Weak breeding seasonality of a songbird in a seasonally arid tropical environment arises from individual flexibility and strongly seasonal moult

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In some tropical birds, breeding seasonality is weak at the population level, even where there are predictable seasonal peaks in environmental conditions. It therefore remains unclear whether individuals are adapted to breeding at specific times of the year or flexible to variable environmental conditions. We tested whether the relative year-round breeding activity of the Common Bulbul *Pycnonotus barbatus* arises due to within-individual variability in breeding dates. We collected data from 827 birds via mist-netting over 2 years with corresponding local weather data. We used a combination of climate envelope and generalized linear mixed models to explore how the timing of breeding is influenced by time of year, individual variation, rainfall and temperature in a West African savannah where seasonal precipitation determines annual variation in environmental conditions. We also pooled 65 breeding records from 19 individuals recorded between 2006 and 2017 based on brood patch occurrence and behavioural observation to compare within-individual and population variability in breeding dates. We show that the breeding dates of individuals may be as variable as for the population as a whole. However, we observed a seasonal peak in juvenile occurrence that varies significantly between years. Models suggest no relationship between nesting and moult, and within-year variation in rainfall and temperature, and birds were unlikely to breed during moult but may do so afterwards. Moult was very seasonal, correlating strongly with day length. We suggest that because environmental conditions permit year-round breeding, and because reproductive output is subject to high predation risk, there is probably a weak selection for individuals to match breeding with variable peak conditions in the environment. Instead, moult, which always occurs annually and successfully, is probably under strong selection to match variable peak conditions in the environment so that long-term survival ensures future reproduction.

Keywords: Afro tropics, annual cycle, birds, food availability, life history evolution, phenology, rainfall, temperature, timing.

Optimal fitness outcomes require organisms to match sequences of annual cycle events to the most suitable environmental conditions (Ricklefs & Wikelski 2002, Reed *et al.* 2009). This may involve control of annual cycle stages by internal biological 'clocks', periodic environmental signals such as day length, and locally variable signals such as rainfall, temperature and food availability (Wingfield 2008, Visser *et al.* 2010, Helm *et al.* 2013). An individual's ability to assess and determine immediate conditions may also be important for a decision to initiate annual cycle stages, and this may depend on the predictability of its environment (Lisovski *et al.* 2017), individual experience and the degree of

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environmental limitation on initiation of such stages (Perrins 1970, Hahn 1998, Tieleman & Williams 2005, Fontaine & Martin 2006, Pimentel & Nilsson 2007, Tökölyi *et al.* 2012).

Timing of breeding is a crucial component of the annual cycle of relatively short-lived organisms but may be less important for long-lived species where fitness may depend more on survival than on annual reproduction. Early ornithological observations outside temperate systems suggested that both the degree of seasonal limitation to the occurrence of breeding and the relative contribution of annual reproduction to overall fitness are low in tropical birds and this was largely attributed to milder food seasonality and high nest predation (Lack 1950a,b, Moreau 1950, Skutch 1950, Thomson 1950, Voous 1950, Ashmole 1963a, Cody 1966). More recent studies (Dittami & Gwinner 1985, Tye 1992, Oschadleus & Underhill 2006, Greeney 2010, Reynolds *et al.* 2014), however, have revealed that breeding strategies are diverse and closely related to species niche, albeit with exceptions such as Ndithia *et al.* (2017) who found no relationship between timing of breeding, invertebrate abundance and weather variables in equatorial larks. Birds in equatorial regions with small variation in day length have sometimes been shown to respond to this minimal environmental variability (Wikelski *et al.* 2000, Quispe *et al.* 2017, Shaw 2017), so year-round breeding at the population level may not necessarily equate to an absence of breeding seasonality due to weak environmental seasonality.

Breeding seasonality is a function of individual flexibility and environmental constraints. However, the strong correlation between breeding and environmental variables in temperate systems limits the appreciation of individual variability as a possible determinant of breeding seasonality, and results in a focus on factors such as food availability and offspring survival (Lack 1948, Ashmole 1963b, Skutch 1967, Lloyd 1999). In environments where birds have multiple breeding opportunities but experience stochastic nest survival, enhancing adult survival via adequate self-maintenance may be a crucial fitness determinant (Williams 1966, Nilsson & Svensson 1996). Such considerations may explain links between age-related survival, future reproduction, environmental seasonality and iteroparity (Schaffer 1974). The need to enhance adult survival could lead to the prioritization of moult over reproduction in adult birds when moult timing is crucial (Stiles & Wolf 1974),

because an unsuccessful moult may have immediate survival consequences for an individual but failure to breed successfully may not be as costly if there are opportunities to breed in the future. Year-round breeding tropical birds may help us better understand how the timing of annual cycle stages which vary differently within and among individuals interacts with environmental seasonality at the population level.

The Common Bulbul *Pycnonotus barbatus* is a long-lived, resident, tropical passerine that breeds non-seasonally in central Nigeria despite clearly seasonal precipitation (Keith *et al.* 2004, Cox *et al.* 2013). However, it is not known whether individual Bulbuls breed consistently at different times of the year or flexibly between years in different environmental conditions. It is also not clear how the timing of breeding events and moult interact in a single annual cycle under seasonal variation in precipitation. Residency and longevity of Common Bulbuls therefore permits repeat observations on individually marked birds at different times of year, thus allowing individual breeding patterns to be differentiated from population breeding patterns.

To test whether the breeding seasonality of Common Bulbul populations arises due to within-individual variability in breeding dates, we studied the annual cycle of the species in a seasonal West African savannah where a single period of annual precipitation improves foraging conditions in the wet season (Brandt & Cresswell 2008, Molokwu *et al.* 2008, Opoku 2017) and is likely to determine peak resources for breeding. We also consider the annual timing of moult, the other main annual life history event for adult resident birds, because this may also impose constraints on the timing of breeding (Siikamaki *et al.* 1994) or be the main focus for selection on seasonality. Specifically, we test whether: (1) the relative timing of breeding and moult in the Common Bulbul follows an annual pattern at the population level, (2) individuals breed flexibly as opposed to seasonally within and between years and (3) the occurrence of breeding and moult are affected by within-year variation in rainfall and temperature.

METHODS

Study site

The study was carried out in the Amurum Forest Reserve (09°52′N, 08°58′E), at the A.P. Leventis

Ornithological Research Institute (APLORI), on the Jos Plateau in Nigeria. The Amurum Forest Reserve is a heterogeneous woodland savannah habitat with inselbergs and riparian forests, surrounded by farmland and human settlements (Nwaogu & Cresswell 2015).

Daily rainfall and temperature data were made available from a weather station located at the APLORI and also from the Nigerian Meteorological Agency at Jos airport, located 26 km from APLORI. However, we used the data from the airport only for modelling the effect of rainfall and temperature on the timing of nesting and moult because there were gaps in data from our local weather station during February 2014 to January 2016; however, records from the two weather stations were strongly correlated (daily maximum temperature = 81%, daily minimum temperature = 74% and rainfall = 87%). We obtained sunset and sunrise data from the United States Navy Oceanography Portal http://aa.usno.navy.mil/data/ (USNO 2012), from which we calculated variation in day length across the year in our study area.

There is a single wet and dry season annually, and this influences food availability. Minor precipitation may be observed before the full onset of the wet season in some years, but the annual rainfall and temperature patterns are largely predictable (see Supporting Information Fig. S1). In APLORI, the wet season usually lasts for approximately 6 months, between mid-April and mid-October. Total monthly rainfall between June and September is usually over 200 mm but may be less in May and October. The duration of the wet and dry seasons may vary slightly between years depending on the onset and termination of the rains. Average daily temperatures vary across the year in a bimodal pattern with amplitudes of about 8 °C around March and April and 6 °C around October and November. Temperatures are lowest during the peak wet season in July and August and the dry, dusty 'harmattan' periods of December and January (Fig. S1). Day length varies with an amplitude of 69 min across the entire year.

Vegetation is mainly grass, shrubs and small trees, with a few large trees around wet gullies, which may dry out after the rains. A few of these gullies hold water throughout the dry season depending on the extent of drought and serve as valuable water sources when water is otherwise largely unavailable in the environment. Insects are more abundant in the wet season than in the dry season, with an especially clear peak in numbers of termites and ants at the onset of the rains (Opoku 2017, C.J. Nwaogu pers. obs.): observations from insect sampling in our study area from 7 March to 19 May 2017 revealed an overall increase in insect abundance at the start of the wet season, with a greater than 10-fold increase in abundance on 7 April due to eruptions of termites and ants from subterranean castes after the first rain. Seeds are more readily available at the end of the wet season (Brandt & Cresswell 2008), whereas nectar and fruits may vary according to phenology of flowering and fruiting plants around the reserve (C.J. Nwaogu pers. obs.). More plants fruit in the wet season and so fruits are abundant and diverse in the wet season than in the dry season, but there is at least one fruiting plant species available at all times of year. Detailed information on variation in food abundance, diet choice and seasonal use of artificial foraging patches by birds around the Amurum Forest Reserve can be found in Molokwu *et al.* (2008, 2010, 2011).

Study species

Common Bulbuls are resident, sexually monomorphic passerines, usually 9–11 cm long and between 25 and 50 g in weight. They have an annual survival probability of 0.67 ± 0.05 (Stevens *et al.* 2013) and individual adults may live for up to 15 years in the wild (unpublished APLORI capture–recapture records). They are territorial throughout the year but may travel up to *c.* 2 km to forage, especially in the dry season when large groups forage on the few available fruiting plants and drink from gullies. They may breed in both the wet and the dry season (Cox *et al.* 2013) and are socially monogamous (C.J. Nwaogu pers. obs.). They always lay two eggs per clutch, but over 79% (*n* = 92 nests in 3 years) of these clutches are lost to nest predation and so pairs may make several repeat breeding attempts in quick succession in the same year. A successful breeding attempt lasts 30–34 days depending on the duration of nest-building and whether egg-laying is initiated immediately after nest completion. Fledglings leave the nest at 66% of adult body size and attain 92% of adult body size 2 weeks after fledging; they start a complete post-juvenile moult 6–8 weeks after fledging (C.J. Nwaogu pers. obs.). Hence the occurrence of young birds is a reliable indication

of recently successful breeding events (Ward 1969). Juveniles remain within their family groups, supported by parents for up to 12 weeks after fledging. Common Bulbuls are largely frugivorous, but nestlings are predominantly fed insects and, later, fruits. Adult birds also feed on insects, and occasionally on nectar or seeds.

Data collection and determination of variables

We mist-netted 827 Common Bulbuls over 2 years from February 2014 to January 2016. Mist-netting was carried out daily from February 2014 to January 2016 except when interrupted by unfavourable weather (day 1 = February 1 for data analysis involving calendar date). We caught at least one Common Bulbul on 257 days of two annual cycles (mean = 3.18 bulbuls/day, sd = 2.82, maximum = 16 in 257 days). We determined the age of all birds on the basis of plumage characteristics or colour of gape, and collected blood samples for molecular sexing by gel electrophoresis. DNA extractions followed methods described by Richardson *et al.* (2001) and genetic sexing was done using the P2/P8 primers (Griffiths *et al.* 1996, Nana *et al.* 2014).

For each adult female, we assessed breeding status and stage on the basis of brood patch occurrence (Redfern 2010). Males do not incubate, so their breeding status cannot be inferred from brood patch scores. Incubation lasts 13–14 days but starts from the date of laying the first egg. Common Bulbuls typically have a clutch of two eggs laid on consecutive days, so egg-laying overlaps with the first 2 days of incubation. Brood patches at stage 4 and 5 (Redfern 2010) may persist after incubation, and thus only females with brood patch scores of 1–3 were considered to be in the nesting phase of reproduction (Nwaogu *et al.* 2017).

Moult status and stage was determined on the basis of feather quality (old, moulting or new) and proportion of primary feather material regrown (Underhill 1985), respectively. In the field, birds were grouped into three moult categories: 'pre-moult', 'in moult' and 'moult completed'. We further scored each primary feather on the scale of 0–5 for use in calculating population moult parameters (duration of primary moult, mean start date of primary moult and standard deviation of start date of primary moult): fully grown new feathers were scored 5 and unmoulted old feathers were

scored 0, and feathers at intermediate stages of growth were scored 1–4 (Ginn & Melville 1983). To model seasonality of moult and the effect of weather variables on the occurrence of moult (Objectives 1 and 3 respectively), birds 'in moult' were scored 1 and birds in the 'pre-moult' and 'moult completed' categories were scored 0. However, to control for effect of moult stage on breeding when modelling the relationship between occurrence of brood patches and weather variables (Objective 3), all three moult categories were used. We considered females trapped between February 2014 and January 2016 (n = 414) when comparing the occurrence of breeding and moult over the annual cycle, but used all 827 records from 2 years of mist-netting when quantifying the occurrence of juveniles in the annual cycle (Fig. 1, Table 1).

To estimate within-individual variation in breeding dates, we considered females that were trapped more than once in breeding condition (Fig. 2) and supplemented these few records from 2014 to 2016 with breeding records of the same individuals from ringing data collected between 2006 and 2013 (Cox & Cresswell 2014), as well as direct nesting observations made between 2014 and 2017. In total, we considered 65 breeding observations of 19 females that were encountered breeding two to nine times between 2006 and 2017 (Fig. 2).

Statistical analyses

Relative timing of breeding, juvenile occurrence and moult

Our first analyses were aimed at predicting the occurrence (binary outcome) of respectively breeding, juvenile occurrence and moult, over the year. Each of these three activities were modelled using a generalized linear model (GLM) with a binomial error structure, with day (from 1 February) as a continuous variable and year as a categorical predictor variable (Fig. 1, Table 1). We included the quadratic and cubic terms of day in all models where they were significant. Year was retained in all our models whether it was significant or not, because we intended to compare best estimates of the timing of annual cycle stages between years.

To model the timing of primary moult in more detail, we estimated population-level annual moult parameters using 771 moult records of adult birds trapped between February 2014 and January 2016 (Table S1). Each moulted primary feather was converted to the proportion of primary feather
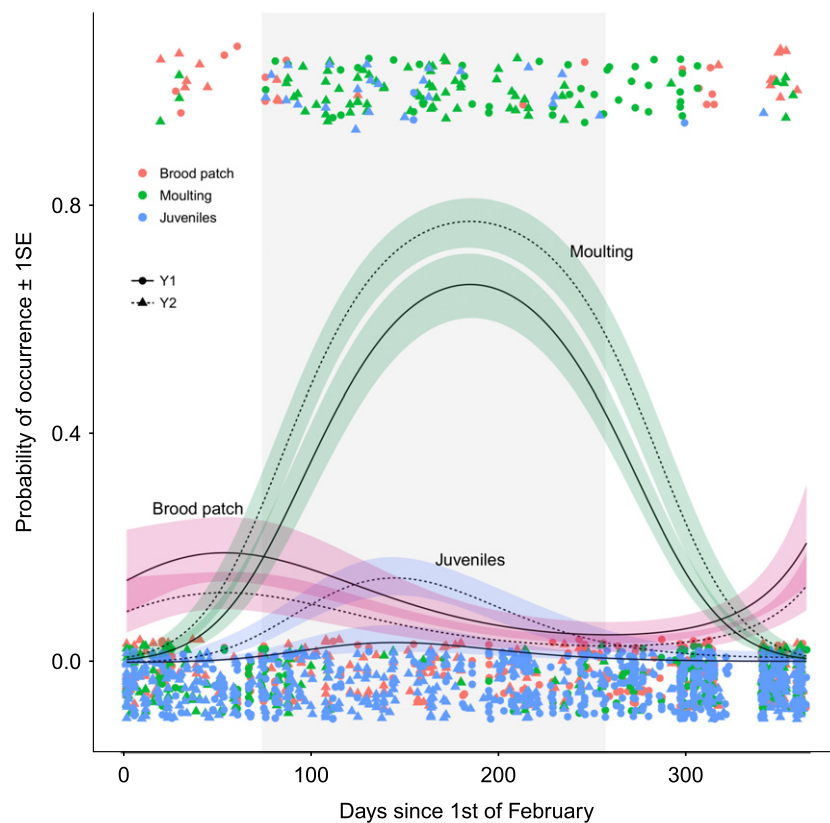
Figure 1. Annual occurrence of annual stages: raw data (plot points are jittered around 0 and 1 for clarity) and annual cycle pattern of presence and absence of brood patch, primary moult and juvenile occurrence in the Common Bulbul *Pycnonotus barbatus* in a West African savannah environment over two annual cycles. Occurrence of brood patches and moult was determined from 414 female birds, whereas for juvenile occurrence, the entire 827 capture records were used. Plot lines are generated from parameter estimates of generalized linear models with binomial error structure (Table 1). Colour bands indicate 1 se of the probability of occurrence of annual cycle stages. Error bands differ in size due to relative difference in the amplitude of annual peaks between years. Grey background indicates the expected start and end of the wet season. Circles and triangles represent 1st year and 2nd year data points, respectively. Day of year is calculated with reference to 1 February for consistency with models estimating moult parameters (see Table S1).

mass regrown at the time of scoring (Underhill 1985, Erni *et al.* 2013) using reference feather masses of fully grown individual primary feathers from Museum specimens at the A. P. Leventis Ornithological Research Institute in Nigeria before fitting the moult model (Erni *et al.* 2013).

Within-individual variation in breeding dates

We estimated individual variation in breeding dates. To do this, we calculated the mean within-individual and population-level coefficient of variation in breeding dates, using the subset of our data which included females with repeat breeding records. The breeding date was recorded as the number of days from 1 February when an individual was encountered with a brood patch or was observed nesting.

Effect of rainfall and temperature on occurrence of breeding and moult

Weather variables may have lag or cumulative effects on life history traits. Hence, we tested the effect of rainfall, minimum temperature, maximum temperature and temperature range on brood patch and moult occurrence over different time windows going back 365 days, using methods described by van de Pol *et al.* (2016). We only used data of females so that effects of rainfall and temperature on the occurrence of breeding and moult were tested for the same individuals. We tested several models for different time windows within 365 days and came up with a top model for each weather variable for a linear and quadratic function, each using aggregate measures: slope, sum, mean and maximum of weather variables within the selected

Table 1. Timing of nesting (active brood patch occurrence), moult and juvenile occurrence in the annual cycle of the Common Bulbul *Pycnonotus barbatus*, modelled by a generalized linear model with binomial error structure using 2 years of capture–mark–recapture data from a West African savannah environment. Occurrence of nesting and moult were modelled from adult female birds only, whereas juvenile occurrence was modelled using all capture records. Year 2014 is set as intercept in the model. Day of year is included as a continuous variable with day 1 = 1 February annually.

	Estimate	Error	Z	P
Nesting				
Intercept	−1.82	0.62	−3.0	**0.003**
2015	−0.54	0.37	−1.4	0.152
day	0.02	0.01	1.0	0.305
day^2	−0.0002	0.0001	−1.7	0.080
day^3	0.0000004	0.0000002	2.1	**0.039**
Juveniles				
Intercept	−9.15	2.02	−4.5	**<0.001**
2015	1.58	0.65	2.4	**0.015**
day	0.09	0.04	2.5	**0.014**
day^2	0.0004	0.0002	−2.1	**0.034**
day^3	0.0000006	0.0000004	1.7	0.093
Moulting				
Intercept	−5.42	0.69	−7.8	**<0.001**
2015	0.55	0.29	1.9	0.056
day	0.07	0.01	8.6	**<0.001**
day^2	−0.0002	0.00002	−9.0	**<0.001**

Number of individuals = 539, total number of observations = 827, number of female observations = 414. Significant *P*-values are presented in bold.

time window (see Supporting Information Tables S3 & S4). Each model quantifies the additional contribution of a weather variable to the fit of a baseline GLMM with brood patch or moult as response variable, day length as continuous predictor variable, and individual identity as random factor (Table 2). Top models for each weather variable are those that generate the largest difference in AIC (relative to the baseline model) after inclusion of the weather variable in the baseline model (Tables S3 & S4). We tested the reliability of these top models by comparing their delta Akaike information criterion (AIC) with the delta AIC of models generated from randomized data; after only 10 randomizations, we found that the suggested weather signals were all likely to be arrived at by chance:

Breeding: Rainfall, $P = 0.99$; T_{max}, $P = 0.99$; T_{range}, $P = 0.97$; T_{min}, $P = 0.96$.

Moult: Rainfall, $P = 0.99$; T_{max}, $P = 0.86$; T_{range}, $P = 0.92$; T_{min}, $P = 0.98$.

The effect of rainfall and temperature were thus not considered further.

All statistical analyses were implemented in R version 3.4.1 (R Development Core Team 2017).

RESULTS

Nesting and juvenile occurrence peaks were seasonally consistent between years

The timing of moult but not breeding was seasonal in the Common Bulbul (Fig. 1, Table 1). Peak occurrence of brood patch and juveniles followed a similar sequence in both 2014 and 2015. Brood patch occurrence peaked weakly prior to the onset of the wet season before the population moult peak, flattened in the wet season during moult, and increased again after the moult peak (Fig. 1, Table 2). Juvenile occurrence peaked within the wet season as did moult, but active brood patches and juveniles still occurred at any time of the year (Fig. 1). The amplitude of juvenile occurrence peaks differed significantly between 2014 and 2015. More juvenile captures were recorded in 2015, despite similar brood patch peaks in both years (Fig. 1, Table 1). The duration and standard deviation of the start date of wing moult did not differ significantly between years or sexes, but males varied significantly in the start date of moult between years. Moult lasted 138 ± 5 days on average. In 2014, males started moulting on 24 April and females on 14 May, whereas in 2015, males started on 16 April and females on 13 May (Table S1).

Breeding dates are variable within individual birds

On average, breeding dates were as variable within individual birds as for the population (mean individual coefficient of variation (CV) = 0.49, population CV = 0.59, Table S2). Within-individual CV in breeding dates ranges from 0.03 to 0.84. Raw data plots (Fig. 2) of observed breeding dates per bird reveal that the same individuals nested at different parts of the same or different year(s).

Within-year variability in rainfall and temperature are weakly associated with the timing of nesting and moult

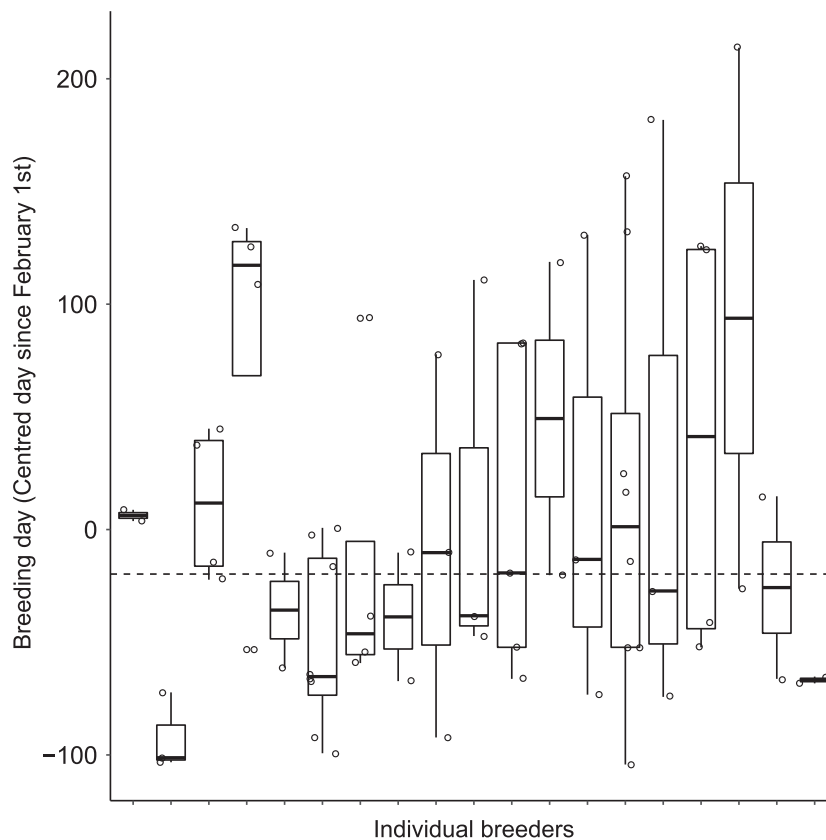Neither the timing of moult nor the timing of breeding were predicted by within-year local

Figure 2. High within-individual variability in nesting dates of Common Bulbuls *Pycnonotus barbatus* in a West African Savannah environment depicted from raw data plots of observed breeding dates per individual bird. Within-individual (0.49) and population (0.59) coefficients of variation in breeding dates were calculated based on number of days since 1 February of brood patch occurrence. Dashed line indicates population median date of brood patch occurrence (65 breeding observations in 19 individuals). First eight and last two individuals (left to right) are less variable compared with the population – this would be the case for all birds if individuals bred seasonally despite weak seasonality at the population level.

variability in rainfall and temperature; this was not due to lag effects of weather variables, because we explored the effect of all weather variables over 365 days before a breeding or moult event. Final models showed that breeding was best predicted by moult ($\chi^2_{2,414} = -1.91 \pm 0.65$, $P < 0.01$) and moult was best predicted by day length ($\chi^2_{1,414} = 0.05 \pm 0.01$, $P < 0.001$; Table 2, Fig. 3).

DISCUSSION

Common Bulbuls showed weakly seasonal nesting at the population level, largely due to individual variability in breeding dates, despite highly seasonal precipitation, and perhaps the need to moult during the wet season (Ward 1969). We found strong evidence for strict seasonal timing of moult based on a correlation of moult with day length. This finding contrasts with the general observation

of breeding being timed to match seasonal food abundance, thus in turn driving the start of moult: a notion which prevails in temperate systems (but see Tomotani *et al.* 2018a,b). We discuss these findings in the context of life history adaptation and environmental variation over the annual cycle of the Common Bulbul, paying particular attention to the benefit of seasonal moult for adult survival and the possible impact of nest predation on re-nesting behaviour.

Seasonality of nesting, juvenile occurrence and moult

The annual cycle of Common Bulbuls suggests weakly seasonal breeding in which peak juvenile occurrence and moult coincide with the start of the wet season even though breeding events were distributed across the annual cycle rather

Table 2. Timing of moult and breeding, measured as occurrence of primary wing moult and active brood patch respectively, in the annual cycle of the Common Bulbul *Pycnonotus barbatus* in a West African savannah. Probability of moult is predicted by day length and breeding status, whereas probability of breeding is predicted only by moult stage. Moult stage was a categorical variable (pre-moult; in moult; moult completed), with the 'pre-moult' stage set as intercept in the model. Breeding status was scored as the presence or absence of an active brood patch in females. Predictor variables in full models included rainfall, maximum daily temperature, minimum daily temperature and daily temperature range.

Trait	Variable	Estimate	Error	Z	P
Breeding	Intercept	−1.72	0.27	−6.27	<0.001
	Moult stage: in moult	−1.91	0.65	−2.94	<0.01
	Moult stage: moult completed	−0.60	0.38	−1.59	0.11
Moult	Intercept	−1.75	0.26	−6.75	<0.001
	Day length	0.05	0.01	5.58	<0.001
	Day length^2	<0.01	<0.001	2.67	0.01
	Breeding status: Breeding	−2.00	0.79	−2.54	0.01

$n = 414$, individuals = 281, estimated random effect variance: breeding model = 0.44 ± 0.66, moult model = 1.22 ± 1.10.

than heavily concentrated in any one part of the year (Fig. 1). The coincidence of juvenile occurrence and moult with the start of the wet season suggests that the annual cycle is organized such that juveniles and adults benefit from the relatively higher insect abundance at the start of the rains. A similar synchrony is reported for the Yellow-vented Bulbul *Pycnonotus goiavier* in Singapore (Ward 1969) and the Common Bulbul in East Africa (Moreau *et al.* 1947). Insects become readily abundant with the first rains but, in contrast to temperate systems, peak insect abundance at the onset of the rains results mostly from termite and ant eruptions (Ward & Jones 1977, Opoku 2017, C.J. Nwaogu pers. obs.). For example, in some parts of Africa, winged termites emerge for nuptial flights from subterranean castes during the early rains (van Huis 2017) and this may not require the vegetation regeneration that drives the seasonal peak in abundance of caterpillars in temperate systems. There may be a lag effect of rainfall on the abundance of insect taxa such as Lepidoptera as in other tropical systems (Vasconcellos *et al.* 2010), but this may simply allow insects to be available for longer periods in the year. Common

Bulbuls raise young year-round, so seasonal variation in insect abundance is unlikely to be the key factor influencing the timing of nesting. It is therefore important to note that peak juvenile occurrence is unlikely to be a direct indication of peak nesting period, because the time interval between peak occurrence of a brood patch in adult females and the peak of juvenile occurrence is longer than the maximum expected 34-day nesting period. Furthermore, the amplitude of juvenile occurrence peaks varied significantly between years but brood patch peaks did not, so the timing of peak juvenile occurrence may be more strongly related to the likelihood of nesting success, which may be variable but more closely related to annual variation in the timing of rainfall than to the occurrence of breeding. Clearly, an understanding of seasonal adult and nestling diet is crucial for a better understanding of breeding phenology in tropical systems.

The wet season may provide better opportunities for juvenile survival and moult (Moreau 1950, Ward 1969, Chapman 1995), but the dry season still supports successful breeding events (Cox *et al.* 2013). Thus, preparation for nesting and a substantial part of the nesting period takes place outside the wet season and this may be supported by the omnivorous foraging behaviour of the Common Bulbul, which allows exploitation of multiple food sources. The dry season, although comparatively more impoverished based on evidence from increased foraging from artificial food patches and lower giving-up densities (Molokwu *et al.* 2010), still must provide sufficient food to allow breeding (Perrins 1970). This further implies that breeding by Common Bulbuls is not specifically triggered by rainfall (Hau *et al.* 2004) and that our study area meets the minimum breeding requirement for the Common Bulbul even before the wet season begins, despite about six preceding months of drought (Fig. S1).

Common Bulbuls were only less likely to breed when in main wing moult and could breed again after moulting (Table 2). Nonetheless, there was an overlap in some individuals of breeding and moult. Our raw dataset (Fig. 1) contains four of 414 (*c.* 1%) females with active brood patches while in main wing moult. All four were trapped after April but before September and one of them, nesting in June, was previously caught incubating in March of the same year. Because juveniles remain with their
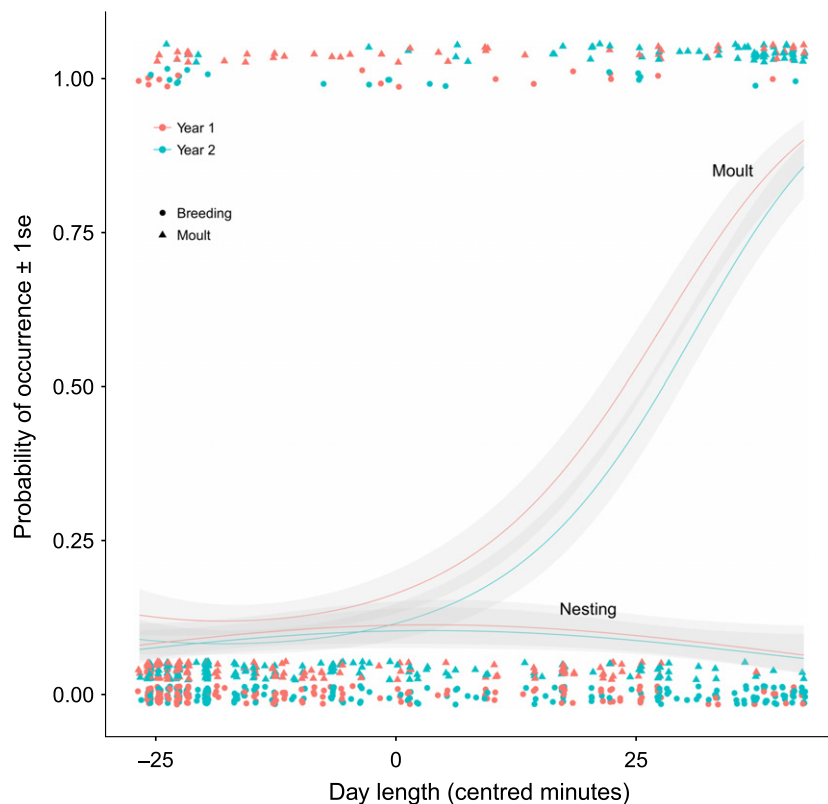
Figure 3. Day length predicts moult but not breeding in the Common Bulbul *Pycnonotus barbatus*: relationship between occurrence of moult and brood patches in female birds, and day length in a West African Savannah environment with slight variation in day length and marked seasonal precipitation. Plot lines are generated from predictions based on a generalized linear model fitted for 414 observations of moult and brood patches in 281 female Common Bulbuls in Amurum Forest Reserve, Jos, Nigeria (Table 2). Moult points are stacked on breeding points for easy identification. Patterns in both annual cycles are plotted to show consistency between years but there was no significant difference between annual patterns. Day length varies with an amplitude of 69 min across the entire year.

parents for up to 12 weeks after fledging, it is likely that the March breeding attempt was unsuccessful and necessitated replacement clutches. Hence, full overlaps between breeding and moult may be an exception rather than a norm (Foster 1974, Camacho 2013). We hypothesize that although individuals are capable of breeding year-round, birds which complete a successful first breeding attempt are unlikely to overlap nesting and moult (Jahn *et al.* 2017). A more common scenario in our study area is to find females with brood patch scores of 4 and 5 (post-nesting stages) already starting wing moult or a few pairs initiating breeding attempts after September when moult is largely complete (Fig. 1). Our observations suggest a tighter schedule for moult than for breeding at the population level. Main wing moult usually lasts about 138 ± 5 days – a period accounting for roughly 80% of the wet season. This duration may be partly influenced by the

21-day delay and larger variability in the start date of moult in females (Table S1).

Flexible individual timing of breeding

Breeding dates within individuals may be as variable as the population as a whole. Thus, weak breeding seasonality at the population level is due to the ability of individuals to breed in different environmental conditions within a year rather than being adapted to specific parts of the year (Fig. 2). Perhaps occurrence of breeding was determined by whether a female was successful or not in a previous attempt to breed, and this may be stochastic. A few individuals that successfully bred before moulting have, however, been observed breeding again after moult. Hence, a sub-annual periodicity where individuals breed at less than annual intervals (Ashmole 1965,

Reynolds *et al.* 2014) or a bimodal breeding season (Greeney 2010) similar to patterns consistent with the bimodal rainfall pattern in east Africa (Moreau 1950, Wrege & Emlen 1991) may be alternative explanations for weak breeding seasonality. A bimodal breeding season is possible if conditions at the start and end of the wet season are similar, but this may be less apparent for Common Bulbuls because breeding events may be spread out due to replacement clutches on both sides of the single moult peak (Fig. 1). This may be the reason for conclusions drawn by Steven (2010), who suggested that the Common Bulbul is an end-of-wet-season breeder, based on juvenile occurrence at the start of the dry season from 1 year of data. Cox *et al.* (2013), on the other hand, suggested a non-seasonal breeding pattern based on similar proportions of brood patch occurrence in four quarters of the year from several years of pooled data.

Only detailed individual observations over several years could confirm individual breeding strategies and allow general conclusions to be drawn about population breeding patterns, because the presence of an active brood patch or nesting event may reflect an individual's decision either to initiate breeding or to replace a depredated clutch or brood. We did not consider differences between initial and replacement clutches, which limits our ability to test whether individuals commence breeding at a similar time in the year. Moreover, a distinction between initial and replacement clutches may be more complicated where birds are capable of breeding year-round. Nonetheless, our conclusion that the environment exerts a weak selection on the timing of breeding for individuals is still valid and opens opportunities for considering alternative explanations for year-round breeding in the Common Bulbul and other tropical species (Ashmole 1965, Wrege & Emlen 1991, Reynolds *et al.* 2014).

Variation in temperature and rainfall do not predict the timing of nesting and moult

Variation in rainfall and temperature did not explain the occurrence of breeding and moult (Tables S3 & S4). Rather, breeding was best predicted by moult, and moult was best predicted by day length. Thus, the relative timing of breeding and moult suggests the use of cues other than rainfall and temperature (Lloyd 1999, Hau *et al.*

2004, Houston 2012, Mares *et al.* 2017). Small changes in day length (Wikelski *et al.* 2000, Quispe *et al.* 2017) and sun rise time (Shaw 2017) have also been suggested as cues used by tropical birds; however, we found no support for the former. There was also no evidence that birds avoided nesting in the wet season (Thomson 1950, Foster 1974, Shaw 2017). Instead our data reveal a seasonal moult (Figs 1 and 3) and a temporal separation of breeding and moult, albeit with high individual flexibility (Fig. 2). This synchronization of moult to the wet season despite flexible individual breeding may be aided by variation in day length, as observed with sunrise and sunset times in African Stonechats *Saxicola torquatus axillaris* (Goymann *et al.* 2012). Common Bulbuls moult during times of above-average day length (Fig. 3) and are able to initiate moult in captivity even when breeding does not take place (C.J. Nwaogu pers. obs.). Nonetheless, we cannot conclude that day length serves as the cue for moult without experiments, because moult may also be controlled by other factors that correlate with day length. Regardless, moult does not seem to be casually linked to breeding, and thus early breeding may relax temporal constraints on the timing of moult (Barshep *et al.* 2013, Tomotani *et al.* 2018a,b).

GENERAL CONCLUSION

We show that year-round breeding by Common Bulbuls probably results from a weak selection for individuals to breed under any specific environmental conditions and perhaps a need to replace stochastically depredated clutches, rather than an individual adaptation to specific conditions at different times of the year. The small seasonal breeding peak at the population level may be related to the onset of the wet season, but the occurrence of individual breeding events is not necessarily determined by rainfall. In contrast, moult is a more seasonal annual event and if selection acts more strongly on timing of moult, then seasonality in breeding may arise because of moult, but not because breeding is timed primarily to specific environmental conditions. Accordingly, we show a temporal separation of breeding and moult with only moult being seasonal. Overall, there appears to be a stronger environmental constraint or a better individual control on the timing of moult compared with breeding in the Common Bulbul.

We hypothesize that where environmental conditions allow multiple breeding opportunities year-round, but there is limited and stochastic annual reproductive output (due to small clutch size and high nest predation, respectively), there will be a weak selection for breeding to match peak environmental conditions. In contrast, there will be a stronger selection to organize the annual cycle such that self-maintaining traits (such as moult) are timed to suitable environmental conditions (Stiles & Wolf 1974, Barta *et al.* 2006, McNamara *et al.* 2011). This is a testable hypothesis that may apply to comparatively long-lived species (Camacho 2013), because an unsuccessful self-maintenance carries an immediate survival, and thus long-term fitness, consequence for an individual, whereas a failed breeding attempt may be relatively less costly.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Annual moult parameters estimated on the basis of proportion of feather material replaced by Common Bulbuls *Pycnonotus barbatus* in a West African savannah environment based on Underhill and Zucchini's primary moult model, using Type II moult data. All estimates are given in days with reference to 1 February annually. Year (although interaction with sex is not significant) is retained in the model to show the consistent difference in mean moult start date of free-living males and females between years.

Table S2. Coefficient of variation in breeding dates of female Common Bulbuls *Pycnonotus barbatus* within individual birds and among all birds in the population. Breeding date was determined as number of days between 1 February and the day of brood patch or nesting behaviour observation.

Table S3. Candidate climate models predicting the occurrence of a brood patch in female Common Bulbuls *Pycnonotus barbatus* over the annual cycle. Delta AIC relative to baseline model, effect time windows and effect sizes are shown for each model. All models are set at 'relative' type to explore time windows within 365 days prior to the observation of an active brood patch. Baseline model is a null generalized linear mixed-effect model with individual identity as random factor. Top climate models for each weather variable are highlighted in bold in the table.

Table S4. Candidate climate models predicting the occurrence of primary wing moult in female Common Bulbuls *Pycnonotus barbatus* over the annual cycle. Delta AIC relative to baseline model, effect time windows and effect sizes are shown for each model. All models are set at 'relative' type to explore time windows within 365 days prior to the observation of primary feather moult. Baseline model is a null generalized linear mixed-effect model with individual identity as random factor. Top climate models for each weather variable are highlighted in bold in the table.

Figure S1. Annual precipitation and temperature patterns are consistent and largely predictable between annual cycles: plots of daily rainfall, minimum, maximum and range of temperature in the Amurum Forest Reserve, central Nigeria, between 15 January 2014 and 15 February 2016.