony by minimising the competitive disadvantage suffered by younger nestlings with respect to the oldest ones.

Breeding time positively affected body mass and tarsus growth, but to a much lesser extent. This may have been due to negative environmental factors like predation pressure and food availability being mitigated by accelerated development in late-hatched nestlings (Hirose *et al*. 2012). In this way, the faster growth of chicks in late broods allows them to fledge at a younger age (Hipfner 1997). Seabird chicks, for example, when under food stress, preferentially allocate resources to the development of body parts (e.g. wings) critical for post-fledging survival (Benowitz-Fredericks *et al*. 2006, Morrison *et al*.

2009). In bittern chicks, the tarsus has the same function, enabling them to walk off through the reeds and escape potential predators (Demongin *et al.* 2007).

Climatic factors affected nestling growth in different ways when biological traits were combined (Reynolds 1996, Siikamäki 1996). Overall, our study confirmed the initial assumptions that the growth of bittern nestlings is influenced by weather conditions. However, our preliminary analysis showed that precipitation and wind speed better explained the variability of growth rate than the three temperature parameters. The negative effect of precipitation on nestling growth has been demonstrated in many bird species, from small passerines to storks (e.g. Bradbury *et al.* 2003, Kosicki & Indykiewicz 2011). These parameters cause the chicks' energy requirements to increase (Denac 2006) while reducing the availability of food delivered by parents (Beintema & Visser 1989b). We also found that growth rates were negatively correlated with wind speed, probably because this, besides precipitation, is a further factor reducing female foraging efficiency. Direct destruction of the nest or the chilling of chicks seems less important because of the protection provided by the dense vegetation around the nests of species occupying reedbeds (Hałupka *et al.* 2008), whereas strong winds whip up waves and increase water turbidity. Bitterns hunt using visual techniques (Voisin 1991, White *et al.* 2006), so prey detection may be hindered in turbid water. The impact of gale-force winds, which reduce the foraging efficiency of adult birds and can lead to starvation among chicks, has also been noted in other heron species (Jakubas 2005). Young bittern nestlings seem to be less exposed to low temperatures because of warming by females, which collect food close to the nest. Moreover, chicks are capable of huddling up to one another to keep warm (White *et al.* 2006).

To conclude, our study shows the importance of brood size, hatching order, laying date, precipitation and wind speed for the development of bittern nestlings. These factors appear to be especially significant in species where the female rears the nestlings solely by her own efforts. Even in food-rich habitats like fishponds, the chicks in the largest broods run the risk of slower growth rates.

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