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Article

Development of intraspecific size variation in black coucals, white-browed coucals and ruffs from hatching to fledging

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Most studies on sexual size dimorphism address proximate and functional questions related to adults, but sexual size dimorphism usually develops during ontogeny and developmental trajectories of sexual size dimorphism are poorly understood. We studied three bird species with variation in adult sexual size dimorphism: black coucals (females 69% heavier than males), white-browed coucals (females 13% heavier than males) and ruffs (males 70% heavier than females). Using a flexible Bayesian generalized additive model framework (GAMM), we examined when and how sexual size dimorphism developed in body mass, tarsus length and bill length from hatching until fledging. In ruffs, we additionally examined the development of intrasexual size variation among three morphs (Independents, Satellites and Faeders), which creates another level of variation in adult size of males and females. We found that 27–100% of the adult inter- and intrasexual size variation developed until fledging although none of the species completed growth during the observational period. In general, the larger sex/morph grew more quickly and reached its maximal absolute growth rate later than the smaller sex/morph. However, when the daily increase in body mass was modelled as a proportion, growth patterns were synchronized between and within sexes. Growth broadly followed sigmoidal asymptotic models, however only with the flexible GAMM approach, residual distributions were homogeneous over the entire observation periods. These results provide a platform for future studies to relate variation in growth to selective pressures and proximate mechanisms in these three species, and they highlight the advantage of using a flexible model approach for examining growth variation during ontogeny.

Keywords: alternative reproductive tactics, birds, body size, growth, sexual size dimorphism

Introduction

Intraspecific variation in body size is ubiquitous, often manifested as sexual size dimorphism (SSD) and linked to different sex roles (Fairbairn 1997). In most sexually reproducing animals, females are larger than males, a pattern explained by fecundity selection

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on females (Shine 1989, Andersson 1994, Fairbairn 1997). However, in many birds and mammals, males are larger than females (Fairbairn et al. 2007), a pattern explained by sexual selection (Székely et al. 2000, 2004). To understand the evolution of variation in body size within species, most previous studies have focused on adults, correlating SSD with a variety of factors such as mating system, habitat preference, activity pattern, body size and phylogenetic relationships (Clutton-Brock et al. 1977, Székely et al. 2004). Although much of the variation in body size arises during early ontogeny (Badyaev 2002), few studies have investigated the development of SSD before fledging, and even fewer have addressed the evolution of developmental patterns themselves.

Occasionally, the variation in size observed within sexes exceeds the size variation observed between sexes (Shuster 1987). This is particularly the case in species with alternative reproductive tactics (ARTs). Species with ARTs are typically characterized by two or three different male mating morphs with nearly discrete size variation (Oliveira et al. 2008a). Large male morphs are larger than females, defend resources, and attempt to dominate other males to obtain matings. In contrast, small male morphs are similar – or even smaller – in size to females and usually adopt alternative mating strategies such as sneaking (Shuster 1987, Taborsky and Brockmann 2010) or female mimicry (Dominey 1980, Shuster 1987, Gonçalves et al. 2005, Jukema and Piersma 2006).

Developmental variation in body size within species may arise through differences in growth rate and/or growth duration (McNamara 1995, Badyaev 2002, Blanckenhorn et al. 2007). The time period when sex differences in body size develop varies among species; differences may be already present at hatching, for instance in the larvae of the solitary predatory wasp *Symmorphus allobrogus* (Budriené et al. 2013), or arise later during development, for example close to sexual maturity, as in humans (Badyaev 2002). Growth rate and growth duration can be influenced by internal (i.e. genetic, physiological and behavioural) and external factors (i.e. food, temperature, parental investment; Rhen 2007). Growth is usually regulated by mechanisms that allow internal and external information to be integrated, thus growth can be adjusted not only in a sex-specific manner, but also according to external conditions (Badyaev 2002, Rhen 2007).

In birds, growth has been typically described as body mass change in relation to age in nestlings or chicks (O'Connor 1984). Most bird species show some form of sigmoidal growth, with an initially small body mass gain that first increases and eventually levels off when approaching the adult body mass. Since the pioneering work of Ricklefs (1968), analyses using sigmoid asymptotic growth models have proliferated, permitting informative comparisons of growth between species (reviewed by Tjørve and Tjørve 2010). In sigmoidal asymptotic models such as the widely used logistic growth model, growth is described by just a few parameters: asymptotic value, maximum growth rate and age at maximum growth rate. These simplistic models assume a pre-determined shape for growth curves and do not allow detection of exactly when differences in growth develop between and within species, and how differences in growth rate shape body sizes during ontogeny.

Generalized additive models are flexible, non-parametric or semiparametric models that can capture the diversity of the growth process without relying on simplistic assumptions about the shape of the growth curve (Katsanevakis 2007). Generalized additive models with maximum likelihood have been widely used to analyse ontogenetic or seasonal growth in vertebrates (Brooks et al. 2011, Hermosilla et al. 2013, Lázaro et al. 2017). The rapidly improving power of computers has enabled a Bayesian approach to run complex additive models with simulation techniques. Recently, the software BAMLSS for fitting generalized additive mixed models (GAMMs) based on Markov chain Monte Carlo simulations that can include random factors has been developed (Umlauf et al. 2018). These GAMMs allow for flexible adjustment of the slope throughout the entire growth period rather than assuming a fixed sigmoidal curve, such as logistic, Gompertz or Bertalanffy growth models. This approach allows the identification of the exact age when differences in growth occur, which is a first step towards understanding the proximate mechanisms and ultimate consequences of discrete size variations during ontogeny.

Here, we use GAMMs to examine when and how intraspecific differences in growth develop in three bird species during ontogeny. The black coucal *Centropus grillii*, the white-browed coucal *C. superciliosus* and the ruff *Philomachus pugnax*, exhibit considerable differences in adult SSD associated with their mating systems. In the sex-role reversed black coucal, adult females are 69% heavier than males, whereas in the socially monogamous white-browed coucal adult females are only 13% heavier than males (Goymann et al. 2015). By contrast, in the polygynous ruff, males are 70% heavier than females (Lank et al. 2013). Further, ruffs feature three male ARTs with large differences in size: Independents, Satellites and discretely smaller female-mimic Faeders (Lank et al. 2013). Morph type is determined by an autosomal inversion, meaning that females also carry the genetic information for morph (Küpper et al. 2016, Lamichhaney et al. 2016). Paralleling differences in males, Faeder females are substantially smaller than Independent and Satellite females (Lank et al. 2013).

The aim of this study was threefold: First, to understand when differences in SSD develop during ontogeny, we compared intersexual variation in growth between males and females from hatching until fledging in all three species. Second, we examined intrasexual variation in growth of the three morphs in both sexes of ruffs during ontogeny. We identified time periods of inter- and intrasexual growth variation and described growth rate differences between and within the sexes. Third, we compared the results of the GAMMs with three commonly used avian growth models (i.e. logistic, Gompertz and Bertalanffy) and assessed their fit. We hypothesized that GAMMs would have a better fit over the entire growth period than the sigmoid asymptotic growth models since GAMMs have a flexible adjustment of their predicted slopes.

Methods

Body size measurements

Black coucals and white-browed coucals

Black coucals and white-browed coucals are altricial, non-parasitic cuckoos of the Old World tropics (del Hoyo et al. 1997) and occur sympatrically in southwestern Tanzania (Baker and Baker 2003). We studied both species in a partially flooded grassland of the Usangu wetland (8°41′S and 34°5′E; 1000 m a.s.l.) in Mbeya Region, Tanzania, during nine breeding seasons (typically January–June) of 2005–2006, 2008 and 2010–2015 (Goymann et al. 2015).

Details on the data collection for coucals are provided by Goymann et al. (2016). Briefly, nests were located by following adult birds carrying nesting material or food in their beaks, or by finding incubating birds that had been equipped with radio-transmitters. After hatching, the body mass (to the nearest g) and tarsus length (to the nearest 0.1 mm) of nestlings were usually measured every other day until they left the nest or the nest was depredated. Black coucal young typically leave the nest when they are about 13 days old and white-browed coucals when they are about 14 days old (Goymann et al. 2015, 2016). For the purpose of this study, we considered the offspring as 'fledglings' at these ages. Note that 'fledgling' here is defined in a broad sense for altricial birds (sensu Ricklefs 1968, Goymann et al. 2016), as the coucal chicks at this age were still unable to fly. Individual nestlings were distinguished by uniquely marking two of the four claws of one foot with coloured nail enamel. At 9–11 days of age, they were ringed with a numbered aluminum ring. In total, we measured 407 black coucals and 431 white-browed coucals from 214 and 192 nests, respectively. This included 66 black coucals and 132 white-browed coucals with just one or two consecutive measurements. Number of measurements of these individuals was reduced either because the respective nests were predated or discovered just before fledging, or because an individual had disappeared from the nest, which often happens to the latest-hatched young of a clutch . To estimate the adult size, we used the measurements from Goymann et al. (2015), which are representative for the respective species (Erritzoe et al. 2012). Nestling sex was determined using the P2–P8 primer set to amplify the chromo-helicase-DNA-binding genes, CHD-Z and CHD-W, located on the avian sex chromosomes, which differ in size (Griffiths et al. 1998). The coucal growth data used in this study were taken from a previous study (Goymann et al. 2016) in which they were analysed using a non-linear logistic regression (Sofaer et al. 2013).

Ruffs

The ruff is a lekking, migratory wader species with pronounced male-biased SSD and three prominent reproductive male morphs: Independents, Satellites and Faeders (Küpper et al. 2016). The precocial chicks hatch after an incubation period of approximately 22 days and fledge (i.e. start to fly) at an age of approximately 20 days (Van Rhijn 1991). We studied the growth of captive ruffs housed at Simon Fraser Univ. in Burnaby, British Columbia, Canada. In captivity, ruffs often destroy eggs and females rarely successfully incubate the eggs until hatching. To enhance offspring survival, we collected the eggs several times per day and incubated them artificially (incubation details are provided in Supplementary material Appendix 1). This procedure did not allow us to identify the mother. Currently we lack parentage information for most chicks used in this study, hence we did not control for genetic relatedness. We hand-raised individually colour-ringed chicks in heterosexual groups under ad libitum food conditions tailored to promote growth and survivorship of ruff chicks (rearing details are provided in Supplementary material Appendix 1). We collected size data from chicks during 11 breeding seasons (2006–2014, 2017 and 2018). Only data from chicks that survived until fledging ($n_{\text{Total}} = 432$; males: $n_{\text{Independents}} = 127$, $n_{\text{Satellites}} = 45$, $n_{\text{Faeders}} = 40$; females: $n_{\text{Independents}} = 138$, $n_{\text{Satellites}} = 49$, $n_{\text{Faeders}} = 33$) were included in the analyses, because many chicks that died before fledging had stopped eating a few days before their death and thus may have deviated from normal growth. As chick mortality in captivity was usually caused by accidents, heterogeneous variation in rearing conditions or infections, we did not compare growth between successful and unsuccessful fledged chicks. Based on records available for six breeding seasons, approximately two thirds of the hatched chicks survived until fledging. While inclusion of all data up to the point of e.g. truly accidental deaths would have added some statistical power to earlier parts of growth curves, because of definitional problems for most of the cases, we took the conservative approach of excluding all potentially problematic cases.

To estimate the development of size variation between sexes and among morphs, we measured body mass (to the nearest 0.1 g) typically daily from hatching to fledging. From fledging until an age of 33 days, juveniles were weighed approximately every three days. In four seasons (2006, 2013, 2017 and 2018, n = 120 chicks), we took measurements of structural growth of tarsus and bill (to the nearest 0.1 mm) approximately every third day from hatching until an age of 33 days. As ruffs are migratory and will put on fat for their annual migration during summer/early autumn even in captivity, we measured adults in November or December during their first winter to determine their asymptotic lean adult body mass. To determine sex we used the *Z-002B* primer set to amplify homologous regions on the Z and W chromosome that differed in size (Dawson 2007) and amplified a W-linked microsatellite (*Calex-31*; Küpper et al. 2007, dos Remedios et al. 2010). We also confirmed sex by sequencing two sex-specific single nucleotide polymorphisms (SNPs) located on the spindlin gene (Dawson et al. 2016) and amplified with the *Z43Bruffsex1* and *RuffSexD7* primer sets (Supplementary material Appendix 1, Table A1).

Morphs were identified using a set of six diagnostic SNPs (Supplementary material Appendix 1, Table A1) based on sequence differences in the inversion region (Küpper et al. 2016). The molecular morph assignments were corroborated by behavioural observations of males (DBL, unpubl.).

Statistical analysis

To analyse when and how differences in body size between and within the sexes develop, we calculated posterior means of biometric measurements (body mass, bill length and tarsus length) and their 95% credible intervals (CrI) in relation to age for each species, sex (all species) and morph (ruffs only) using GAMMs with the R package BAMLSS (Umlauf et al. 2018). The advantage of this package is that it takes the uncertainty of the curve's shape into account. BAMLSS uses thin plate spines as smoothing functions and does regularization with scale-dependent priors (Umlauf et al. 2018). We modeled each factor separately because BAMLSS does not allow to include fixed effects and our main interest was to examine differences in the shape of growth curves. Thus for the comparison between sexes we modeled each species and each sex within species separately whereas for the analyses within sexes in ruffs we modeled each morph within sex separately. We included all individuals with at least one measurement, independent of how many measurements we had per individual (Supplementary material Appendix 1 Table A3, A4) For each model we z-transformed biometric measurements and ages by setting their means to 0 and their standard deviation to 1. Biometric measurements were z-transformed to enable BAMLSS to find the intercept. We included 'Individual ID' and an interaction between 'Individual ID' and 'age' as a random factor in all models to allow for individual specific growth curves. For models of males and females in ruffs, we included morph and year as random factors to account for different sample sizes among morphs and to account for among-year variation, because rearing conditions differed slightly among years. For models of morphs in ruffs, we only included year as random factor. In both coucal species, we included the identity of the nest, the number of siblings and year as random factors to account for repeated measurements of chicks from the same nests, and for potential effects of genetic relatedness, sibling competition and environmental variation among years on growth (Bortolotti 1986, Fresneau et al. 2018). In separate models, we additionally estimated posterior means and 95% CrI of the proportion of adult size (body mass, tarsus length and bill length), growth rate and relative growth rate in relation to age. We calculated the proportion of adult size, growth rate and relative growth rate for each individual with the following formula:

$$\text{proportion of adult size} = W_t \,/\, W_{Ad}$$

where W_t is the biometric measurement at age $\bar{t}$ and W_{Ad} is the adult size.

$$\text{growth rate} = \left(W_t - W_s\right) / \left(\bar{t} - \bar{s}\right)$$

where W_s is the preceding measurement to W_t at age $\bar{s}$.

$$\text{relative growth rate} = \left(\left(W_t - W_s\right) / \bar{t} - \bar{s}\right) / W_s$$

We modeled relative growth rate only for body mass, because the growth process differs between our measured traits. Growth is a consequence of cell growth and cell division. For body mass the absolute increase depends on the actual body mass. However, for length growth of tarsus and bill this is different. Length growth of tarsus and bill in length happens mainly in restricted regions, such as the epiphyseal plates of the tarsi (Hunziker 1994) and at the base of the growing beak (Schneider and Helms 2003). This means, that length growth of bill and tarsus is only weakly influenced by their actual length.

Because the coucals dispersed after leaving the nest, we were unable to obtain the individual adult biometric values. Instead, we used the mean reported adult size for males and females from Goymann et al. (2015) as an estimate for W_{Ad}. To compare growth between sexes and among morphs in ruffs, we extracted the following estimates of the posterior distribution from each model: growth rate at hatching ($\bar{K}_0$), maximum growth rate ($\bar{K}_{max}$), age at the maximum growth rate ($\bar{t}_I$, i.e. the age at $\bar{K}_{max}$), growth rate at fledging ($\bar{K}_F$), size at hatching (W_0), size at fledging (W_F), size at maximum growth rate (W_I, i.e. size at $\bar{t}_I$) and W_{Ad}.

For comparisons with other studies and to evaluate how GAMMs growth models deviated from the models typically used to describe avian growth, we analysed the growth data using the following traditional growth models: (1) Gompertz growth model, $W_t = W_{As} \times \exp(-\exp(-K \times (t - t_I)))$, (2) Logistic growth model, $W_t = W_{As}/1 + \exp(-K(t - t_I)))$ and (3) Bertalanffy growth model, $W_t = W_{As} \times (1 - (\exp(-K(t - t_I))/3))^3$ (Ricklefs 1968). In these models, W_{As} represents the asymptotic value, K the growth coefficient inherent to each model and t_I the age at maximum growth. In the Gompertz model, t_I occurs when 37% of the asymptote is attained, in the Logistic model at 50% and in the Bertalanffy model at 30%. As these parameters are not directly comparable to any of the parameters or estimates of the GAMMs, we assessed model differences and residual distributions graphically and calculated standard deviations and natural logarithm of the likelihoods to compare the model outputs.

For the analyses with sigmoid asymptotic models, we determined model parameters for each individual to obtain individual specific growth curves. For this, we used Markov Chain Monte Carlo simulation using 'Just Another Gibbs Sampler' (JAGS; available online at <https://sourceforge.net/projects/mcmc-jags/files/>) with 100 000 iterations, a burn-in phase of 5000 and a thinning rate of 10 and 2 chains. We determined broad priors excluding only completely unrealistic values (Supplementary material Appendix 1, Table A2), as priors that are much broader than the effective knowledge do not influence parameter estimates markedly (Gelman and Hill 2006). For this analysis we included only individuals with at least three measurements (black coucal: n = 341, white-browed coucal: n = 299, ruff: n = 432). We assessed convergence using number of effective samples, i.e. number of independent draws from the posterior distribution, and additionally checked the model fit graphically, by plotting the biometric measurements of each individual against age and including the estimated growth curves. In case the number of effective samples were lower than 2000 or the estimated growth curve showed unrealistic estimates like e.g. a decrease of the biometric measurement over time despite the real data showing an opposite trend (0.02% of the models), we ran the model once again. After the second run, all models had converged. To obtain group estimates, we then modeled W_{As}, K and t_I for each growth model and for each biometric measurement with a linear mixed model (lmer) and improper prior distribution, using the same random structure as in the GAMMs. To obtain model estimates we simulated 2000 values from the joint posterior distribution of the model parameters using the function *sim* of the package *arm* (Gelman and Hill 2006). We present means and the 95% CrI of the model parameters.

Results

Development of SSD

Sex differences in body size developed in all three species before fledging (Fig. 1, Table 1) and were more pronounced for body mass (Fig. 1) than for tarsus length (Fig. 2) or bill length (Supplementary material Appendix 1, Fig. A1). Across all species and biometric measurements, maximal growth rates were reached during the first half of the pre-fledging period. In all cases, the larger sex was characterized by higher

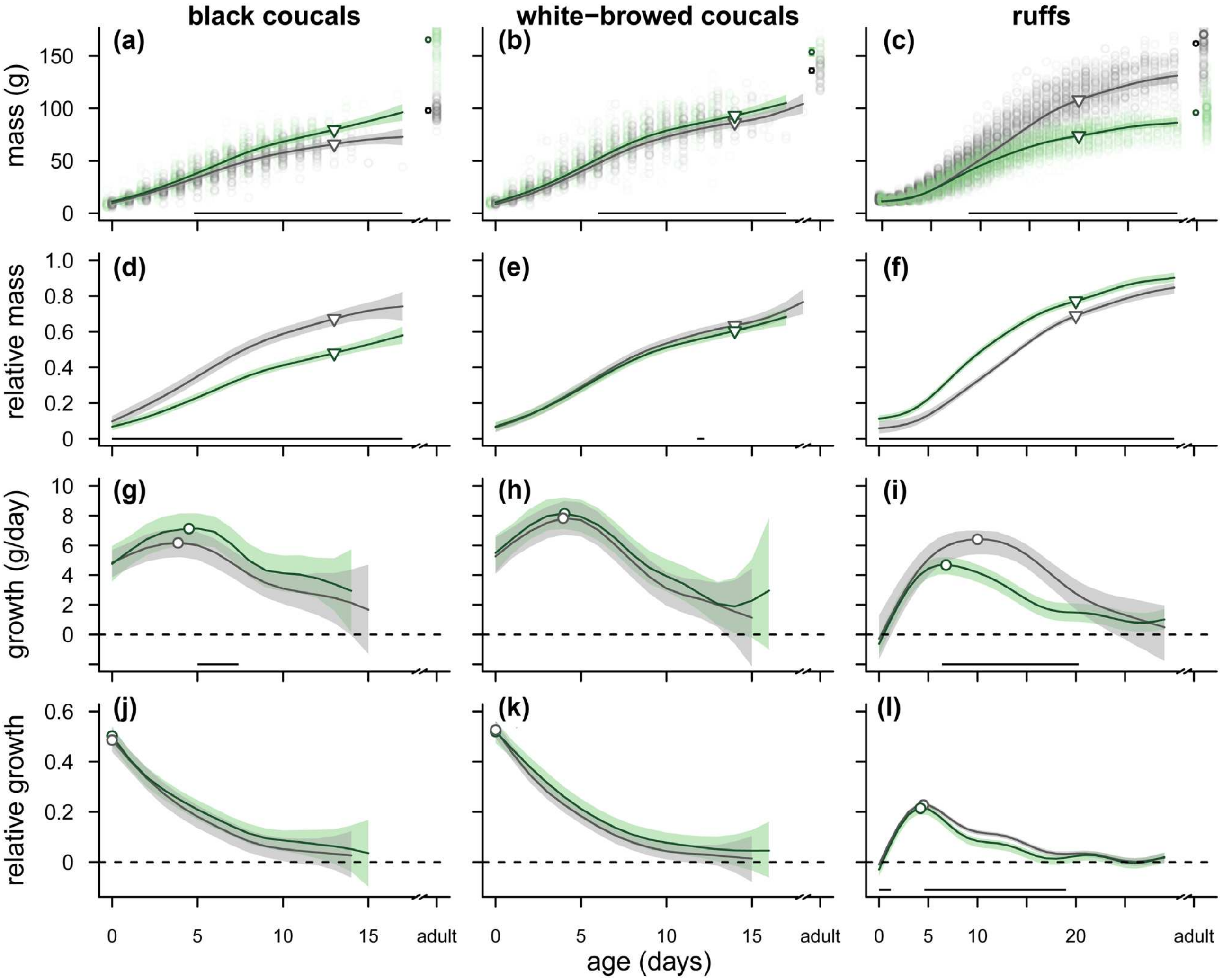

Figure 1. Development of sexual size dimorphism in juvenile body mass of three bird species. Mean ± 95% CrI of males in grey and females in green. Open circles in (a), (b), (c) refer to mean adult mass. Open circles in (g)-(l) refer to points of maximal growth. Open triangles in (a)-(f) show the absolute mass at fledging, the developmental endpoint of the study, and relative to adult mass. Black bars at the bottom of the diagram indicate time-periods where means did not fall within the CrIs of the other sex.

Table 1. Sexual size dimorphism at fledging in black coucals (BC), white-browed coucals (WBC) and ruffs. Fledging ages are 13 days for BC, 14 days for WBC and 20 days for ruffs. SSD is presented as the percentage by which the larger sex exceeds the smaller sex: ((larger sex/smaller sex) − 1) × 100. Direction of sexual size dimorphism is indicated in parentheses (m: males, f: females).

	BC (f > m)	WBC (f > m)	Ruffs (m > f)
Body mass			
SSD at 13 days	21	7	24
SSD at 14 days	22	7	28
SSD at 20 days	–	–	46
SSD of adults	69	13	70
Tarsus length			
SSD at 13 days	4	2	18
SSD at 14 days	4	3	18
SSD at 20 days	–	–	22
SSD of adults	2	3	17
Bill length			
SSD at 20 days	–	–	9
SSD of adults	–	–	15

maximal growth rates and also reached its inflection point at an older age than the smaller sex. The time periods with highest variation in absolute growth occurred shortly after the larger sex reached its maximal growth rate. However, only in black coucals and ruffs means did not fall within the CrIs of the other sex. In ruffs, maximal absolute growth rate was reached first in tarsus and bill lengths, and then in body mass, whereas in black coucals and white-browed coucals maximal growth rates were reached simultaneously for body mass and tarsus length (Fig. 1, 2, Supplementary material Appendix 1, Fig. A1).

Body mass

Adult SSD in black coucals and ruffs were of similar magnitude, and larger than that in white-browed coucals (Fig. 1, Table 1). For all three species body mass at hatching was similar between sexes (Fig. 1, Supplementary material Appendix 1, Table A3). Statistically clear differences in body mass developed first in black coucals, then in white-browed coucals and last in ruffs, at ages of 5, 6 and 9 days, respectively (Fig. 1).

None of the species reached their respective adult body mass during the observation period. The relative (to adult) mass was always higher in the smaller sex (Fig. 1). At fledging, black coucal females were 21% heavier than males, white-browed coucal females were 7% heavier than males and ruff males were 46% heavier than females (Table 1, Fig. 1).

In contrast to both coucal species, ruff chicks initially lost mass during the first day, meaning that their absolute and relative growth rates were negative (Fig. 1). Relative growth rate curves showed remarkably similar shapes between the sexes, but their shapes were different across species. Coucal species showed continuously decreasing relative growth rates throughout the observation period, whereas ruffs first increased their relative growth rates, reaching their maximal values at 5 days of age before the rates decreased (Fig. 1).

Tarsus length

In adults, the degree of SSD in tarsus length was most pronounced in ruffs (males 17% larger than females), intermediate in white-browed coucals (females 3% larger than males) and lowest in black coucals (females 2% larger than males; Fig. 2, Table 1). Sex differences in tarsus length in black coucals and white-browed coucals developed towards the end of the observation period, whereas in ruffs males showed longer tarsi than females from day 1 onwards (Fig. 2). Only ruffs reached adult values of tarsus length during the observation period at an age of 11 days in males and females (Fig. 2).

Bill length

Adult ruffs had moderate SSD in bill lengths, with males having 15% longer bills than females (Table 1, Supplementary material Appendix 1, Fig. A1). In juveniles, the differences between sexes in bill length were statistically clear from day 12 onwards. Juveniles did not reach adult bill length during the observation period.

Development of size variation among morphs in ruffs

Intrasexual variation in growth among the three morphs was statistically clear for body mass, but not for tarsus or bill length. Thus, we only compared body mass growth among Independents, Satellites and Faeders in males and females. Body mass was highest in Independents, intermediate in Satellites and lowest in Faeders (Fig. 3, Supplementary material Appendix 1 Table A4). In adult males, Independents were on average 5% heavier than Satellites and 27% heavier than Faeders. In adult females, Independents were on average 6% heavier than Satellites and 26% heavier than Faeders. By contrast, hatching body masses were similar among the morphs (Fig. 3, Supplementary material Appendix 1, Table A4). At fledging size variations among morphs had already developed, but were less pronounced than in adults. Differences in body mass among the three morphs became statistically clear from day 1 onwards in males and from day 7 onwards in females. Differences between sexes were consistent among morphs. At fledging, Faeders had reached the highest proportion of their adult mass, followed by Satellites and lastly Independents. Absolute growth rates increased similarly among morphs until reaching maximal values in Faeders. Thereafter Independents and Satellites continued increasing growth rates until reaching maximal values first in Satellites and lastly in Independents. The shapes of the curves for relative growth rates were very similar across morphs (Fig. 3), with maximal values at an age of 5 days in both sexes (Fig. 3, Supplementary material Appendix 1, Table A4).

Comparison of GAMM estimates and parameters of traditional growth models

The GAMMs provided the most precise estimates of all models, with the smallest standard deviations of

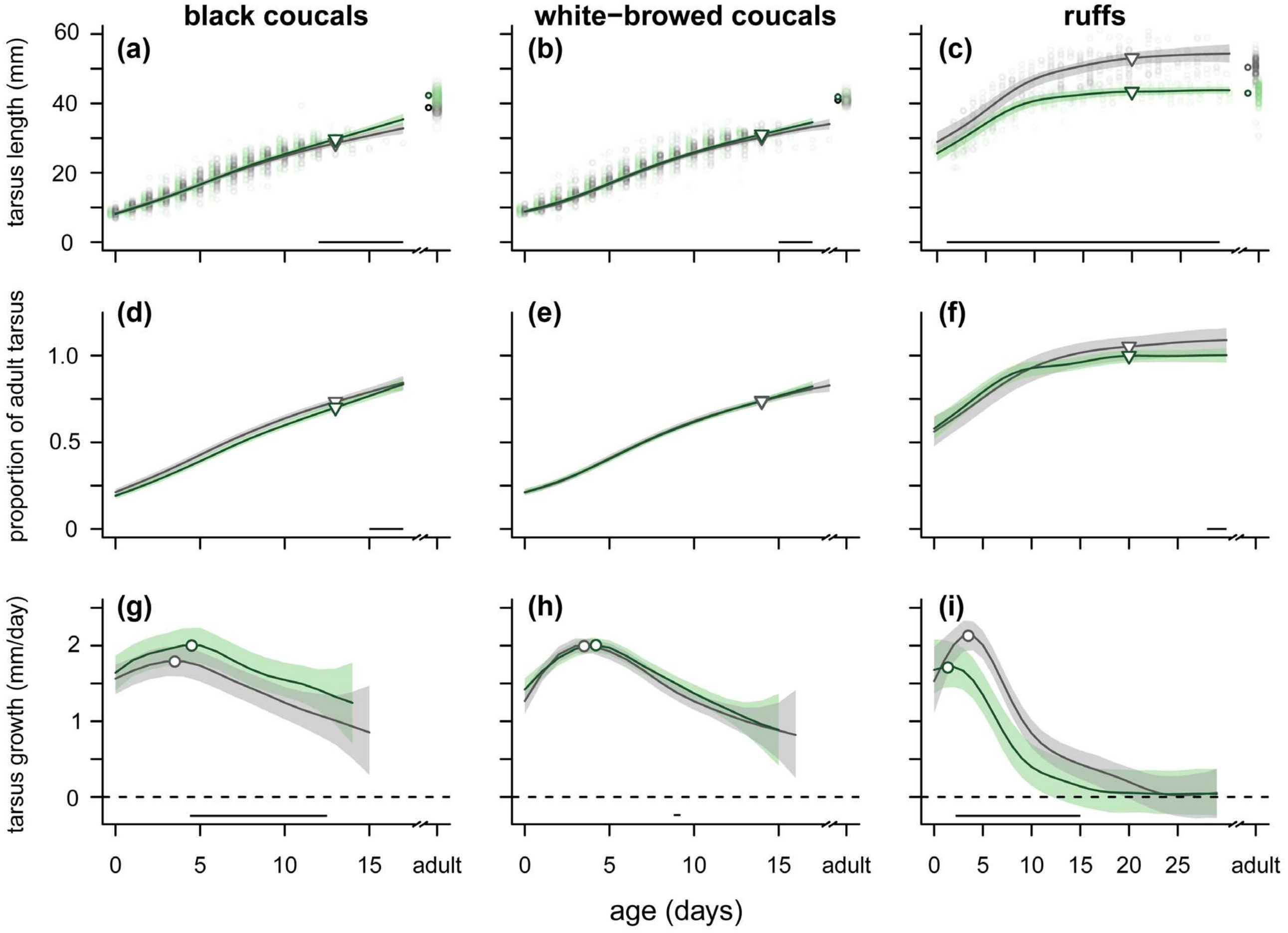

Figure 2. Development of sexual size dimorphism in tarsus length in juveniles of three bird species. Mean ± 95% CrI of males in grey and females in green. Open circles in (a), (b), (c) refer to mean adult tarsus length. Open circles in (g), (h), (i) refer to points of maximal growth. Open triangles in (a)-(f) indicate absolute tarsus length at fledging, the developmental endpoint of the study, and relative to adult length. Black bars at the bottom of the plots indicate time-periods where means did not fall within the CrIs of the other sex.

residuals and log likelihoods (Fig. 4, Supplementary material Appendix 1, Fig. A2, Table A5). Despite a similarity at a broad scale between GAMMs and traditional growth models, estimates at specific ages deviated substantially among models, especially during the first days after hatching and late in the observation period for body mass, and in the middle of the observation period for tarsus and bill lengths (Fig. 4, 5, Supplementary material Appendix 1, Fig. A2, A3). Among sigmoidal asymptotic models, growth in black coucals was best described by the logistic model in males and by the Bertalanffy model in females. In white-browed coucals, growth was best described by the Gompertz model and in ruffs growth was best described by the logistic models (Supplementary material Appendix 1, Table A5). For comparison with other studies, estimates of W_0, W_P, W_I, W_{Ad}, $\bar{K}_0$, $\bar{K}_{max}$, $\bar{K}_I$ and $\bar{t}_I$ modeled with GAMM (Supplementary material Appendix 1, Table A3), as well as growth parameters estimated with logistic, Gompertz and Bertalanffy models are provided (Supplementary material Appendix 1, Table A6).

Discussion

Development of size variation

Examining the development of inter- and intrasexual size variation in three species, we found that size variation developed before fledging through differences in growth rates almost from the point of hatching. Interestingly, the shapes of relative growth rates were similar within all three investigated species. However, between species, the degree of SSD at fledging, as well as the growth rate patterns, varied strikingly. The GAMMs had the best fit over the entire observation period, and allowed us to precisely identify time periods with inter- and intrasexual growth variation.

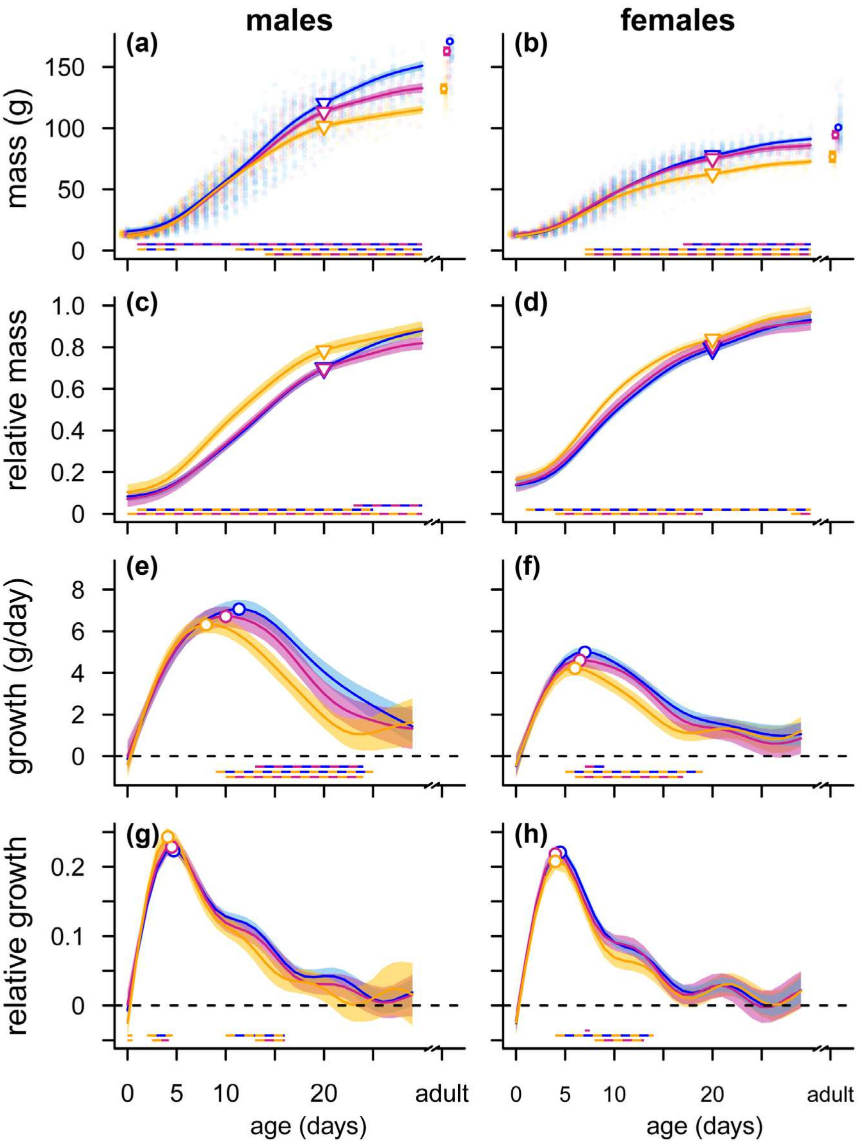

Figure 3. Development of intra-sexual size variation in juvenile body mass of ruffs. Mean ± 95% CrI for each morph (Independents in blue, Satellites in violet and Faeders in orange) is given. Open circles in (a), (b) refer to mean adult mass. Open circles in (e)-(h) refer to points of maximal growth. Open triangles in (a)-(d) show the absolute mass at fledging, the developmental endpoint of the study, and relative to adult mass. Bicolored bars at the bottom of the plots indicate time-periods where means did not fall within the CIs of the other morph, i.e. Independents versus Satellites (blue-violet), Independents versus Faeders (blue-yellow) and Satellite versus Faeders (violet-yellow).

For body mass, the larger sex had no apparent head start at hatching. Instead, in all three species the intersexual size variation in body mass developed during the period before fledging even though individuals had not yet reached their adult sizes by the end of our observation periods. At fledging, the smaller sex had reached a larger proportion of its adult body mass than the larger sex (Fig. 1, Supplementary material Appendix 1, Table A3). These results are consistent with growth patterns described for other sexually size-dimorphic species (Ricklefs 1968, Teather and Weatherhead 1994). Among our study species, ruffs are precocial whereas coucals are altricial. Ricklefs (1968) evaluated the shape of growth rate models by fitting either logistic, Gompertz or Bertalanffy models in birds. From this, he concluded that the developmental mode should affect growth in two ways. First, precocial species should have lower growth rates than altricial species. Second, the shape of growth rates should be similar between precocial and altricial species. Consistent with Ricklefs' first finding, we found that precocial ruffs had overall a lower relative growth rate compared to the altricial coucal species, even under a system of ad libitum food tailored to their dietary needs. However, contrary to Ricklefs' second finding, our flexible modelling approach revealed that this was driven by growth rate differences during the first few days after hatching (Fig. 1). Altricial coucals showed the

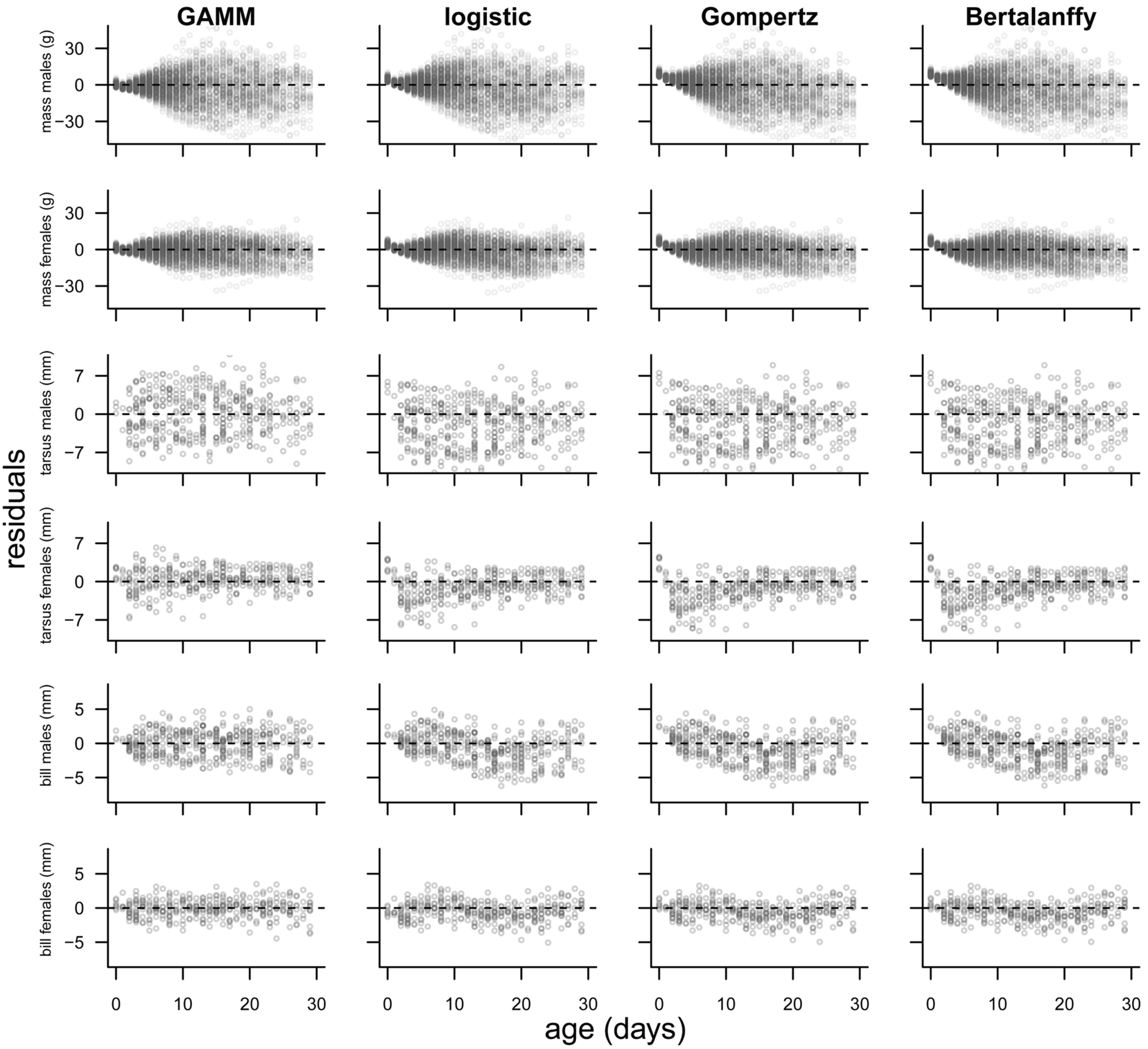

Figure 4. Comparison of fit for different growth models: Residual distribution for body mass, bill and tarsus length over the entire set of observations in ruffs.

highest relative growth rates right after hatching, probably because they were fed by their parents. In contrast, precocial ruff chicks first lost mass until they learned to forage, reaching their maximal relative growth rate at an age of 5 days. The delay in reaching maximal relative growth rates in ruffs compared to coucals could thus be a matter of developmental mode. Non-growth or negative growth shortly after hatching is also apparent in other precocial shorebirds (Catlin et al. 2013, Grønstøl et al. 2013, Tjørve and Tjørve 2017, Loonstra et al. 2018) but this fact cannot be captured with traditional growth models. However, we note that it is also possible that for ruffs the artificial rearing conditions, such as the absence of living food, were less stimulating and thus foraging motivation was reduced.

The degree of SSD at fledging varied among species, being relatively small in both coucal species compared to ruffs. Ruffs had developed an approximately two times higher degree of SSD at fledging than black coucals, even though the degree of adult SSD was similar in the two species (Fig. 1, Table 1). There are several explanations for the observed differences between species. First, coucal data were collected in the wild, where chicks likely experienced constraints such as limitation of food, whereas ruff data were taken in captivity with food ad libitum and optimized rearing conditions. Food limitation is reported to affect growth of the larger sex more than that of the smaller sex (Blanckenhorn 2005, Blanckenhorn et al. 2007, Loonstra et al. 2018, Rohner and Blanckenhorn 2018). Therefore, the growth of female black coucals could have

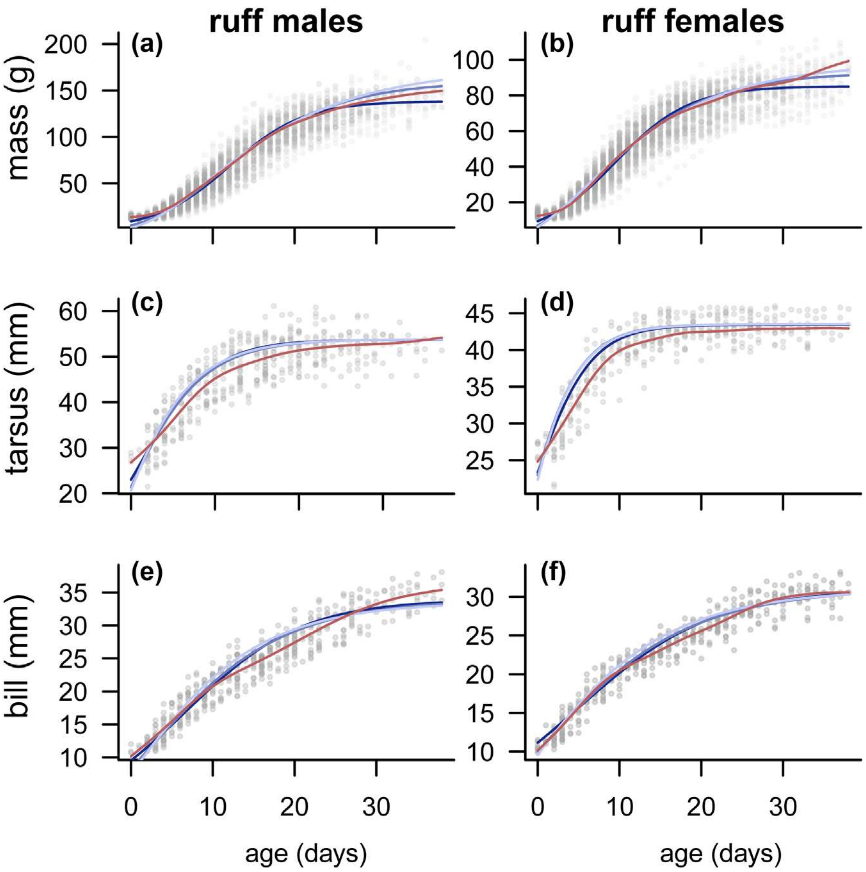

Figure 5. Comparison of growth models: Logistic (dark blue), Gompertz (blue), Bertalanffy (light blue) and GAMM (red). Mean values of each model for body mass, tarsus length and bill length.

been more constrained by food limitation than the growth of conspecific males. Second, in coucals, fledging was defined as the age when chicks left the nest, whereas in ruffs fledging was defined as the age when chicks started to fly. Coucals that left the nest were still not able to fly and thus in an earlier developmental stage than ruffs at our defined 'fledging' age. Third, mechanisms related to reversed SSD may have further contributed to the discrepancy between ruff and black coucal SSD at fledging: for birds with female-biased SSD, slightly lower growth rates relative to body size are reported for the larger sex compared to species with a male-biased SSD (Teather and Weatherhead 1994, Blanckenhorn et al. 2007).

Generally, variation in tarsus and bill length in adults was lower than in body mass (Table 1, Fig. 1, 2, Supplementary material Appendix 1, Fig. A1). This is most likely because size changes in length measurements are isometric, whereas size changes in body mass have a cubic effect. During the pre-fledging period, ruffs developed the most pronounced sex differences in tarsus length. There are at least two explanations for this. First, species with more pronounced SSD in adults also show a more pronounced SSD at fledging (Teather and Weatherhead 1994). Second, allometric growth of leg length is more pronounced in precocial than in altricial species (Ricklefs 1983) because functionally developed legs are essential for precocial foraging after hatching, but become relevant in altricial species only from fledging onwards (O'Connor 1984).

The duration of tarsus growth was similar in male and female ruffs (Fig. 2). For all other morphometric measurements we could not evaluate growth duration, because growth was not completed during our observation periods (Fig. 1, 2, Supplementary material Appendix 1, Fig. A1). It has been previously stated that the larger sex takes longer to reach its adult size than the smaller sex (Ricklefs 1967, Teather and Weatherhead 1994). However, this general assumption was derived from sigmoid asymptotic growth models. In our study, absolute growth rates did not follow a sigmoidal growth pattern over the entire period from hatching until fledging (Fig. 1, 2). In addition, asymptote values were often lower than adult values, rendering it difficult to estimate the completion of growth. When we modelled growth rates as a percentage of body mass (relative growth rate), the variation between sexes decreased. Maximal growth rates then occurred at a similar age in males and females. At the end of our observation periods, differences in growth rates between sexes were non-significant. This suggests a similar timing in growth regulation between sexes. Thus, the differences observed in absolute growth rate at the end of the observation period are the result of a similar relative mass gain, based on the already-existing differences in body mass. A methodological implication of this observation is that growth rates need to be corrected for initial size because low absolute growth rates are always easier to detect in the larger sex than in the smaller sex.

Across all three species, SSD developed via faster growth of the larger sex right after hatching (Fig. 1, 2, Supplementary material Appendix 1, Fig. A1). These differences will have to be matched by differences in metabolism, as the sex with faster growth needs more energy for growth and to maintain a larger body mass. If the sexes differ in their energy demand due to different developmental trajectories, the larger sex is expected to experience a higher mortality when conditions are limiting (Benito and González-Solís 2007, Villegas et al. 2013, Loonstra et al. 2019, but see Magrath et al. 2007). Thus, selection should shift sex ratios from hatching onwards towards more females in ruffs and towards more males in black coucals. In white-browed coucals a more balanced sex ratio is expected. Consistent with this, migrant populations of juvenile ruffs are female-biased (Jaatinen et al. 2010), male-biased in black coucals and seemingly unbiased in white-browed coucals (Goymann et al. 2015). Furthermore, a sex bias in the juvenile mortality of shorebirds has been shown to influence mating and parental care systems (Eberhart-Phillips et al. 2017, 2018). Biased sex-specific survival among chicks may be more pronounced when environmental conditions are bad than under benign conditions. However, in coucals, increased mortality of males could also occur through sibling competition if larger chicks are better at competing for food and thus overcome the energetic constraints (Bortolotti 1986).

The proportion of adult mass attained at fledging has been used as an indicator of developmental stage when nestlings leave the nest (Teather and Weatherhead 1994, Cheng and Martin 2012). The sex differences in proportion of adult size reached at fledging point towards differences in developmental rate between sexes. Our results that the smaller sex had attained a higher proportion of its adult size than the bigger sex are in line with the general observation that the smaller sex is more developed at fledging than the larger sex (Fig. 1, 2, Supplementary material Appendix 1, Fig. A1) (Ricklefs 1968, Weatherhead and Teather 1991, Teather and Weatherhead 1994). However, adult body mass is plastic and affected by environmental conditions. Direct measurements, such as thermoregulatory ability, feather growth or flying ability, may provide a better measure of the developmental stage than body mass.

Development of size variation among morphs in ruffs

The development of intrasexual variation in ruffs was strikingly analogous to the pattern observed between the sexes, although the differences among morphs were less pronounced. In both sexes, Independents, the largest morph, showed the highest growth rates, Satellites had intermediate and Faeders the lowest growth rates. The age of maximal relative growth rate was similar among morphs (Fig. 2). This result supersedes the lack of differences in Gompertz growth parameters between Independent and Satellite males reported by Lank et al. (1995). Although a trend towards lower growth by Satellites was present, the earlier study lacked sufficient statistical power to demonstrate a difference. The similarities between the development of inter- and intrasexual size variation support the hypothesis that the mechanisms that generate size differences between the sexes are similar to the mechanisms that generate size differences within the sexes in ART morphs (Oliveira et al. 2008b).

The flexible growth models may also point to time periods when physiological variation manifests itself. We still know surprisingly little about the underlying proximate mechanisms mediating the growth variation between and within sexes. Between the sexes, growth variation is related to differential regulation of autosomal genes by sex-linked loci (Rhen 2007, Bachtrog et al. 2014, Ledón-Rettig et al. 2017) and/or sex steroids (Gatford et al. 1998, Badyaev 2002, Rhen 2007). Testosterone and its metabolites are proposed to have a stimulatory effect on growth and development of SSD in vertebrates (Badyaev 2002). However, the majority of studies suggesting such a role for testosterone have focused on model species with a male-biased SSD (reviewed by Cox and John-Alder 2005). Studies on reptiles showed that species with a female-biased SSD did not conform to this pattern (John-Alder et al. 2007, Cox and John-Alder 2005), instead suggesting a stimulatory effect of testosterone on male growth in species with a male-biased SSD and an inhibitory effect of testosterone on male growth in species with a female-biased SSD (Cox et al. 2005). In black coucals, male nestlings express higher levels of testosterone than females, but only female tarsus growth is positively related to testosterone concentration (Goymann et al. 2005). These data are consistent with a potentially inhibitory effect of testosterone on male growth and a stimulatory effect on female growth, similar to the effects observed in reptiles (Cox et al. 2005). We are not aware of any other study investigating the proximate mechanisms of growth variation in bird species with a female-biased SSD. The identification of time periods with growth variation in black coucals and white-browed coucals, two sympatric and closely related species with different degrees of female-biased SSD, opens the opportunity to further evaluate growth regulation in birds with a female-biased SSD.

In species with ARTs, sex steroids also have an important role in the regulation of size variation (Oliveira et al. 2008b). Morph-biased expression of steroidogenic enzymes during critical periods related to sexual differentiation shapes the ontogeny of fixed alternative reproductive morphs, suggesting similar time windows for morph differentiation and sexual differentiation (Oliveira et al. 2008b). This observation is in line with our results, as variation in growth among morphs had a similar pattern to the variation between the sexes (Fig. 1, 2). In ruffs, several genes within the inversion are involved in steroid hormone metabolism and growth

(Küpper et al. 2016), and thus could either directly influence cell division or indirectly mediate growth hormone metabolism. Analogous to sexes, we expect variation in morph-biased hormone metabolism during the identified time-periods of relative growth variation (Fig. 2). Investigating the proximate mechanisms related to growth variation among ruff morphs has the potential to elucidate how the genetic differences within the inversion bias hormone metabolism and its regulatory effects, independent of sex and environmental conditions. Further, morph differences in hormone metabolism during the identified periods of variation in growth could also represent a mechanism for organizational effects determining morph-specific behavior.

Comparison of GAMM estimates and parameters of traditional growth models

The identification of time periods of variation in growth required a flexible modelling approach. Although growth followed a sigmoidal pattern on the broad scale, at specific ages sizes were over- or underestimated by sigmoidal growth models, depending on the species and morphometric trait (Fig. 5, Supplementary material Appendix 1, Fig. A3). This was reflected in consistently smaller residuals (Supplementary material Appendix 1, Table A5) and a more homogeneous residual distribution over time for GAMMs, than for sigmoidal models (Fig. 4, Supplementary material Appendix 1, Fig. A2). How well the growth parameters (W_{As} and t_I) of sigmoidal-asymptotic models corresponded with the estimates W_{Ad} and $\bar{t}_I$ of GAMM was influenced by how well growth followed a sigmoidal shape and depended on species and biometric measurement. This was especially the case for t_I and $\bar{t}_I$ (Supplementary material Appendix 1, Table A3, A6). In contrast, W_{As} was similar to W_{Ad}, when growth was almost completed. Yet, in black coucals and white-browed coucals, females seem to have a second growth period after fledging and thus W_{As} was lower than W_{Ad}. While $\bar{K}_{\max}$ was always higher in the larger sex/morph, this was not always the case for K of Logistic, Gompertz or Bertalanffy models (Supplementary material Appendix 1, Table A3, A6). Note that K is a unitless growth rate constant in sigmoidal models and thus can not be compared with real growth rates ($\mathrm{g\,Day}^{-1}$) estimated with GAMMs. In birds, the large majority of growth analyses have used a sigmoidal growth model, providing useful insight into broad patterns of growth variation. However, when growth does not follow a sigmoidal curve, estimates can be misleading. This is the case, when growth does not follow the assumed symmetry between the time periods before and after t_I, or if body mass loss occurs, e.g. directly after hatching, before fledging or in response to ecological stressors . The improved computing power and the availability of statistical packages for complex growth modeling have allowed us to obtain a more precise and accurate description of patterns of growth variation. This is necessary to get a deeper understanding of the proximate mechanisms, and the ultimate consequences, of growth variation between and within the sexes.

Conclusions

Examining the development of inter- and intrasexual size variation in three bird species, we found that much of the size variation developed before fledging through higher absolute and relative growth rates in the larger sex/morph since hatching. The shapes of relative growth curves within species were similar between sexes and among morphs, suggesting synchronized regulatory mechanisms of inter- and intrasexual growth variation. Between species, however, growth rate patterns and the degree of intersexual size variation at fledging varied strikingly. The GAMMs provided the best fit over the entire observation period and enabled identification of time periods that show variation in growth within and between the sexes. Identification of such time periods provides a basis for future studies to relate ultimate and proximate mechanisms to growth variation in bird species with female-biased SSD and ARTs.

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Author contributions – LMGD, DBL, WG and CK conceived the study. IS and WG collected coucal growth data, DBL and LMGD collected ruff growth data. MS designed morph-specific SNP markers and DAD designed sex-specific SNP markers for ruffs. TB supervised molecular work. LMGD performed statistical analyses and wrote the manuscript with input by CK and contributions of all other authors. All authors approved the final version of the manuscript.

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Permits – The study was conducted according to the legal requirements in Canada and Tanzania.

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Supplementary material (available online as Appendix jav-02440 at <www.avianbiology.org/appendix/jav-02440>). Appendix 1.