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The seasonality of breeding in savannah birds of West Africa assessed from brood patch and juvenile occurrence

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Abstract In order to maximise breeding success in a seasonally fluctuating environment animals breed during periods of increased resource abundance and avoid times of resource constraint. In tropical savannahs, variation in resources in time and space is dependent on the amplitude of the rains and their predictability. We quantified the degree to which tropical savannah birds have concentrated their breeding around predicted periods of increased food availability coincident with rainfall. We used the proportion of adults caught with brood patches and/or the juvenile-to-adult ratio in 25 species of small savannah bird which were caught over a 10-year period in Nigeria, West Africa, to assess the degree to which there were clear seasonal peaks in breeding activity. We found two-thirds of species bred in all seasons (68 %), but that most species showed distinct seasonal peaks (96 %) in the timing of their breeding. Over one-half of species (60 %) varied the timing of their breeding across the years. Granivorous species bred later than insectivorous and frugivorous species, which probably indicates synchronisation with their respective peak abundance in food type. Overall we found distinct seasonal peaks in breeding effort (i.e. breeding seasons), and this is most likely in response to changing resource availability brought about by seasonal rainfall. We also demonstrated the potential utility of using brood patches to test for patterns in breeding in multi-species long-term datasets.

Keywords Brood patches · Breeding indicators · Feeding guilds · Juveniles · Rainfall · Seasonality

Zusammenfassung

Saisonalität von Brutzeiten bei Vögeln der Savanne Westafrikas, abgeleitet aus dem Auftreten von Brutfleck und Jungvögeln

Um den Fortpflanzungserfolg in einer saisonal fluktuierenden Umwelt zu maximieren, wählen Tiere für die Fortpflanzung Perioden mit erhöhter Ressourcenverfügbarkeit und vermeiden Perioden in denen Ressourcen stark limitiert sind. In der tropischen Savanne ist die zeitliche und räumliche Variabilität von Ressourcen abhängig von der Amplitude und Vorhersagbarkeit von Niederschlag. Wir quantifizierten das Ausmaß, mit dem Vögel der tropischen Savanne ihre Brutaktivität um vorhersagbare Perioden mit erhöhter Ressourcenverfügbarkeit, welche mit Regen zusammenfallen, konzentrieren. Um zu untersuchen, in welchem Ausmaß es saisonale Höhepunkte in der Brutaktivität gab, analysierten

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wir einen Datensatz von 25 Arten kleiner Savannenvögel, welche über einen Zeitraum von zehn Jahren in Nigeria, West Afrika, gefangen wurden, hinsichtlich des Anteils Adulter mit Brutfleck und/oder des Anteils Juveniler zu Adulten. Wir fanden, dass zwei Drittel aller Arten zu jeder Jahreszeit brüteten (68 %), die Mehrheit allerdings klare saisonale Höhepunkte in der Brutaktivität aufwies (96 %). Mehr als die Hälfte der Arten zeigte eine zeitliche Varianz in der Brutzeit zwischen den Jahren (60 %). Granivore Arten brüteten später als insektivore und frugivore Arten, was möglicherweise eine Synchronisierung mit dem Höhepunkt der Verfügbarkeit der jeweiligen Nahrung widerspiegelt. Generell wird deutlich, dass die Brutaktivität klare saisonale Höhepunkte aufweist (Brutzeiten) und dass dies sehr wahrscheinlich eine Antwort auf sich ändernde Ressourcenverfügbarkeit ist, welche durch saisonalen Niederschlag hervorgerufen wird. Wir demonstrieren weiterhin die potentielle Möglichkeit, Brutflecken zu verwenden, um in Datensätzen von mehreren Arten, die einen langen Zeitraum umfassen, nach Mustern in der Brutaktivität zu suchen.

Introduction

Breeding is the most costly life history activity, with energetic expenditure peaking while parents are rearing nestlings (e.g. Bryant 1988; Nilsson and Råberg 2001). Animals reduce the costs of reproduction by timing their breeding around periods of increased resource availability (Martin 1987; Bennett and Owens 2002), thereby ensuring maximum reproductive output for each breeding attempt by synchronising the production of young with seasonal peaks of resource abundance to enable rapid growth and to increase juvenile survival (e.g. Perrins 1970). Adult survival during breeding is also maximised because breeding is only initiated when there is an expectation of sufficient food availability for females during egg formation (e.g. Nager et al. 1997) without there being a significant risk of starvation to the female (Perrins 1970; Martin 1987).

In many tropical environments, variation in the timing of breeding in time and space is dependent on both the amplitude of the rains and their regularity (Wingfield et al. 1992; Komdeur 1996; Moore et al. 2005). In those environments where the dry period is less pronounced, clear breeding seasons may be absent (Voous 1950), and there is a greater diversity across species in the timing of peak breeding (e.g. Thomson 1950; Brown and Britton 1980). A study conducted in Limonochocha National Biological Nature Reserve in equatorial Ecuador, for example, where rainfall and temperature remain relatively constant, found that 26 species of antbirds (Formicariidae) displayed almost no breeding seasonality (Tallman and Tallman 1997). However, most tropical environments are distinctly seasonal in terms of rainfall and, correspondingly, the timing and length of the breeding season may be both species- and population-specific (Komdeur 1996; Hau et al. 2000; Moore et al. 2005; Wikelski et al. 2003).

Seasonal rainfall drives fluctuations in food availability, which is a key factor for many species in determining annual fecundity, number of broods and the time taken between renesting attempts (Martin 1987, 1995; Konig and Gwinner 1995; Komdeur 1996). In almost all tropical habitats food availability across the breeding season fluctuates in relation to rainfall (e.g. Janzen 1973; Wolda 1978; Poulin et al. 1992; Mulwa et al. 2012); thus, with seasonally predictable rainfall patterns we expect to see predictable periods of increased food availability. Therefore, although there is an extended season when birds can possibly breed (and many tropical species may be capable of breeding for much of the year; e.g. Franklin et al. 1999), a predictable period of increased food availability and subsequently higher juvenile survival means that there will be a strong selective pressure to breed during these periods. How a bird experiences seasonality will depend on the response of its foraging niche to variation in rainfall. The high degree of niche specialisation in the tropics thus leads to a diverse variety of breeding strategies, with the timing and predictability of seasonal fluctuations in food availability appearing to be the driving force determining the timing of breeding in most species (Poulin et al. 1992, 1993; Komdeur 1996; Moore et al. 2005; Hau et al. 2008). However, other factors, such as nest predation (e.g. Morton 1971), climate (e.g. Tye 1991) or juvenile survival during post-natal dispersion (Young 1994), might also be important in determining when to be species and population specific and dependent on environmental conditions at the site (Moore et al. 2005). Where there is not a season of particularly high starvation risk, individual pairs may initiate breeding outside of the main breeding season, thus giving a false impression of year-round reproduction at the species level (Miller 1965; Wingfield et al. 1997), even though most individuals of the species may breed during a defined season. This season may vary, however, with different feeding guilds, such as insectivores timing their breeding to coincide with the insect peak of the early rains and granivores with the seed peak at the end of the rains (Poulin et al. 1992).

There has been a lot of interest in the breeding seasons of species in humid tropical forests (e.g. Fogden 1972; Wikelski et al. 2000) in East Africa. However, there have been no quantitative across-species studies in West Africa, where the presence of a single, predictable wet season may mean that birds are more constrained in when they can breed. Ideally, a study would follow a species at an individual level, tracking a large number of colour-ringed individuals and recording breeding success, number of broods, time taken between nesting attempts and survival of fledged juveniles (e.g. Grzybowski et al. 2005; Nesbitt Styrsky and Brawn 2011). Unfortunately, this is not practical in a multispecies study in most tropical environments, where population densities are often low, nests are hard to find, and individuals are difficult to track. We therefore used temporal changes in two breeding indicators, namely, the proportion of adults with brood patches and changes in juvenile-to-adult ratios within a population, to quantify the degree to which there are specific periods of increased breeding costs, which occur during egg laying, incubation and chick provisioning. This may provide insights into how seasonality affects the timing and length of the breeding seasons in a strongly seasonal savannah environment in West Africa. We used these indices to test two specific hypotheses: (1) that species will show a distinct seasonal peak in breeding activity even though individuals of most species can potentially nest throughout the year; (2) that seasonal peaks are coincident with predicted peaks in food availability so that timing of breeding will depend on the feeding guild.

Methods

We estimated the seasonality of breeding in small tropical birds in the Amurum Community Forest Reserve, working out of the A.P. Leventis Ornithological Research Institute (APLORI), Jos, Nigeria. This forest reserve is situated on the Jos Plateau (09°55′N, 08°53′E), in the centre of the Guinea savannah forest zone, which is characterised by very strong seasonality due to a single rainy season. The Reserve consists of 120 ha of four main habitat types: degraded guinea savannah woodland, gallery forest, rocky outcrops (inselbergs) and farmland. Much of the land surrounding the reserve has been degraded by anthropogenic pressures. In West African savannahs, the seasons are divided into a distinct wet and dry season. Daily rainfall summaries between January 2002 and November 2011 were obtained from Jos Airport (09°52′N, 08°53′E), located in the centre of Jos Plateau and 26 km from the Amurum Forest Reserve. In Amurum, the rainy season lasts for approximately 6 months—from 10 April ± 9 days to 13 October ± 11 days during the period 2001–2011. During this period, there was an annual rainfall of 1,337 ± 159 mm, 97.4 % of which fell within the wet season, with the heaviest rainfall occurring in August (290 ± 28 mm). The maximum temperatures in this area range from between 20–25 °C (<10 °C in extreme cases) during the coldest months rising to 30–35 °C at the end of the dry season. Amurum is located 1,270 m a.s.l., with a daylength that varies annually by 68 min.

During the study period, we caught 9,228 individuals of 25 species (Table 1). To avoid under-representation of adult birds breeding over several years, we retained individuals retrapped in different years in the analysis, yielding 2,280 records of 25 species. Birds were trapped using mist nets between January 2002 and November 2011. Trapping occurred year-round but was concentrated as a constant effort site (CES) ringing scheme in Amurum for two 14-day periods annually–at the end of the dry season (March–April) and at the end of the wet season (September–October), respectively. During the CES ringing, 272 m of four shelf nets was used between 0600 and 1030 hours (although there were few captures after 0930 h). Where possible, birds were aged and sexed. Species were assigned to feeding guilds (Fry et al. 1992–2004). This methodology was repeated outside of the CES ringing scheme, with the exception that netting occurred opportunistically throughout the year, and there was variation in the number of net metres used. However, the overall annual netting effort was approximately the same as a single CES ringing scheme.

Determination of variables

The presence of brood patches and of juveniles was used to identify timing of breeding periods. The assessment of brood patches was made using a six-stage scoring system: 0 (no brood patch); 1 (patch forming; defeathering process has begun); 2 (breast and belly fully de-feathered, some wrinkling of skin evident and signs of oedema); 3 (skin of belly opaque and engorged, broad swollen wrinkles); 4 (skin shows thin wrinkles, no longer engorged); 5 (refeathering; Redfern 2008). It was assumed that tropical species show a similar progression of brood patch development as temperate species. Stages 2–4 generally occur during the period of incubation and brooding (Bailey 1952; Hinde 1962; Jones 1971); however, a bird is also breeding at stages 1 and 5 (Redfern 2010). We therefore included all stages as an indication of breeding. To standardise across species where sexes could and could not be distinguished in the hand, all birds with brood patches were included in analyses irrespective of sex since males of a number of species included here are also known to incubate (e.g. Fry et al. 2004). We only included species for which there were more than ten adults with brood patches.

Trapped birds were aged as juvenile if they had a complete juvenile plumage containing no adult feathers; immature, if they had a mixture of juvenile and adult feathers, or had moulted into their sub-adult plumage (e.g. the African thrush *Turdus pelios*); adult, if birds no longer retained any juvenile feathers and as such were considered to be capable of breeding. Juvenile feathers were identified by feather shape and structure, as feathers tend to be weaker and looser than following generations of feathers (Svensson

Table 1 The seasonality of breeding in 25 species of savannah birds caught between 2002 and 2011 in West Africa

Species	Number of adults	Number of adults with brood patches	Number of juveniles	Brood patch: season	Brood patch: year	Brood patch: rain	Juvenile: season	Juvenile: year	Juvenile: rain	Season minimal breeding^a	Month maximal breeding^b	Breeding all seasons	Guild^c
COLIIFORMES													
Coliidae													
Speckled Mousebird *Colius striatus*	385	–	16	–	–	–	$<0.0001^d$	0.03	0.01	–	*E. June (12)*	No	F
CORACIIFORMES													
Meropidae													
Red-throated Bee-eater *Merops bulocki*	130	–	18	–	–	–	0.009	0.0009^d	0.02	–	*S. March (6)*	No	I
PICIFORMES													
Capitonidae													
Yellow-fronted Tinkerbird *Pogoniulus chrysoconus*	342	109	–	0.002^d	0.0004^d	0.05	–	–	–	2	S. August (16)	Yes	I
PASSERIFORMES													
Pycnonotidae													
Common Bulbul *Pycnonotus barbatus*	573	45	–				–	–	–	4	E. May (10)	Yes	I/F
Turdidae													
African Thrush *Turdus pelios*	508	18	22	0.03			$<0.0001^d$	$<0.0001^d$		1	S. August (16)		Yes
Muscicapidae													
Familiar Chat *Ceromela familiaris*	107	14	18	$<0.0001^d$	$<0.0001^d$		$<0.0001^d$	$<0.0001^d$		3/4	S. May (9)	Yes	I
Cisticolidae													
Grey-backed Camaroptera *Camaroptera brachyura*	293	35	14	0.0003^d			0.002^d			3	S. September (18)	Yes	I
Zosteropidae													
Yellow White-eye *Zosterops senegalensis*	271	64	–	0.01			–	–	–	1	E. September (19)	Yes	F
Nectariniidae													
Red-chested Sunbird *Chlcomitra senegalensis*	379	21	41	0.002^d			$<0.0001^d$		0.04	1	S. September (18)	Yes	N

Table 1 continued

Species	Number of adults	Number of adults with brood patches	Number of juveniles	Brood patch: season	Brood patch: year	Brood patch: rain	Juvenile: season	Juvenile: year	Juvenile: rain	Season minimal breeding^{a}	Month maximal breeding^{b}	Breeding all seasons	Guild^{c}
Variable Sunbird *Cinnyris venustus*	314	16	35	<0.0001^{d}	<0.0001^{d}	0.0005^{d}				2	S. September (18)	Yes	N
Green-headed Sunbird *Cyanomitra verticalis*	178	14		0.003^{d}	0.0001^{d}	0.0003^{d}	–	–	–	1	S. September (17)	Yes	N
Malaconotidae													
Black-crowned Tchagra *Tchagra senegalus*	82	18	–	0.0001^{d}	<0.0001^{d}		–	–	–	1	S. September (17)	Yes	I
Ploceidae													
Village Weaver *Ploceus cucullatus*	601	66	73	<0.0001^{d}			<0.0001^{d}	<0.0001^{d}	0.004^{d}	1	E. October (21)	Yes	G
Little Weaver *Ploceus luteolus*	120	11	13	<0.0001^{d}	<0.0001^{d}		0.002^{d}	<0.0001^{d}		½	S. November (22)	Yes	G
Black-necked Weaver *Ploceus nigricollis*	222	–	16	–	–	–	0.001^{d}			–	*E. October (21)*	Yes	G
Vitelline Masked Weaver *Ploceus vitellinus*	242	42	47	<0.0001^{d}	0.0002^{d}		0.0006^{d}	0.03	0.03	1	E. October (21)	Yes	G
Northern Red Bishop *Euplectes franciscanus*	2045	515	369	0.0002^{d}			<0.0001^{d}	<0.0001^{d}		1	S. December (24)	No	G
Estrildidae													
Lavender Waxbill *Estrilda caerulescens*	668	61	23	<0.0001^{d}	0.0004^{d}	0.05	<0.0001^{d}			2	E. September (18)	Yes	G
Red-cheeked Cordon-bleu *Uraeginthus bengalus*	739	168	32	<0.0001^{d}	0.003^{d}		<0.0001^{d}	0.002^{d}		1	E. November (23)	Yes	G
Black-bellied Firefinch *Lagonosticta rara*	92	21	–	<0.0001^{d}	0.003^{d}	0.05	–	–	–	1	S. December (25)	Yes	G
Bar-breasted Firefinch *L. rufopicta*	98	25	–	<0.0001^{d}	<0.0001^{d}		–	–	–	2	S. December(24)	No	G
Rock Firefinch *L. sanguinodorsalis*	541	71	49	<0.0001^{d}			<0.0001^{d}	<0.0001^{d}		1	E. December (26)	Yes	G
Red-billed Firefinch *L. senegala*	655	150	50	0.0002^{d}	<0.0001^{d}					2	S. December (24)	Yes	G

Table 1 continued

Species	Number of adults	Number of adults with brood patches	Number of juveniles	Brood patch: season	Brood patch: year	Brood patch: rain	Juvenile: season	Juvenile: year	Juvenile: rain	Season minimal breeding[a]	Month maximal breeding[b]	Breeding all seasons	Guild[c]
Bronze Mannikin *Lonchura cucullatus*	609	49	145	<0.0006[d]			<0.0001[d]			1	S. October (20)	Yes	G
Emberizidae													
Cinnamon-breasted Rock-bunting *Emberiza tahapisi*	315	31	18	<0.0001[d]	<0.0001[d]					2/3	E. November (23)	Yes	G

General linear models for each species were used to test the effect of season, year and variation in rainfall on two response variables, namely, the proportion of adults caught with brood patches and/or the proportion of juveniles to adults. Pooling data across years for each species, we show the season with the lowest proportion of adults with brood patches (Season minimal breeding) and the approximate start (S.) or end (E.) of the month which best fits the 2-week period of the highest breeding activity (also numbered 1–26). From the literature we identified a species' feeding guild

[a] The season which showed the lowest breeding activity, calculated from the proportional brood patch data: 1 = end of dry season, 2 = start of wet season, 3 = end of wet season, 4 = start of dry season

[b] The start (S.) or end (E.) of the month which showed the highest annual breeding activity. Where possible this was calculated from the proportional brood patch data. Where BP data was insufficient we subtracted 1 month from peak juvenile abundance (italics)

[c] F, frugivorous; G, granivorous; I, insectivorous; N, nectivorous

[d] Predictor variable was significant after sequential Bonferroni correction (Rice 1989)

1992). Ringing has been conducted in the reserve since 2001, and species can usually be reliably aged from plumage characteristics; birds of uncertain ages were excluded from the analysis. After fledging, birds only maintain their juvenile plumage for a short period before they undergo post-juvenile moult. Therefore, if a bird is caught with juvenile plumage it is possible to *estimate* the number of days since fledging and subsequently when it hatched. Most species of northern temperate passerines undergo post-juvenile moult between 3 and 8 weeks after leaving the nest (e.g. Jenni and Winkler 1994), and tropical passerines may follow a similar timeframe (Franklin et al. 1999; Jones et al. 2002). If the mean fledging period for tropical passerine species is approximately 16.8 days (standard error ± 0.37; $n = 204$; derived from data in Byers et al. 1995; Feare et al. 1998; Cheke et al. 2001), then we can estimate when the chick hatched. Large confidence limits linked to the uncertainty of our estimate of individual variation in the timing of post-juvenile moult should be considered against the low temporal resolution of the study (i.e. 3-month seasons; see below). Across the 15 species for which sufficient data were available, the period between peak juvenile abundance and the peak presence of brood patches correlated with the estimate of the number of days between presence of juveniles and hatching dates (see below). Therefore, we assumed that the presence of juveniles could be used as an estimate of the timing of breeding in adult birds. Immature birds were assumed not be to actively breeding and so were excluded from the analysis. Only species for which there were records for more than ten juveniles were included in the analysis.

Statistical analysis

In total we identified 1,594 individuals with brood patches and 999 juveniles. We assumed that the peak timing of breeding for the adults coincided with peak brood patch abundance and used brood patch data within the same species to then determine how peak juvenile abundance related to the timing of peak breeding. For each of the 15 species we modelled how the response variable varied across 26 two-week periods, commencing on 1 January, included as a factor. The response variable was the relative proportion of birds with brood patches or of juveniles to the total number of adult birds caught. This variable was included in the model as the real relative frequency of adult birds with brood patches, or of juveniles, to the number of adult birds without brood patches, or adults. We used the cbind command in the R (ver. 2.14.0) statistical environment ® Development Core Team 2011) to do the statistics and the lme4 package (Bates and Maechler 2010).

The 2 weeks of peak breeding was then calculated from the parameter estimates. For each species we estimated the number of days between peak presence of brood patches and peak juvenile abundance, before averaging across species to estimate a lag of 35 ± 17 days. The presence of juveniles in catches was therefore considered to be a suitable method of identifying breeding periods. We subsequently used this estimate to calculate peak breeding for the three species where there was insufficient brood patch data (Table 1). However, where both measures were available, the presence of brood patches was considered to be a more precise measure of breeding and was used over the presence of juveniles.

We categorised the year into four seasons of distinctly different resource availability correlated to the approximate start and finish of the rains: end of dry season (10 January–9 April); start of wet season (10 April–9 July); end of wet season (10 July–9 October); start of dry season (10 October–9 January). We estimated variation in seasonal rainfall as a covariate by dividing the actual rainfall (mm) for a season within year by the average rainfall (millimetre) for that season across years: thus, a value of >1 indicated a season in which rainfall was above the seasonal average.

We tested for variation in seasonal breeding across species by building a generalized linear mixed model (GLMM) with a binomial error structure and with species as a random factor. We modelled how the response variable (proportion of adults with brood patches (across 22 species) or proportion of juveniles to adults (across 18 species), constructed with the cbind command in R, varied seasonally and annually or was affected by variation in rainfall. We justify the validity of fixed effects models across species because the variance absorbed by the random effect was relatively small (Table 2), allowing us to rerun each model as a GLM (i.e. without the random effect). We compensated for overdispersion in the GLM by fitting an empirical scale parameter. However, this suggested that the GLMM may also be overdispersed, which was compensated for by including a random effect for each species/season combination. This allowed for an additional variance component within species at the level of the linear predictor. As the GLM and GLMM provided consistent estimates for the effects of each predictor variable, we present the results of the GLMM (Table 2).

For each species we modelled the occurrence of seasonal breeding by building a GLM with a pseudo-binomial error structure, logit link function and empirical scale parameter. We tested the statistical significance of season, year and variation in seasonal rainfall on our response variables by dropping each from the full model and applying a likelihood ratio test (Table 1). We corrected for multiple tests using sequential Bonferroni correction (Rice 1989). For each species and season we calculated the proportion of adults with brood patches or juveniles to adults predicted by the model by back-transforming the parameter estimates. We used a stepwise model as opposed to an Akaike Information Criteria (AIC) approach to specifically test for the effect of predictor and confounding variables on the response variable. We provided further support for our model by excluding the predictor variable season and rerunning the model before comparing AIC values. Across all species we found that the model was significantly improved by including season.

Table 2 Estimates from mixed effects models testing seasonal variation in the occurrence of brood patches across 22 species (brood patch; no brood patch) and juveniles across 19 species (juveniles; adults), both as a proxy for breeding, while controlling for possible year effects and inter-annual variation in rainfall (included in the models below but parameter estimates not shown)

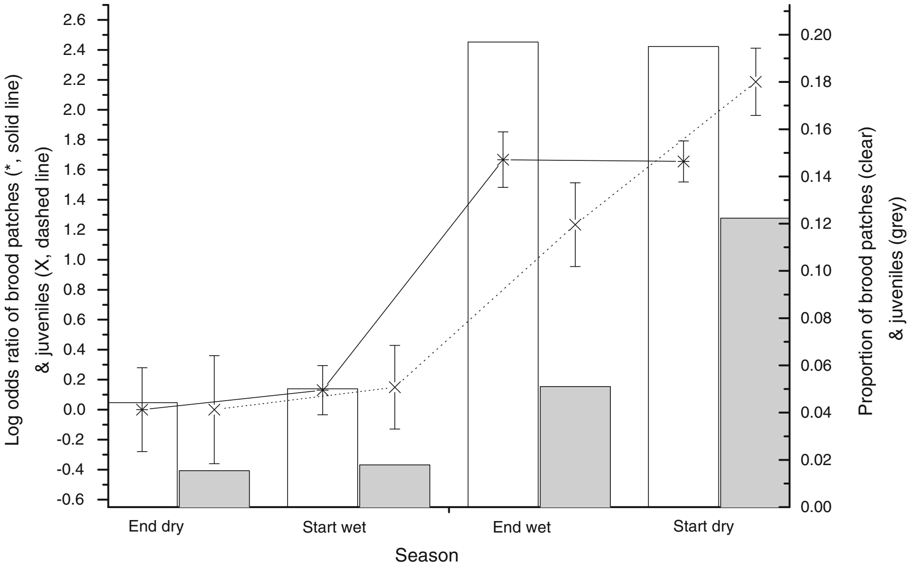
Mixed effects models	Estimate	Standard error	*Z* value	*P*
Brood patch				
Intercept	−3.30	0.28	−11.6	<0.0001
Start wet	0.13	0.16	0.8	0.4
End wet	1.67	0.18	9.0	<0.0001
Start dry	1.65	0.14	12.0	<0.0001
Species	Variance 0.45	SE 0.67		
Random	Variance 0.55	SE 0.74		
Juveniles				
Intercept	−3.29	0.36	−9.1	<0.0001
Start wet	0.15	0.28	0.5	0.6
End wet	1.23	0.28	4.4	<0.0001
Start dry	2.19	0.22	9.7	<0.0001
Species	Variance 0.25	SE 0.50		
Random	Variance 1.65	SE 1.29		

For each species we calculated the 2-week period of peak breeding (as above), either from the 2 weeks with the highest proportion of brood patches or the 2 weeks with the highest proportion of juveniles minus the mean lag period between peak juveniles and peak brood patches (37 days). We built a linear model to test whether the 2 weeks of peak breeding (included as a continuous variable) varied by feeding guild across species.

Results

There was strong evidence for the seasonality of breeding *across* savannah species. Mixed effect models testing for the effect of season, while controlling for the possible confounding effects of year and variation in rainfall, on the proportion of brood patches (across 22 species) or juveniles (across 18 species) showed that across species there was a

Fig. 1 Average seasonal timing of breeding. Log odds ratios (as a measure of the effect size and non-independence of the two binary response variables) and proportions of adult birds caught with brood patches (across 22 species) and juveniles to adults (across 18 species)



seasonal effect (Table 2). Most species showed reduced breeding towards the end of the dry season before increasing breeding after the onset of the rains (Fig. 1).

There was strong evidence for the seasonality of breeding *within* most savannah species. Of the 22 species for which there were sufficient numbers of adults with brood patches caught, we found seasonal variation in 21 (95 %) species (Tables 1, 3). Only the Common Bulbul *Pycnonotus barbatus* showed no significant evidence of seasonal breeding (Fig. 2a). All three species for which sufficient brood patch data were lacking showed significant seasonal variation in the proportion of juveniles (Table 1). Of the 15 species for which there were sufficient data, 12 (80 %) showed seasonal variation in both juveniles and brood patches (Table 1).

Overall (using the presence of brood patches, or in the case of insufficient data for these, the presence of juveniles), 24 species (96 %) varied their timing of peak breeding within any 1 year [20 species (80 %) significantly after sequential Bonferroni correction and 4 marginally significant species (16 %); Table 1]. Fifteen species (60 %) also varied their timing of peak breeding across years [12 species (48 %) significantly after sequential Bonferroni correction and 3 marginally significant species (12 %); Table 1]. Seasonal variation in rainfall only affected breeding in seven species [28 %; 1 species (4 %) significantly after sequential Bonferroni correction and 6 species (24 %) marginally; Table 1). We found evidence of breeding in all seasons in 20 species (80 %; Tables 1, 3).

The timing of peak breeding across species was variable, with there being a strong interaction between season and species in the 21 species which showed seasonal variation in the proportion of brood patches (season × species added to model in Table 2, $df = 69$, deviance = 1,026, $P < 0.0001$) and the 15 species which showed seasonal variation in the proportion of juveniles (season × species added to model in Table 2, $df = 51$, deviance = 1,049, $P < 0.0001$). A minimum of one species showed a peak of breeding in each season [Table 3; compare *Tchagra senegalus* (Fig. 2b) with *Lonchura cucllatus* (Fig. 2c, d) that shows intra-annual variation in rainfall]. Annual variation in seasonal rainfall was not found to influence breeding across species in the proportion of birds with brood patches ($df = 1$, deviance = 999, $P = 0.1$), but it did influence the proportion of juveniles to adults ($df = 1$, deviance = 678, $P = 0.006$). This result suggests that in a tropical environment such as our study site where rainfall is predictable across years, most species may time their breeding independent of annual environmental variation; seasonal rainfall, however, may influence productivity and juvenile survival. At an increased temporal resolution, the 14-day period of peak breeding varied by feeding guild ($F_{3,22} = 8.5$, $P < 0.001$), with granivores breeding later in the year than insectivorous and frugivorous species (Table 4; Fig. 3).

Discussion

Our study tested for seasonality in breeding in a large dataset and showed that although two-thirds of species (68 %) in the savannah environment of West Africa were capable of breeding in all four seasons, most species (96 %) showed distinct seasonal peaks in breeding activity which was coincident with predictable seasonal rainfall and dependent on feeding guild.

Methodological considerations

Modelling seasonal breeding at a population level through the use of a breeding indicator, such as the presence of

Table 3 The proportion of adults with brood patches and/or the proportion of juveniles to adults caught per season in 25 species of West African savannah bird

Species	Percentage of adults with brood patches				% Juveniles			
	End dry season	Start wet season	End wet season	Start dry season	End dry season	Start wet season	End wet season	Start dry season
Colius striatus	–	–	–	–	0.0	7.0	6.7	2.8
Merops bulocki	–	–	–	–	23.8	19.8	0.0	0.0
Pogoniulus chrysoconus	25.1	22.9	46.6	42.9	–	–	–	–
Pycnonotus barbatus[a]	7.3	12.4	9.5	5.1	–	–	–	–
Turdus pelios	1.4	4.8	12.1	4.9	0.0	2.3	22.6	8.8
Cercomela familiaris	12.3	16.4	0.0	0.0	1.8	22.6	22.5	23.2
Camaroptera brachyuran[b]	3.4	8.8	3.3	21.8	0.7	0.3	10.0	21.8
Zosterops senegalensis	12.2	30.3	58.2	25.7	–	–	–	–
Chalcomitra senegalensis[b]	2.2	5.7	22	3.0	4.2	4.5	19.1	27.2
Cinnyris venustus	8.3	0.0	2.3	10.7	13.7	6.5	12.7	9.0
Cyanomitra verticalis	2.0	3.9	9.9	7.5	–	–	–	–
Tchagra senegalus	6.0	24.9	46.4	19.9	–	–	–	–
Ploceus cucullatus[b]	0.8	7.9	17.7	20.5	0.9	5.0	11.4	20.9
Ploceus luteolus	0.0	0.0	13.5	18.5	2.4	5.3	5.2	13.1
Ploceus nigricollis	–	–	–	–	3.2	6.3	25.6	37
Ploceus vitellinus[b]	15.4	6.0	5.7	18.1	4.7	2.0	14	22.5
Euplectes franciscanus	0.0	1.3	49.0	33.0	0.0	0.0	1.2	18.9
Estrilda caerulescens[b]	6.1	2.6	25.4	27.4	2.6	0.5	6.1	12.6
Uraeginthus bengalus	2.1	7.3	19.5	39.1	1.8	0.0	0.0	9.6
Lagonosticta rara	6.2	11.6	75.0	47.5	–	–	–	–
Lagonosticta rufopicta	20.8	0.0	29.7	33.8	–	–	–	–
Lagonosticta sanguinodorsalis	11.2	9.0	25.4	36.4	3.6	0.0	1.0	15.9
Lagonosticta senegala[b]	22.4	9.1	26.7	32.6	9.9	10.8	2.7	5.9
Lonchura cucullatus[b]	3.5	10.1	19.6	23.9	0.9	0.6	16.1	53.7
Emberiza tahapisi	9.7	0.0	0.0	20.9	7.0	2.1	0.0	4.7

The data were pooled by season between 2002 and 2011

[a] The only non-seasonal breeder

[b] Species which both incubated eggs and successfully fledged chicks in all four seasons

brood patches or juveniles, appears to provide a robust method of using existing ringing datasets to investigate patterns of breeding across species. Identification of either a brood patch or a juvenile in the hand is a straightforward field technique for estimating the most costly stage of breeding for parent birds (Walsberg and King 1978; Redfern 2010). Although the presence of a brood patch may not be a reliable indicator of breeding in some bird guilds (Tranquilla et al. 2003), in small passerine birds the different stages of brood patch development has been closely linked to breeding stages (Redfern 2008, 2010), such as nest building (brood patch score 1), egg production and incubation (brood patch score 3) or parental care (brood patch score 4 and 5; Hinde 1962; Jones 1971). However, there are limitations to the resolution in breeding activities which can be inferred from using brood patches as a breeding indicator, as the stage of brood patch development may vary relative to actual egg production (Hinde 1962; Zann and Rossetto 1991) and the extent of brood patch formation in males may vary (Zann and Rossetto 1991). Further work is needed to determine the extent of individual variation, both within and across species and guilds, in the development of brood patches in relation to stages of breeding.

We found that three species (*Cinnyris venustus*, *Lagonosticta sanguinodorsalis*, *Emberiza tahapisi*) showed seasonal variation in the proportion of brood patches but not in the proportion of juveniles (Table 1). This result

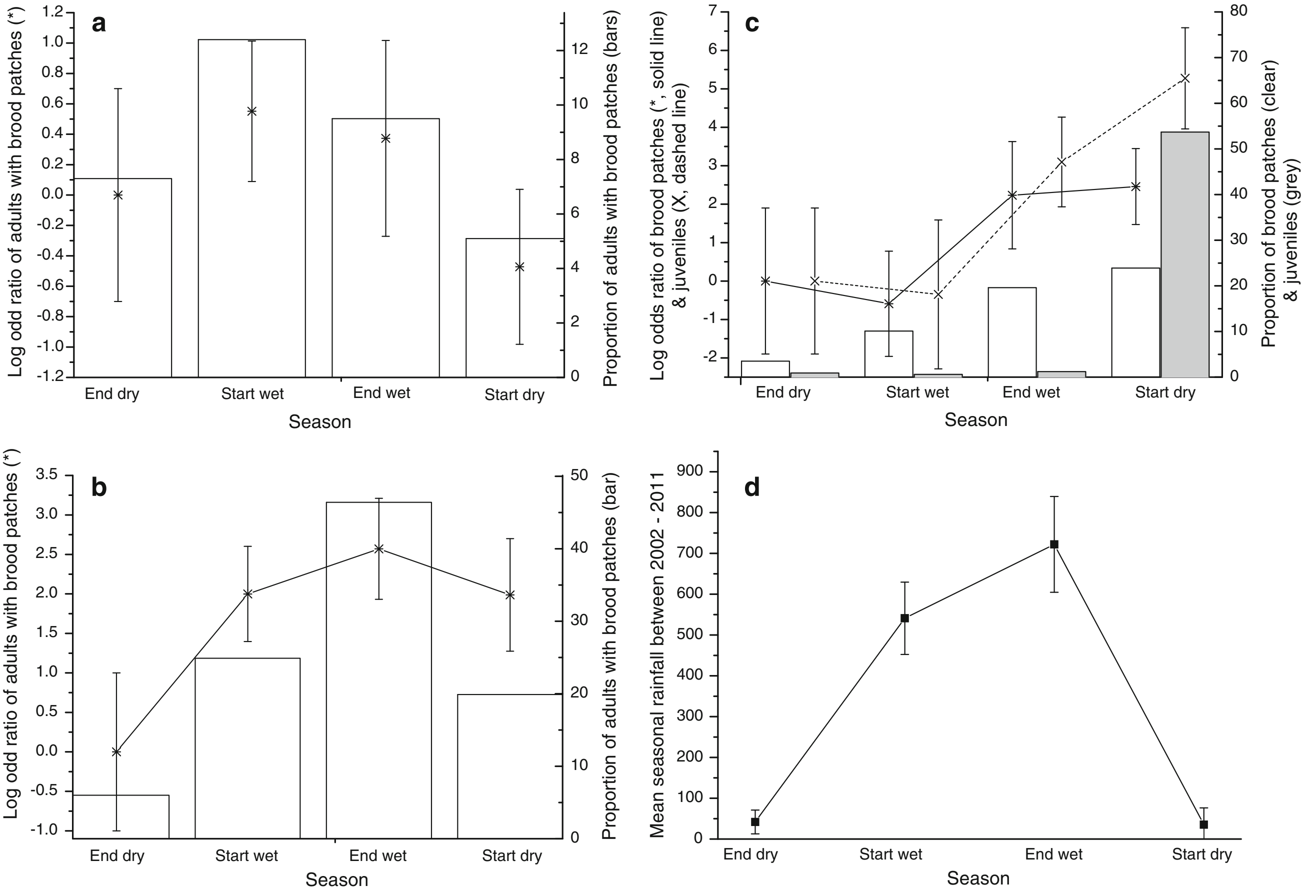


Fig. 2 Examples of seasonal timing of breeding for individual species. Log odds ratios (as a measure of the effect size and non-independence of the two binary response variables) and proportions of adult birds caught with brood patches and/or juveniles to adults in three case study species: a species showing no significant seasonal peak in brood patch abundance (*Pycnonotus barbatus*; **a**); a species which showed a peak in brood patch abundance at the end of the wet season (*Tchagra senegalus*; **b**); a species which showed a peak in brood patch abundance at the start of the dry season (*Lonchura cucullatus*; **c**). Mean seasonal rainfall (2002–2011; **d**) is also shown to demonstrate the general driver of these patterns

Table 4 A general linear model of how the 2-week period of peak breeding activity varied by feeding guild across 25 species of West African Savannah species

Guild	Estimate	Error	t	P
Intercept (frugivore)	15.7	2.2	7.2	<0.0001*
Granivore	7.0	2.4	2.9	0.009*
Insectivore	−1.5	2.6	−0.6	0.6
Nectivore	2.0	3.1	0.6	0.5
Adjusted R^2	0.49			

* Significant at $P < 0.5$

suggests that the proportion of juveniles as a breeding indicator may be confounded by seasonal variation both within and across species by factors such as the number of days before commencing post-juvenile moult (Ginn and Melville 1983) and variation in clutch size (Ludvig et al. 1995). Therefore, where possible, the proportion of adults with brood patches was used over the proportional presence of juveniles. However, despite these potentially confounding factors we found a strong correlation between our breeding indicators. There was a reasonably consistent lag (37 ± 17 days) between the peak abundance of adults with brood patches and the peak presence of juveniles; therefore, we consider that the presence of juveniles is likely to be a reliable indicator of peak breeding activities for the three species (*Cloius striatus*, *Merops bulocki*, *Ploceus nigricollus*) where there was insufficient brood patch data. Clearly it is better to use brood patch data whenever possible but, on average, juvenile ratio data is also likely to indicate seasonality of breeding at a population level at a seasonal temporal scale.

Average seasonality of breeding

Almost three-quarters of species (16 of the 22 species for which sufficient brood patch data were available) showed evidence of incubating eggs in all four seasons, while seven of these species (out of the 10 for which data were available) also managed to successfully fledge chicks in all seasons, indicating that breeding is possible outside of the main breeding season. Aside from the possible density-dependent advantages of breeding out of season, such as reduced competition, selection should favour breeding during peak food availability. Therefore, we suggest that individuals which breed out of season may be doing so opportunistically, capitalising on localised increases in food availability. The common occurrence of a few individuals breeding outside the main season means that studies with small sample sizes, or accounts of a few nests found in any one time of year, should be treated with caution in terms of drawing conclusions on general seasonality (or aseasonality) of breeding in the tropics.

Most species showed a peak in breeding during the late wet and/or early dry season; however, it is important to point out that this finding only indicates what is happening *on average*. Although most species time their peak breeding to occur at the end of the rains, some species will specialise as dry season breeders: the lack of a season in which resources are constrained, such as winter in the Northern hemisphere, has allowed species to evolve to occupy a wide variety of niches. For example, the Familiar Chat *Cercomela familiaris* forages on ground-dwelling invertebrates, the abundance of which may not vary across the seasons (Poulin et al. 1992), and thus foraging may become more predictable at the end of the dry season due to a reduction in grass cover. At the higher temporal resolution of our 2-week sampling periods, the timing of peak breeding was dependent on feeding guild, with species probably synchronising their peak breeding season with their particular feeding niche. Insectivorous and frugivorous species showed peak breeding during the wet season, likely coinciding with the explosion in invertebrate numbers and peak fruit abundance, respectively (Poulin et al. 1992). In contrast, granivorous birds bred later with respect to rainfall, probably concentrating their breeding at the start of the dry season when the grain crop is at its peak (Fig. 3; Crowley and Garnett 1999). Specialised seed-eating finches may breed later than other guilds because they experience greater increased seasonality in their food availability, with seeds being negligible at the start of the rains, increasing to being in superabundance when seeds ripen and fall (Crowley and Garnett 1999; Brandt 2007). Carry-over effects from the wet season probably mean that foraging for invertebrates to feed chicks remains reasonably predictable into the dry season and that concomitantly seed availability becomes superabundant, thereby allowing parents to efficiently forage for themselves while providing for chicks. We also suggest that breeding may be favourable during this period for some species due to increased nest survival as a result of changes in grass cover (e.g. Hovick et al. 2012). Some species, such as the cinnamon-breasted Rock Bunting *Emberiza tahapisi*, which breeds largely in the dry season, may then trade-off these benefits with declining invertebrate availability.

Seasonal breeding in West African savannahs

The savannahs of West Africa act as a model system for understanding how the seasonality of resources affects synchrony in breeding across species. The reason for this is that although daylength and temperature remain relative constant across the year, the rains drive a single wet and single dry season, each of which is associated with distinctly different resource availability. Where rainfall is less constrained, such as in humid tropical forests or in East Africa, where there are two wet seasons, the seasonality of food availability is likely to be reduced because organisms experience a longer period when water is abundant, which tends to result in species which reproduce more slowly and, consequently, live longer. However, increased seasonality leads to a period of increased density-dependent mortality; therefore, there is more food available when species start to breed, which leads to larger clutch sizes and subsequently reduced survival (McNamara et al. 2008). We might therefore predict an increase in breeding synchrony (and clutch size) within and across species relative to regions where rainfall is less constrained because species respond to large peaks in food availability (Griebeler et al. 2010). However, although some species in our study displayed distinct breeding seasons, three-quarters of the species

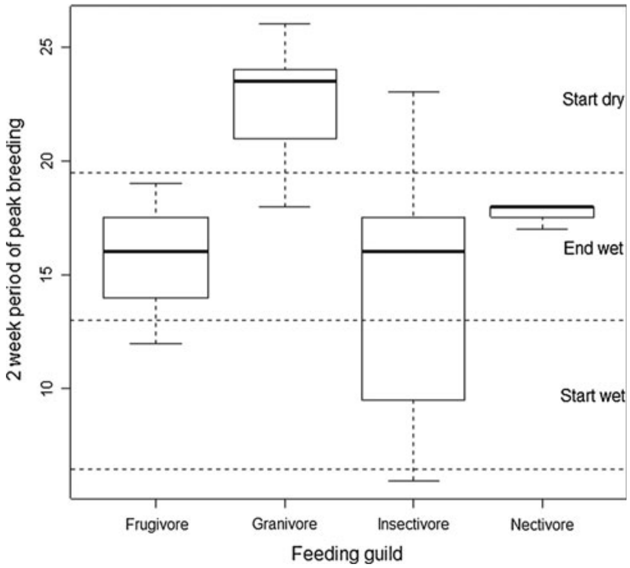


Fig. 3 Variation in peak breeding in 2-week periods and seasons (*dashed line*) by feeding guild in 25 species of small West African savannah birds. Week 1 begins on 1 January, continuing throughout the year

from all four feeding guilds initiated breeding in all four seasons, suggesting that despite relatively high seasonality, food availability for many species may not be constrained in any particular season.

The savannah communities of West Africa are dynamic, with species movements on many scales as populations follow seasonal variations in food availability (e.g. Elgood et al. 1973; McGregor 2005; Cresswell et al. 2009). Thus, an increase in the numbers of competitors and conspecifics at source habitats could result in the amount of food available per individual not increasing significantly. Therefore, the timing of breeding is likely to be more species, population and breeding pair specific, with individuals capitalising on local increases in food availability. As a consequence, birds are unable to support the larger clutch sizes found in seasonal environments, and instead clutch sizes in many species are more comparable to those of humid forest species (Fry et al. 1992–2004).

General conclusions

Overall, most species of West African savannah birds sampled in our study bred seasonally, the timing of which was dependent on feeding guild, which likely means it is related to peak food availability. However, small numbers of individuals of two-thirds of the species sampled were also able to incubate and successfully fledge young outside the main breeding season. The ability to breed throughout the year suggests that these birds are not exposed to a high risk of starvation in the non-breeding season. Nevertheless, the existence of a seasonal peak in food abundance will select for an apparent breeding season as individuals are selected to breed at the optimum time. Other constraints on timing of breeding may of course also select for a fixed breeding season, such as moult or migration. In addition, the correlation in peak timing between our breeding indicators provides support for the reliability of using brood patches to access the stages of breeding in small savannah birds.

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Ethical note Although the research work described here does not require any licences within Nigeria, all ringing was directly carried out and supervised by BTO (British Trust for Ornithology) C or A permit ringing licence holders (or European equivalent), to the standards required for ringing in the UK. All ringing activities were also approved in advance by the APLORI Scientific Committee which oversees research ethics at the sites using the Association for the Study of Animal Behaviour ethical guidelines. We thank two anonymous referees and the Editor for useful comments pertaining to the revision of our paper.

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