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3 **Breeding limits foraging time: evidence of interrupted foraging response from body mass**
4 **variation in a tropical environment**

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12 **Abstract**

13 Birds should store body reserves if starvation risk is anticipated; this is known as an ‘interrupted
14 foraging response’. If foraging remains unrestricted, however, body mass should remain low to limit
15 the predation risk that gaining and carrying body reserves entails. In temperate environments mass
16 gain in female birds during breeding is often attributed to egg formation and mass loss after
17 incubation to flight adaptation or the effect of reproductive workload, rather than as a result of an
18 adaptive interrupted foraging response to the limited foraging time or unpredictable foraging
19 conditions that breeding demands. In tropical environments, foraging conditions vary more within
20 the breeding season than in temperate environments, and so studies in tropical environments are
21 more suited to decouple the potentially confounded effects of increase in body reserves versus egg
22 formation on the body mass of breeding birds. In this study, we test whether breeding results in an
23 interrupted foraging response in a tropical savannah system using body mass data collected over a
24 15-year period from female Common Bulbuls *Pycnonotus barbatus*. This species breeds both in the
25 wet and dry season, despite fewer resources being available in the dry season. Breeding stage
26 predicted female body mass: body mass peaked abruptly during incubation, but was not closely
27 associated with the egg-laying stage, and declined during brood rearing. Breeding females were
28 heavier in the dry season than in the wet season. In the dry season, heavier birds were more likely to
29 incubate eggs or brood chicks. These observations suggest that increased body reserves are required
30 to buffer the consequence of limited foraging time or impoverished foraging conditions, which may
31 be most pronounced during incubation and in the dry season, respectively. Such mass increases are
32 consistent with an interrupted foraging response, which may apply to temperate zone birds
33 experiencing foraging restrictions during breeding.

34

35 **Key words**

36 Body reserves, breeding status, food availability, foraging unpredictability, reproduction, starvation-
37 predation risk, tropical seasonal variation, tropical birds.

38 Introduction

39 Foraging time in breeding birds may be restricted by breeding roles, such as territoriality, mate
40 guarding, nest building, incubation and brood rearing, as well as the constraints of having to forage
41 in a central place and deliver food to a fixed nest site. As a consequence, breeding birds may carry
42 extra body reserves to reduce the risk of starving due to limited foraging time or unpredictable
43 foraging conditions, even though this may increase predation risk (Lima 1986; Gosler et al. 1995).
44 This body mass gain strategy is called the 'interrupted foraging response' (Lima 1986; Macleod and
45 Gosler 2006): unpredictable foraging leads to increase mass reserves whether this is, for example,
46 shorter day length in winter or shorter available time to forage during the breeding season.

47 The interrupted foraging response may then provide a simple universal explanation for body
48 reserves carried by breeding birds beyond the egg laying stage in addition to the unavoidable
49 additional mass that increased size of reproductive organs and egg production entail. For example,
50 body mass gained during breeding has been shown to correlate positively with adult survival
51 probabilities in tropical savannah birds (Cox and Cresswell 2014), which suggests that body reserves
52 carried during breeding decrease starvation risk and increase survival likelihood when foraging
53 opportunities become relatively unpredictable for breeding birds. However, body reserves in birds
54 should reflect a trade-off between their costs and benefits (see Witter & Cuthill 1993). Hence, if
55 starvation risk is low, body mass should remain relatively low even during breeding to limit
56 predation risk (Macleod et al. 2005; Macleod et al. 2008).

57 Differences in body reserves carried between breeding stages should reflect relative starvation risk
58 between these stages or how available foraging time is constrained by each stage. For example, in
59 the Blue Petrel *Halobaena caerulea*, body mass before and after incubation bouts, and food
60 availability at sea during foraging may predict incubation duration and foraging bouts, likelihood of
61 temporary egg neglect, rate of body mass gain during foraging and overall breeding success
62 (Chaurand and Weimerskirch 1994). Within a breeding attempt, foraging time may be most limited
63 during incubation because incubating birds have to spend a fixed amount of time on their eggs in
64 order for them to develop and hatch as quickly as possible. Larger body reserves may then be
65 particularly valuable if the foraging environment is relatively unpredictable during incubation
66 because birds are less likely to obtain sufficient food in each foraging bout.

67 Body mass variation in breeding birds has received considerable attention in temperate
68 environments compared with tropical ones. In temperate environments, body mass gain before
69 incubation in female birds has been attributed to the increased size of reproductive organs (Vezina &
70 Salvante 2010), while mass loss after or during incubation is attributed to the effect of reproductive
71 workload or adaptation for better flight performance during nest provisioning (Merkle & Barclay
72 1996; Neto & Gosler 2010; Boyle, Winkler & Guglielmo 2012). Pre-incubation body mass gain due to
73 increased size of reproductive organs is largely undisputed (see Vezina & Salvante 2010), but the
74 reproductive stress and flight adaptation hypotheses have been tested using experimental food
75 supplementation to temperate breeding birds (Moreno 1989; Merkle and Barclay 1996). However,
76 body mass response to food supplementation in experimental set-ups may be uninformative if non-
77 supplemented control breeding birds do not anticipate any foraging unpredictability. Experimental
78 reduction of food may also be less practical in natural systems where birds move freely and can use
79 other resources. An alternative approach, however, might be to model patterns of breeding body

80 mass from long-term data of individual birds ringed within the same environment with clear
81 resource seasonality for bird species with protracted breeding periods.

82 Such data are available in a tropical savannah breeding environment for the Common Bulbuls
83 *Pycnonotus barbatus*, which can breed throughout the year (see also Cox *et al.* 2013). By using brood
84 patch presence and development as indicators of breeding occurrence and stage, respectively
85 (Redfern, 2008; Redfern 2010), we assessed how body mass varied within the breeding period and
86 between environmental conditions. The different stages of brood patch development are closely
87 linked to breeding stages in European passerines (Redfern 2010; Myers & Redfern 2011). We assume
88 that savannah bird species show a similar progression of brood-patch development (Table S1). We
89 expect that body reserves will increase with breeding stages that constrain foraging such as
90 incubation but with an interaction with availability of resources. For the Common Bulbuls, the dry
91 season in a tropical savannah is expected to be less favourable for breeding than the wet season
92 because insect abundance is low, and food and water are less widely distributed (Molokwu *et al.*
93 2008; Molokwu *et al.* 2010; Brandt and Cresswell 2008). The occurrence of moult may confound the
94 effect of breeding on body mass variation (Gosler 1994) and, therefore, we also consider the
95 possible confounding effects of moult here. We therefore expect that body reserves will offer a
96 greater reproductive advantage under less favourable foraging conditions (Smith & Moore 2003),
97 resulting in more pronounced body mass gain for breeding birds in the dry season in our study area.
98 We, therefore, test two hypotheses:

- 99 1. Body mass within a breeding attempt varies in accordance with the level of foraging
100 unpredictability at different breeding stages independently of mass gains due to egg
101 formation. Foraging unpredictability is expected to peak during incubation.
- 102 2. Body mass during breeding varies seasonally with peaks in the dry season when foraging is
103 expected to be most unpredictable.

104 **Methods**

105 *Study site*

106 Our study was carried out in Amurum Forest Reserve (09°52'N, 08°58'E), at the A.P. Leventis
107 Ornithological Research Institute (APLORI), on the Jos Plateau in Nigeria. The Amurum Forest
108 Reserve consists of four main habitat types: a regenerating savannah woodland, riparian forests,
109 rocky outcrops (inselbergs) and farmlands. Much of the land surrounding the reserve, like the
110 reserve itself before 2001, is degraded by anthropogenic pressure from farming, bush fires and
111 livestock grazing. There is a single wet and dry season per year lasting about six months each.
112 Generally, the wet season spans from May to mid-October while the dry season spans from the end
113 of October to April. Total monthly rainfall is above 150mm in the wet season except for May and
114 October when it may be lower, while there is almost entirely no rainfall in the dry season.
115 Temperatures vary across the year: temperatures are lowest (8 - 14 °C) during the dry cold windy
116 periods in December and January when relative humidity may be as low as 10% and also at the peak
117 of the wet season in July and August; temperature maxima (28 - 32 °C) are in March and April before
118 the start of the wet season (Cox *et al.* 2011; Figure S1).

119 *Study species*

120 The Common Bulbul is widespread throughout Africa. They are sexually monomorphic, usually 9 - 11
121 cm and weigh 25 - 50g. They have an annual survival probability of 0.67 ± 0.05 (Stevens *et al.* 2013),
122 but some adults can live for up to 15 years in the wild. The Common Bulbul breeds in both the wet
123 and the dry season in our study area with an average clutch size of two. Most breeding attempts fail
124 due to nest predation. Nest building takes 3 - 5 days, egg laying 2 - 3 days, incubation 13 - 14 days,
125 and nestlings leave the nest at 12 days after hatching. Breeding roles are shared by parents. Females
126 build the nest while being guarded by the males. Females incubate the eggs while the male perches
127 close by until both go foraging between incubation bouts. Males feed nestlings during the early
128 nestling phase while females brood chicks. Later, females feed nestlings while males guard the nest
129 from a nearby perch. Both parents continue to feed chicks after fledging and Bulbuls may still remain
130 in family groups for 12 weeks after the chicks have left the nest. Bulbuls moult almost exclusively in
131 the wet season, although a few individuals may start before or at the end of the wet season
132 depending on annual rainfall variability. Common Bulbuls are largely frugivorous but nestlings are
133 predominantly fed insects. Adult birds may also occasionally feed on insects, nectar and seeds.
134 Fruits are available to Bulbuls year round but from different fruit plants, which vary in fruiting
135 phenology, so that food availability may be constrained by the distribution of a specific fruiting plant.
136 Moreover, insect abundance peaks occur in the wet season while seeds are more readily available at
137 the end of the wet season and start of the dry season.

138 *Data collection and determination of variables*

139 Birds were caught using mist nets from 06:00 to 10:30 hours between 2001 and 2015, inclusively. In
140 the years 2001 and 2013, trapping was mostly concentrated at Constant Effort Sites (CES) during a
141 CES ringing project, which takes place 5 times each year for six consecutive days each. During the
142 CES, 272 meters of nets were used in total. In 2014 and 2015, in addition to the regular CES captures,
143 trapping was carried out repeatedly throughout the entire year with variable lengths of mist nets in
144 addition to the use of playback devices, depending on the trapping area covered.

145 We trapped 1,422 birds in total, and 271 individuals were trapped repeatedly a total of 673 times.
146 From all birds trapped, there were 135 females with brood patches and 69 identified non-breeding
147 female birds; 50 of these females were caught more than once but at least once with a brood patch.
148 In total these 50 females were caught 147 times. Where possible, caught birds were aged and sexed
149 by the presence of a gape and a brood patch, respectively.

150 Because only the sexes of breeding female Common Bulbuls are reliably determined by field
151 observations, we considered only adult females for this study. Breeding status and stage were
152 assessed on the basis of brood patch occurrence and development (Table S1). In addition, we
153 verified the relationship between brood patch development and breeding stages in female Common
154 Bulbuls that were caught raising young or incubating eggs. Also note that Common Bulbul females
155 incubating or brooding chicks have a brood patch score of 3 while those feeding chicks may have a
156 brood patch score of 3 or 4, depending on whether females are still brooding. We are confident that
157 only female Common Bulbuls have brood patches and so birds can be sexed reliably based on brood
158 patch occurrence; however, we verified the sexes of birds with brood patch score of 5 from our
159 molecular sexing data because males undergoing moult may be erroneously scored as having a
160 brood patch of 5.

161 For each trapped bird, we recorded wing length ($\pm 1\text{mm}$), moult status, pectoral muscle score, fat
162 score, brood patch score and body mass ($\pm 0.1\text{g}$, Ohaus Scout). Moult was scored as present or
163 absent: an individual actively replacing main wing or tail feathers was scored 1; otherwise, it was
164 scored as 0 (Svensson 1991, Redfern and Clark, 2001). Birds were labelled as caught during the wet
165 or dry season, based on the usual precipitation in the period when they were caught. The 16th of
166 October to the 30th of April was considered to be dry season, while the 1st of May to the 15th of
167 October was considered the wet season.

168 *Statistical analyses*

169 To test the hypothesis that breeding birds vary body mass in accordance with the level of foraging
170 unpredictability at different breeding stages but controlling for the timing of mass gains due to egg
171 formation, we built a General Linear Mixed Model (GLMM) with body mass as a response variable
172 and brood patch score as a predictor. We controlled for the effect of body size and seasonal
173 variability by including wing length and season of capture in the model, respectively. We also
174 controlled for inter-annual and individual variability between capture years and individuals,
175 respectively, by including year of capture and individual identity in the model as random factors.
176 Individual identity did not significantly improve overall model fit (contribute any additional variance)
177 and so was dropped from the final model.

178 To test the hypothesis that breeding body mass depends on environmental conditions during
179 breeding, we built a General Linear Mixed effect Model (GLMM) fitted by Restricted Maximum
180 Likelihood (REML). Only incubating and chick rearing females differed in body mass from non-
181 breeding birds (see results below), thus only these categories were considered as breeding birds for
182 between season comparisons of body mass. Variation in body mass was predicted by season and
183 breeding status. We controlled for the effect of body size and moult on body mass by including wing
184 length and moult status as predictor variables in the model. The effect of moult status on body mass
185 variation was not significant; hence, it was dropped from the final model. We accounted for
186 individual variability and inter-annual variation between capture years by including individual
187 identity and year of capture in the model as random variables.

188 We relied on actual body mass as a proxy for body reserves because visible fat reserves are rarely
189 observed in tropical savannah birds and pectoral muscle scores mostly vary between scores of 2 and
190 3. However, we are confident that body mass corrected for size is a reliable measure of relative body
191 reserves size, even in tropical birds based on previous observations of mass gain in intra-African
192 migrants (Nwaogu and Cresswell 2016). Prior to fitting the minimal adequate model, all GLMMs
193 were fitted by Maximum Likelihood (ML) rather than Restricted Maximum Likelihood REML to allow
194 comparison of models with different fixed factors using Akaike Information Criteria (AIC). Normality
195 and homogeneity of variance were tested using the Shapiro–Wilk normality test and residual plots,
196 respectively. The final models were then fitted with REML, which gives a better fit for models with
197 random effects, because we were interested in modelling body mass variation at the individual level.
198 All analyses were carried out in R version 3.1.0 (<http://cran.r-project.org/package=nlme>, R,
199 Development Core Team 2015).

200 **Results**

201 *Body mass variation at different stages of breeding*

202 Body mass was significantly higher in incubating and brood rearing (Brood patch score 3, 4 & 5)
203 compared to non-breeding females (Table 1, Table S2). During incubation, breeding birds were 8.1%
204 heavier than non-breeders after controlling for body size, and inter-annual and individual variation
205 (Table 1, Fig. 1). Body mass peaked during incubation but decreased during the brood-rearing stages
206 (Fig. 1). The observed pattern is consistent with the assumed available foraging time at the different
207 breeding stages (Table S1). Body mass during egg laying (Brood patch score 2) was low and this did
208 not differ significantly from the non-breeding or post incubation stages (Fig 1). Heavier females were
209 more likely to incubate eggs and brood chicks but this effect was more pronounced in the dry season
210 (Fig. 2).

211 *Body mass variation when breeding in different seasons*

212 Difference in body mass between breeding (incubating and chick rearing) and non-breeding female
213 birds differed significantly during the dry season (Table 2, Fig. 3). During the dry season, breeding
214 birds were on average 5.7% heavier than non-breeding birds, after controlling for body size and
215 inter-annual and individual variation (Table 2). Breeding birds were also on average 2.6% heavier
216 during the dry season than in the wet season. However, in the wet season, breeding and non-
217 breeding females did not differ in body mass (Fig. 3).

218 **Discussion**

219 Body mass variation in female Common bulbuls was consistent with an interrupted foraging
220 response (Macleod and Gosler 2006). We showed that females maintained body reserves according
221 to the likely availability of foraging time in different breeding stages (Table S1) and with seasonally
222 dependent foraging conditions. Body mass increase was more pronounced during incubation and in
223 the dry season, when foraging time is most limited and less food may be encountered, respectively.
224 In the dry season, only heavy females were likely to incubate eggs or brood chicks (Fig. 2).

225 *Body mass variation at different stages of breeding*

226 Our results were consistent with the first hypothesis that female birds will maintain a higher body
227 mass during incubation because time available for foraging is most restricted during incubation.
228 Carrying body reserves may be adaptive allowing females to timetable breeding activities as a
229 priority rather than foraging. For example, body reserves may function to keep on/off bouts minimal
230 and sustain longer incubation duration, thus reducing nest visibility to predators by reducing activity
231 around the nest (Basso & Richner 2015). As a consequence, the survival probabilities of incubating
232 birds and nests may be higher because they are less likely to be predated upon (Lima 1986; Macleod
233 & Gosler 2006; MacLeod *et al.* 2007).

234 Less pronounced differences between breeding stages in the wet season (Fig. 1) may result from
235 confounding moult effects (Gosler 1994) or variation in food availability within the wet season.
236 Moulting is largely restricted to the wet season and moulting birds may carry larger body reserves
237 (Gosler 1994). Fluctuations in food availability peaks within the wet season due to inter-annual
238 variation in rainfall pattern may also cause birds to vary body reserves accordingly depending on
239 individual strategies (Cresswell 1998; Babbitt & Frederick 2008; Durant, Hjermand & Handrich 2013).

240 We did not find any suggestion that body mass variation was due to egg mass or increased size of
241 reproductive organs as previously suggested for temperate birds (Redfern, 2010), which is consistent

242 with our first hypothesis. Our results (Table 1) show clearly that the body mass of breeding female
243 Common Bulbuls was significantly higher than non-breeding females only at the onset of incubation.
244 This suggests that while egg-laying females may be as light as non-breeding ones, incubating or
245 chick-rearing females (well after the egg-laying period) are not. It is unclear if the body mass
246 variation observed during the egg phase in the wet season (Fig. 1) is (partly) due to fluctuating
247 reproductive organ mass. The effect of mass gain due to egg or reproductive organs will likely
248 depend on the timing of weighing, and so body mass is expected to be highly variable during the egg
249 phase (Vezina and Williams 2003) for different individuals weighed before or after laying. Moreover,
250 variation in body mass associated with reproductive organs may also depend on the length of the
251 laying period and the likelihood of successive broods.

252 In other species male cooperation may compliment a female's foraging effort and allow more
253 efficient foraging within restricted time (Afton 1979; Chaurand & Weimerskirch 1994; Curlee &
254 Beissinger 1995). Males accompany females to forage during bouts between incubation, so this may
255 improve vigilance or search efficiency for females or both. But the role of male Bulbuls is not clear:
256 they mate-guard females during nest building, incubation and brood rearing, and they also assist
257 with nestling feeding, especially when females still brood nestlings, and so we might expect males to
258 also have foraging time constraints.

259 Females continue brooding chicks after hatching when males feed chicks. This behaviour may be
260 sustained by the body reserves carried during incubation, and females may lose these reserves
261 rapidly before they take over feeding nestlings. This brooding behaviour in the absence of
262 provisioning from their mate may explain body mass loss after incubation (Fig. 1). By brooding
263 nestlings and losing stored body reserves, females may adapt their body mass for better flight
264 performance during nest provisioning. This post-incubation loss of mass is similar to patterns
265 observed in other species (Moreno 1989; Merkle and Barclay 1996; Neto & Gosler 2010). Thus, our
266 observations suggest that the reproductive stress and flight adaptation hypotheses are not mutually
267 exclusive and probably explain why there is no clear experimental support for each. Moreover, in
268 temperate environments, foraging conditions during breeding may not be sufficiently unpredictable
269 to drive significant changes in body mass between experimentally supplemented and controlled
270 birds in normal years.

271 *Body mass variation when breeding in different seasons*

272 As predicted by the second hypothesis, body mass increases for incubating and brood-rearing female
273 Common Bulbuls were more pronounced in the dry season probably due to higher starvation risk
274 imposed by fewer foraging opportunities (Fig. 3, Table 2). We were able to rule out two potentially
275 confounding factors. There was no indication from the seasonal population body mass pattern (Fig.
276 S2) that predation risk varies seasonally in our study area. A difference in predation risk between the
277 wet and the dry season should lead to a difference in population body mass average between
278 seasons depending on the anti-predation strategy employed (see Lima 1986; Gosler, Greenwood &
279 Perrins 1995), which we did not find. Furthermore, Common Bulbuls moult almost entirely in the
280 wet season (Fig. S2) so that any increases in body mass during moulting should not be confounded
281 with the observed body mass gain in the dry season.

282 The difference in food availability between the wet and the dry season is a fundamental assumption
283 in this study. We believe this assumption to be reasonable because it is based on empirical

284 observations from previous studies in the same study area (Molokwu *et al.* 2008; Molokwu *et al.*
285 2010; Brandt & Cresswell 2008). Furthermore, insect abundance is generally lower in the dry season
286 as in other seasonal tropical environments (Karr 1976; Frith & Frith 1985; Arun & Vijayan 2004; Silva,
287 Frizzas & Oliveira 2011) so that parents may work harder to raise young when they breed during the
288 dry season. Moreover, differences in precipitation (Fig. S1) influence productivity in tropical
289 savannah environments and for a largely frugivorous bird like the Common Bulbul, fruits are
290 obviously less readily available in the dry season (Ting, Hartley & Burns 2008; Williams & Middleton
291 2008).

292 Our observation of higher body mass during incubation and in the dry season supports observations
293 of higher body mass gain during breeding in species with higher survival probabilities (Cox &
294 Cresswell 2014). Adult survival and, thus, repeat breeding may be the main determinants of fitness
295 in the Common Bulbul because only 1 in 10 nests survive predation on average (pers. obs.).
296 Accordingly, breeding pairs make repeated attempts to breed. In this case, selection should favour
297 traits that enhance adult survival during breeding, therefore increasing the likelihood of future
298 reproduction because there is a high chance that any breeding attempt will turn out unsuccessful.
299 For example, incubating Blue Petrels *Halobaena caerulea* were found to temporarily neglect eggs
300 once body mass fell below a threshold (Chaurand & Weimerskirch 1994). Body mass regulation
301 during breeding may help birds manage less favourable foraging conditions in the dry season and
302 still invest in self-maintaining processes.

303 *General conclusions*

304 Intra-individual analyses of females breeding in both the wet and dry season are crucial for
305 understanding whether this behaviour is consistent or flexible in individuals, depending on
306 immediate foraging conditions or trade-offs that may result from other factors. We observed some
307 level of consistency in a few individuals with breeding records between seasons but lack sufficient
308 observations to test this; moreover, breeding records were generally few and repeated individual
309 captures are stochastic.

310 Understanding body mass variation during breeding as a response to limited foraging time may
311 provide a better appreciation of how birds manage breeding costs, depending on environmental
312 conditions and life-history challenges. Our observations suggest that body reserves are required to
313 buffer the consequence of restricted foraging opportunities during breeding, which may be most
314 pronounced during incubation and in the dry season. Such mass increases during breeding are
315 consistent with an interrupted foraging response, which also seems likely to apply to temperate
316 birds experiencing similarly high restrictions on foraging time. This study, using capture-mark-
317 recapture data from a West African Savannah environment also highlights the relevance of long-
318 term bird ringing operations. It brings to light the added value of tropical seasonality, protracted
319 breeding periods and brood patch scoring to understanding animal ecology (Redfern, 2008; Redfern,
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443

444 **Table 1.** Variation in body mass of female Common Bulbuls *Pycnonotus barbatus* between breeding
 445 stages in a tropical savannah environment. Variation in body mass was modelled by Linear Mixed-
 446 effects Model fit by Restricted Maximum Likelihood. Body mass in breeding females was compared
 447 to females with brood patch score of '0' (non-breeding females), set at the intercept in the model.
 448 Including season of capture did not improve model fit (AIC 929.55 Vs 929.57, L. Ratio = 1.98, $p=0.16$).
 449 Shapiro-Wilk normality test: $W = 0.99$, $p\text{-value} = 0.4$. Brood patch scores are explained in Table S1.

Parameters	Estimate	Error	<i>df</i>	<i>t</i>	<i>p</i>
Intercept	36.27	0.31	177	116.8	<0.001
Wing length	0.24	0.07	177	3.4	0.001
Brood patch score 1	0.60	0.79	177	0.8	0.45
Brood patch score 2	0.76	0.51	177	1.5	0.13
Brood patch score 3	2.94	0.61	177	4.8	<0.001
Brood patch score 4	1.81	0.68	177	2.7	0.01
Brood patch score 5	1.44	0.52	177	2.8	0.01

450 Random effects: Year (N=15); overall sample size = 196; sample size per brood patch score: 0 = 69, 1 = 12, 2 = 40, 3 =23, 4 = 18, 5 = 37.
 451 Significant p -values are given in bold.

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454 **Table 2.** Seasonal difference in body mass of breeding and non-breeding female Common Bulbuls
 455 *Pycnonotus barbatus*, modelled by linear mixed-effects model fit by Restricted Maximum Likelihood.
 456 Breeding birds and the dry season were set at the intercept in the model. Shapiro-Wilk normality
 457 test: $W = 0.99$, p -value = 0.5.

Parameters	Estimate	Error	<i>df</i>	<i>t</i>	<i>p</i>
Intercept	36.30	0.32	93	112.4	<0.001
wing length	0.27	0.09	93	3.0	<0.01
Season (Wet)	0.59	0.51	93	1.1	0.25
Breeding status (breeding)	2.37	0.45	93	5.3	<0.001
Season : Breeding status	-1.54	0.68	93	-2.3	0.03

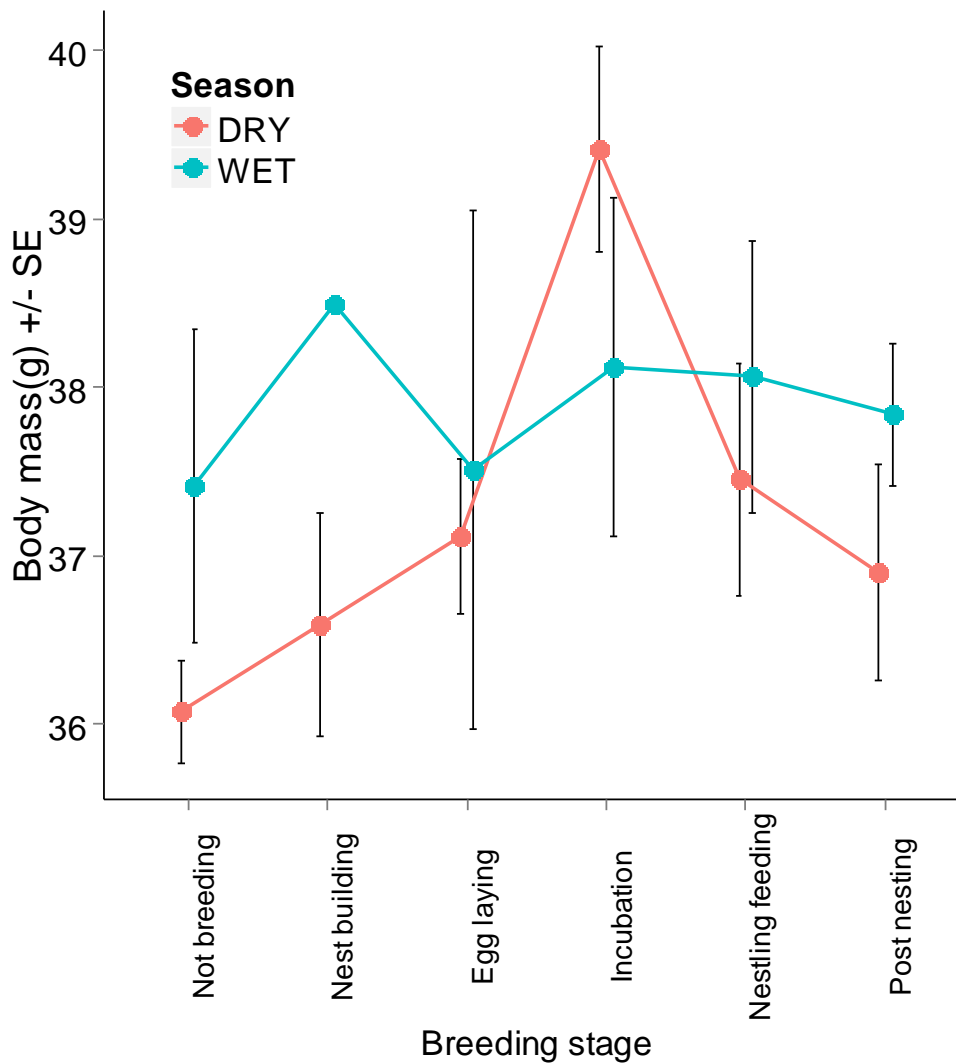
458 Random effects: Year and individual identity; number of individuals = 50, overall number of observations = 147. Significant p -values are
 459 given in bold.

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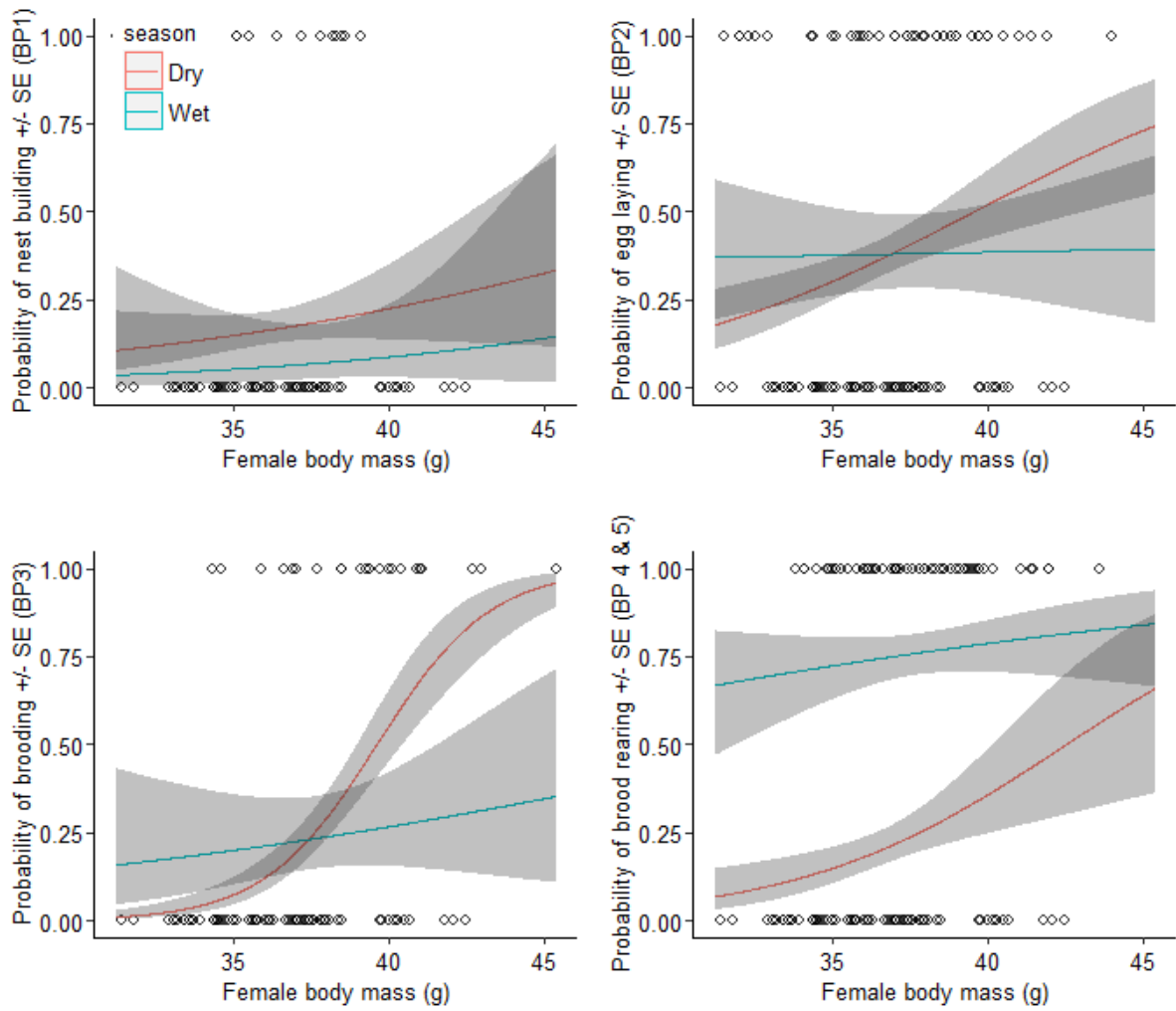
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463 **Figure 1.** Variation in body mass of breeding female Common Bulbuls *Pycnonotus barbatus* at
464 different breeding stages in a tropical savannah environment (determined by brood patch score, see
465 Table S1), means \pm SE calculated from raw data used in Linear Mixed-effect Model (Table 1).
466 Breeding females were heaviest when incubating but lost body mass as brood rearing progressed.



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473 **Figure 2.** In the dry season, there is a high probability that only heavy female Common Bulbuls
474 *Pycnonotus barbatus* are able to incubate eggs or brood chicks. The occurrence of brood patch
475 stages (BP, see Table S1) in female Common Bulbuls predicted by body mass using a logistic
476 regression from a Generalised Linear Model.

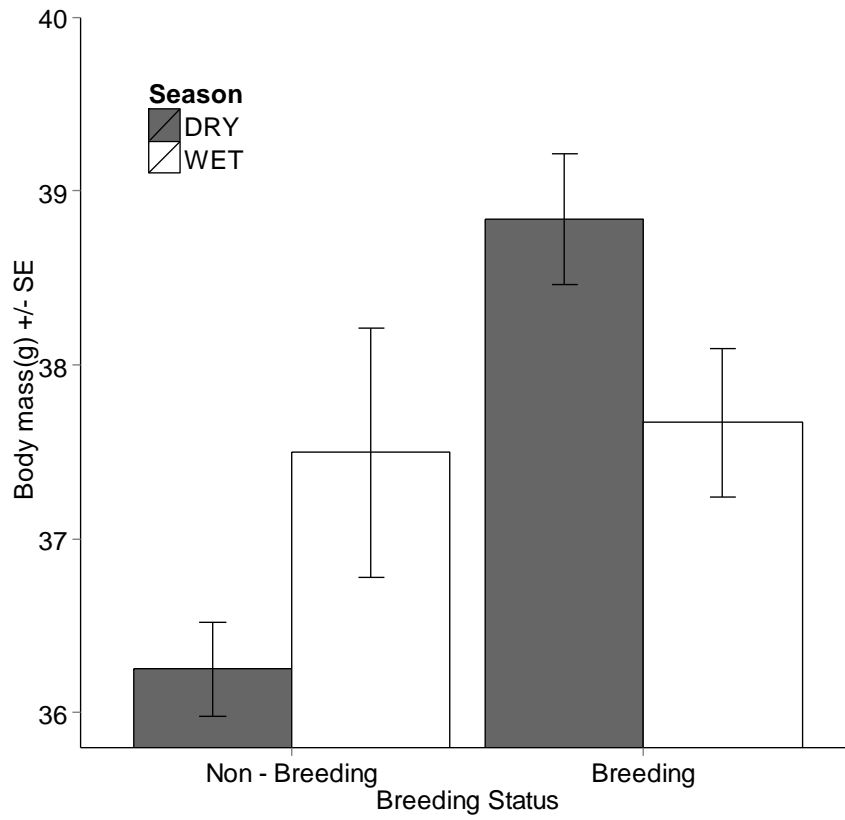


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480 **Figure 3.** Incubating and brood-rearing female Common Bulbuls *Pycnonotus barbatus* were heavier
481 when breeding during the dry season in a tropical savannah environment. Mean body mass \pm SE
482 calculated from raw data used in Linear Mixed-effect Model (Table 2).



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489 **Supplementary information**

490 **Table S1.** Breeding status and stage was assessed based on the presence and development of brood
 491 patches, respectively. Expected sensitivity to flight performance and available foraging time are
 492 scored as low, moderate and high across breeding stages, based on flight requirements and
 493 restriction to foraging, respectively.

Patch score	Patch development	Breeding stage	Sensitivity to Flight performance	Available foraging time
0	No brood patch	Not breeding	Moderate	High
1	De-feathering breast and belly region	Nest building	High	Moderate
2	Vascularisation of breast and belly region/ loose skin	Egg laying	Moderate	Moderate
3	Moderate and marked oedema/ breast muscle obscure and swollen.	Incubation/hatching/ chick brooding	Low	Low
4	No oedema/ skin stretched with marked wrinkles.	Nestling feeding/ fledging	High	Low
5	Re-feathering (white feathers and pins)/ tighter skin.	“Post nesting phase”	Moderate	Moderate

494 Scoring of brood patches were carried out using a six-stage scoring system according to Redfern (2008, 2010) with confirmation from field
 495 observations on the Common Bulbuls *Pycnonotus barbatus*.

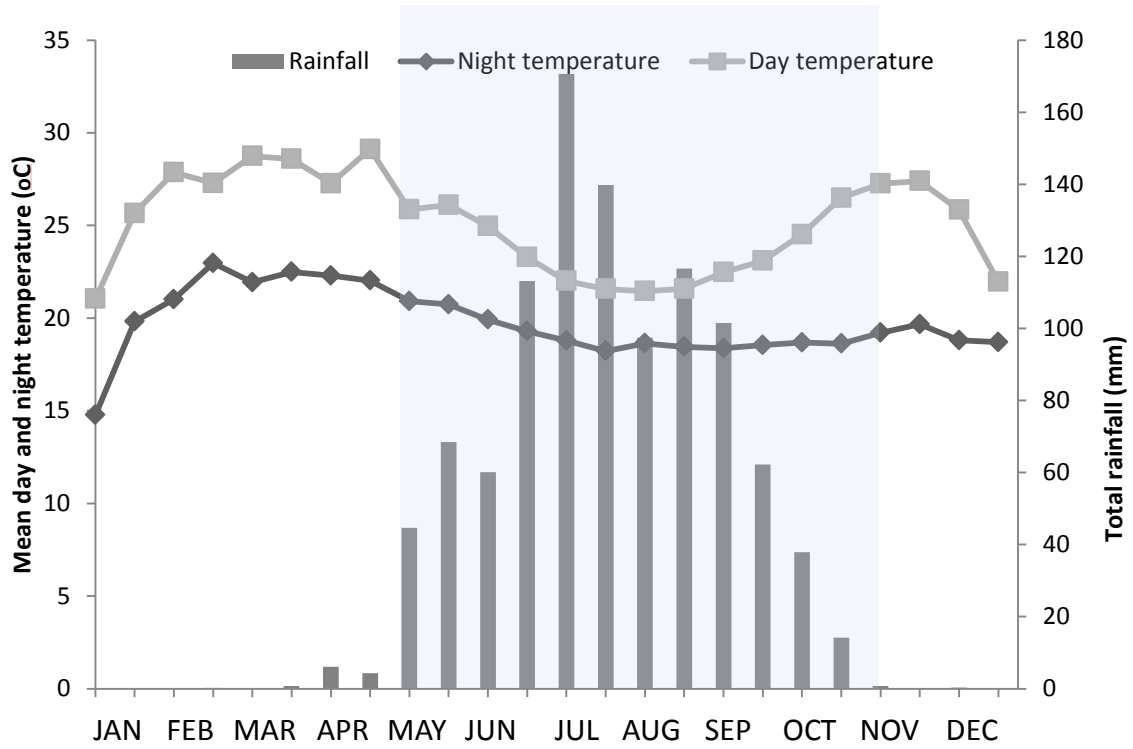
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497 **Table S2.** Pairwise comparison of body mass between breeding stages, based on brood patch
 498 occurrence in female Common Bulbuls *Pycnonotus barbatus* in a tropical savannah environment.
 499 Variation in body mass was modelled by Linear Mixed-effects Model fit by Restricted Maximum
 500 Likelihood (Table 1), followed by a multi-comparison of breeding stages using Tukey test from the
 501 Multcomp package.

Parameters	Estimate	Error	z	p
Brood patch score 1 - Brood patch score 0	0.60	0.79	0.8	0.97
Brood patch score 2 - Brood patch score 0	0.76	0.51	1.5	0.65
Brood patch score 3 - Brood patch score 0	2.94	0.61	4.8	<0.001
Brood patch score 4 - Brood patch score 0	1.81	0.68	2.7	0.08
Brood patch score 5 - Brood patch score 0	1.44	0.52	2.8	0.06
Brood patch score 2 - Brood patch score 1	0.16	0.83	0.2	1.00
Brood patch score 3 - Brood patch score 1	2.34	0.90	2.6	0.09
Brood patch score 4 - Brood patch score 1	1.21	0.94	1.3	0.78
Brood patch score 5 - Brood patch score 1	0.84	0.84	1.0	0.91
Brood patch score 3 - Brood patch score 2	2.18	0.66	3.3	0.01
Brood patch score 4 - Brood patch score 2	1.05	0.73	1.4	0.69
Brood patch score 5 - Brood patch score 2	0.68	0.58	1.2	0.84
Brood patch score 4 - Brood patch score 3	-1.13	0.80	-1.4	0.71
Brood patch score 5 - Brood patch score 3	-1.50	0.67	-2.2	0.21
Brood patch score 5 - Brood patch score 4	-0.37	0.73	-0.5	1.00

502 Random effects: Year (N=15); overall sample size = 196; sample size per brood patch score: 0 = 69, 1 = 12, 2 = 40, 3 =23, 4 = 18, 5 = 37.
 503 Significant p-values are given in bold.

504 **Figure S1.** Variation in rainfall and temperature across the annual cycle of the Common Bulbul
 505 *Pycnonotus barbatus* in a tropical Savannah environment, calculated from local weather data
 506 collected between 2012 and 2015 in the Amurum Forest Reserve, north-central Nigeria. Means per
 507 2-week intervals. Blue shading indicates the wet season.



531 **Figure S2.** Annual cycle processes in the Common Bulbul *Pycnonotus barbatus* in a tropical savannah
 532 environment. Top panel – mean monthly body mass of female Common Bulbuls across the year.
 533 Middle panel – mean proportion of suspended molts and proportion of molting birds per 2-week
 534 interval. Bottom panel – mean proportion of breeding females based on occurrence of brood
 535 patches and proportion of juvenile birds in total captures per 2-week interval. All data were
 536 collected between 2001 and 2015 in the Amurum Forest Reserve, North central Nigeria. The wet
 537 season is indicated by the shaded area.

