

Patterns of seasonal and yearly mass variation in West African tropical savannah birds

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Birds in the northern hemisphere usually increase mass reserves in response to seasonal low temperatures and shorter day length that increase foraging unpredictability and so starvation risk. In the lowland tropics, relatively low temperatures and short day lengths are absent and so the risk of starvation may be reduced, leading to much smaller seasonal effects on mass. Nevertheless, other factors such as high temperatures and water and food availability may vary greatly between tropical wet and dry seasons, leading to variable starvation risk and seasonal mass effects. Using data collected from 47 species of birds caught over a 10-year period in a tropical savannah region in West Africa we tested for seasonal variation in mass in response to a predictable, strongly seasonal tropical climate. Many species (91%) showed seasonal variation in mass, and this was often in a clear annual pattern that was constant across the years. Many species (89%) varied their mass in response to seasonally predictable rainfall. Annual variation in mass was also important (45% of species). Relatively few species (13%) had a seasonal pattern of mass variation that varied between years. Feeding guild or migratory status was not found to affect seasonal or annual mass variation. Seasonal mass change was on average 8.1% across the 21 species with a very large sample size and was comparable with both northern and southern temperate species. Our study showed that biologically significant consistent seasonal mass variation is common in tropical savannah bird species, and this is most likely in response to changing resource availability brought about by seasonal rainfall and the interrupted foraging response due to the constraints of breeding.

Keywords: fat regulation, interrupted foraging, life history, mass-dependent predation, West Africa.

Birds regulate their mass as part of the trade-off between the risk of starvation and the risk of predation (Brodin 2001). For example, birds lay down fat deposits to ensure against unpredictable foraging opportunities in winter, when day length and temperature are reduced (Cresswell 1998, Brodin 2007). Carrying fat, however, bears a cost in terms of increased mass-dependent predation risk, due to

reduced acceleration during escape flights of fatter birds (Lima 1986, McNamara & Houston 1990, Houston & McNamara 1993, Witter & Cuthill 1993) and higher metabolic costs and extended exposure to predation while foraging (Lima 1987). Therefore fat reserves are not maintained when starvation risk is reduced, such as during the summer in northern temperate regions when temperatures are higher and foraging is more predictable. A bird's mass is therefore a reflection of environmental conditions (Pravosudov & Grubb 1997).

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Regular low temperatures and short day length occurring in the winter of temperate and boreal regions are the main reason for the seasonal weight variation in birds occurring in northern latitudes (Rogers & Heath-Coss 2003). In the tropics, however, temperature and day length remain relatively constant throughout the year, and so there is no season when birds have a particularly high risk of starvation due to longer and colder nights (Brodin 2007). Warmer, shorter nights, followed by predictable foraging conditions, suggest that tropical birds can afford to avoid the cost of carrying elevated fat reserves throughout the year. Furthermore, the cost of increased fat reserves may be higher in the tropics. Perceived or actual risk of predation may be different in the tropics compared with northern temperate regions (Brandt & Cresswell 2009) because survival rates appear to be higher (Jullien & Clobert 2000, Peach *et al.* 2001, McGregor *et al.* 2007) and there is an increase in the density and diversity of predators (Thiollay 1991, 1999). Nevertheless, significant adaptive mass variation has been recorded in tropical birds (McNeil 1971, Fogden & Fogden 1979, Brandt & Cresswell 2009), although there are surprisingly few studies that have measured this in non-migrating birds. For example, across its geographical range, 59 different populations of a common African species (Common Bulbul *Pycnonotus barbatus*) have been shown to display a degree of plasticity in their weight variation in response to varied environmental conditions. Individual birds tended to be heavier at sites with lower temperatures and populations responded to increased seasonality by increasing their body mass in colder months (Crowe *et al.* 1981).

Although the risk of starvation caused by seasonal low temperatures may be less important in determining seasonal mass change in tropical birds, other factors may still cause mass reserves to vary seasonally. In particular, tropical environments are characterized by rainfall seasonality, with the monsoon rains driving predictable peaks in the abundance of food sources and the availability of standing water (Osborne 2000). Seasonal availability of water (Macmillen 1990) and its interaction with high diurnal temperatures (Goulart & Rodrigues 2007) have both been shown to affect mass reserves in birds. Consequently, many tropical species schedule costly activities, such as breeding, moult and migration, seasonally (Fogden 1972, Elgood *et al.* 1973, Sinclair 1978, Dittami &

Gwinner 1985, Cruz & Andrews 1989, Abrams 1991, Poulin *et al.* 1992). However, any effects of seasonal variation in starvation risk because of variable rainfall may be dependent on feeding guild. Granivores may have a peak of food availability after the rains as grasses set seed (Crowley & Garnett 1999, Brandt & Cresswell 2009), whereas insectivores may have a peak of food availability during the rains as invertebrate numbers peak (Dingle & Khamala 1972).

Temporally variable resources may also result in seasonal movements on many scales (Elgood *et al.* 1973, Karr 1976, Newton 2008). Seasonal mass change could be expected to occur in intra-African migrants as they increase their fuel reserves in preparation for migration (Fry 1967, Jones & Ward 1977, Ward & Jones 1977) due to the high energy demands of migration (King & Farnier 1965, Ramenofsky 1989). Starvation risk, and therefore mass reserves in the tropics, might also be caused by density-dependent processes associated with a higher population density of conspecifics and competitors (Rohde 1992, Gaston 2000). For example, spatial redistribution of birds due to migration may change local competition levels and so seasonal foraging uncertainty for both migrants and residents that the migrants join or leave, again leading to seasonal mass variation (Rogers 1987).

In this paper we use data collected over a 10-year period in a tropical West African savannah to test two hypotheses: (1) that tropical bird species vary their mass seasonally and (2) species that vary their mass do so in response to seasonally variable foraging opportunities characterized by a dry and wet season, moderated by their foraging guild and migratory status.

METHODS

Study site

We estimated the seasonal weight variation of small tropical birds in Guinea savannah woodland at the A. P. Leventis Ornithological Research Institute (APLORI) Amurum Forest Reserve on the Jos Plateau (09°52'N, 08°58'E) and at Yankari Game Reserve (09°45'N, 10°30'E) in Nigeria: we caught 13 353 individuals of 47 species (Table 1). All retraps of birds were excluded from the analysis to avoid pseudoreplication or over-parameterization of the model. We included all species for which more than 60 individuals were caught: species with

Table 1. Seasonal mass variation in 47 species of West African savannah birds captured by mist-netting over a 10-year period in central Nigeria.

Species	<i>n</i>	Guild	<i>W</i> ₁	Δ	Season	Year	Season*Year	Rain	Age	Sex	Wing	ΣS	ΣY	$\Sigma S*Y$	Min. mass (g)	Max. mass (g)	% difference	Mean mass (g)	Season min. mass	Season max. mass	No. of dry season CFS captures	No. of wet season CFS captures	Migratory
Columbiformes																							
Columbidae																							
<i>Streptopelia hypopyrrha</i>	159	F	0.44	3			-			-		0.45	0		32.14	37.71	17	36.58	3	4	113	3	T
<i>Stigmatopelia senegalensis</i>	85	G	0.5	2			-			-		0.6	0		40.69	48.45	19	45.72	3	1	70	15	T
<i>Turtur abyssinicus</i>	230	G	0.41	2			-			-		> 0.99	> 0.99	> 0.99	35.45	39.71	12	37.41	4	2	32	16	R
Collifformes																							
Coliidae																							
<i>Colinus striatus</i>	298	F	0.18	6			-			-		0.48	> 0.99	0.42	51.01	57.09	12	52.27	4	3	117	103	R
Coraciiformes																							
Meropidae																							
<i>Merops bulcocki</i>	205	I	0.26	4			-			-		0.15	0.03		22.77	24.45	7	23.91	3	1	131	31	T
Piciformes																							
Capitonidae																							
<i>Pogonius chrysoconus</i>	239	F	0.23	6			-			-		0.81	0.37		10.50	10.84	3	10.86	1	4	131	50	T
<i>Lybius vieilloti</i>	62	F	0.21	5			-			-		0.45	0		32.14	37.71	17	36.58	3	4	27	14	R
Indicatoridae																							
<i>Indicator indicator</i>	111	I	0.22	4			-			-		0.6	0		40.69	48.45	19	45.72	3	1	47	31	R
Passeriformes																							
Pycnonotidae																							
<i>Pycnonotus barbatus</i>	614	F	0.65	2			-			-		> 0.99	> 0.99	> 0.99	35.45	39.71	12	37.41	4	2	176	113	R
Turdidae																							
<i>Turdus pelios</i>	516	I	0.38	3			-			-		> 0.99	0.09		64.51	69.68	8	65.28	1	3	242	48	T
Muscicapidae																							
<i>Cossypha niveicapilla</i>	176	I	0.36	3			-			-		0.99	0	0	34.00	37.23	10	36.28	2	1	53	13	T
<i>Ceromela familiaris</i>	117	I	0.43	1			-			-		0.69	0		15.59	17.37	11	16.88	4	2	40	11	T
<i>Myrmecocichla cinnamomeiventris</i>	63	I	0.28	3			-			-		0.59	0		39.03	45.59	17	39.35	1	2	18	9	R
Sylviidae																							
<i>Eremomela pusilla</i>	70	I	0.34	2			-			-		0.11	0.29		6.88	7.43	8	7.03	1	2	17	8	T
Cisticolidae																							
<i>Camaroptera brachyura</i>	226	I	0.66	1			-			-		0.66	> 0.99		10.76	11.64	8	10.87	1	3	37	38	R
<i>Prinia subflava</i>	64	I	0.38	3			-			-		0.64	0		6.45	9.33	45	8.40	2	4	11	9	R
<i>Cisticola aberrans</i>	85	I	0.3	4			-			-		0.17	0.04		13.20	13.68	4	13.26	1	3	24	12	R

Table 1. (Continued)

Species	<i>n</i>	Guild	<i>W</i> ₁	Δ	Season	Year	Season*year	Rain	Age	Sex	Wing	ΣS	ΣY	$\Sigma S*Y$	Min. mass (g)	Max. mass (g)	% difference	Mean mass (g)	Season min. mass	Season max. mass	No. of dry season CES captures	No. of wet season CES captures	Migratory
Monarchidae																							
<i>Terpsiphone viridis</i>	84	I	0.59	2								0.96	0.01		13.81	14.68	6	14.21	1	4	35	5	T
Platysteiridae																							
<i>Batis senegalensis</i>	68	I	0.38	3								0.29	0		7.92	10.82	37	9.88	2	4	22	7	T
<i>Platysteria cyanea</i>	94	I	0.38	2								0.1	0.98		13.94	14.86	7	13.79	1	1	18	23	R
Zosteropidae																							
<i>Zosterops senegalensis</i>	241	F	0.4	2								0.55	0.02		9.42	9.66	2	9.42	2	3	60	47	R
Nectarinidae																							
<i>Cyanomitra verticalis</i>	130	N	0.78	1								0.91	0.02		11.52	12.87	12	12.15	2	4	36	37	R
<i>Chlomitra senegalensis</i>	476	N	0.39	3								0.97	> 0.99		10.69	11.13	4	10.23	4	3	185	75	T
<i>Cinnyris venustus</i>	354	N	0.14	8								0.87	0.64		6.15	6.43	5	6.26	3	1	141	51	T
<i>Cinnyris pulchellus</i>	201	N	0.58	2								0.05	0.03		7.11	8.05	13	6.98	4	3	17	15	R
Malacoitidae																							
<i>Laniarius barbarus</i>	82	I	0.34	4								0.46	0.53		46.78	51.84	11	48.89	1	4	24	10	T
Passeridae																							
<i>Petronia dentata</i>	64	G	0.46	2								0.89	0		15.61	23.84	53	18.00	1	3	20	2	T
<i>Sporopipes frontalis</i>	62	G	0.15	7								0.25	0.09		17.06	19.10	12	17.02	1	3	22	15	R
Ploceidae																							
<i>Ploceus luteolus</i>	147	G	0.42	1								0.7	> 0.99		13.67	14.79	8	14.44	2	3	28	22	R
<i>Ploceus vitellinus</i>	284	G	0.33	3								0.63	0.35		17.94	21.61	20	20.18	2	4	59	27	T
<i>Ploceus heuglini</i>	81	G	0.35	3								0.48	0.02		20.95	27.91	33	23.61	3	4	56	10	T
<i>Ploceus cucullatus</i>	738	G	0.61	2								0.99	> 0.99	0.99	36.45	40.25	11	36.38	2	3	203	107	R
<i>Ploceus nigricollis</i>	209	G	0.43	2								> 0.99	0.31		25.01	26.63	6	26.40	1	4	59	46	R
<i>Euplectes hordeaceus</i>	169	G	0.86	1								> 0.99	0.01		17.15	21.95	28	19.99	2	4	94	23	T
<i>Euplectes franciscanus</i>	1762	G	0.38	2								> 0.99	> 0.99	> 0.99	14.67	15.46	5	15.22	1	3	246	1335	T
Estrilidae																							
<i>Estrilda melpoda</i>	88	G	0.27	3								0.34	0.14		7.06	7.93	12	7.21	4	3	23	7	T
<i>Estrilda caerulescens</i>	530	G	0.27	4								0.49	> 0.99	0.05	8.92	9.46	6	9.22	4	3	158	73	T
<i>Estrilda troglodytes</i>	149	G	0.23	3								0.48	0.92		7.79	8.17	5	7.62	1	4	56	26	T
<i>Uraeginthus bengalus</i>	692	G	0.46	3								0.78	> 0.99		9.72	10.22	5	10.08	4	3	81	207	T
<i>Oryzopsis atricollis</i>	139	G	0.22	6								0.98	0		10.31	11.11	8	10.58	1	3	74	39	R
<i>Lagonosticta rufopicta</i>	113	G	0.24	3								0.6	0.13		9.43	10.23	9	9.27	4	3	13	21	R
<i>Lagonosticta senegala</i>	763	G	0.46	2								> 0.99	0.93		8.06	8.60	7	8.69	2	4	79	194	T
<i>Lagonosticta sanguinodorsalis</i>	480	G	0.54	1								> 0.99	> 0.99	0.97	9.98	11.05	11	10.45	1	3	60	71	R
<i>Lagonosticta rara</i>	84	G	0.18	5								0.17	0.44		9.73	10.37	7	9.82	1	3	35	8	T
<i>Spermestes cucullatus</i>	768	G	0.5	2								> 0.99	> 0.99	> 0.99	8.75	9.22	5	8.94	2	3	286	142	T

Table 1. (Continued)

Species	n	Guild	W_1	Δ	Season	Year	Season*year	Rain	Age	Sex	Wing	ΣS	ΣY	ΣS^*Y	Min. mass (g)	Max. mass (g)	% difference	Mean mass (g)	Season min. mass	Season max. mass	No. of dry season CES captures	No. of wet season CES captures	Migratory
Viduidae																							
<i>Vidua chalybeata</i>	71	G	0.31	3	■		-	■		-	■	0.51	0		11.55	12.48	8	12.24	2	4	10	16	R
Emberizidae																							
<i>Emberiza tahapisi</i>	361	G	0.2	6	■		-	■		-	■	0.62	0.18		13.36	14.50	9	13.50	3	4	147	35	T

Results of models to test whether there was seasonal (S), annual (Y) or variation in mass controlling for rainfall, age, sex and wing length. We used AICc to calculate the Akaike weight (W_1) of the top model and the number of models which show equal support for the top model (Δ , $\Delta < 2$). We present which variables were present (■) or absent () in the top models (– denotes that the variable was not analysed in the model), and the relative importance (Σ) of a predictor as the sum of the W_1 of the models in which the predictor was present. Minimum and maximum mass and the proportional maximum mass change between seasons are given along with the season of the minimum and maximum mass. We identified species guilds from diet in Elgood *et al.* (1994), Urban *et al.* (1997) and Fry *et al.* (2004): I, insectivore; F, frugivore; N, nectivore; G, granivore. Transient status was identified over resident status by a > 50% change in capture rate between dry and wet season CES.

smaller sample sizes did not have a sufficient spread of captures across seasons and years to allow meaningful analysis.

Birds were trapped using understorey mist-nets between November 2001 and March 2011. Trapping occurred year round but was concentrated at a Constant Effort Site (CES) conducted biannually in Amurum for a 14-day period at the end of the dry season (March–April) and at the end of the wet season (September–October). During the CES, 272 m of four shelf-nets was used between 06:00 and 10:30 h WAT (although there were few captures after 09:30 h). Trapped birds were aged and sexed where possible. Maximum wing-chord was measured using a stopped wing rule to 1 mm (Svensson 1992). Mass was measured to 0.1 g using digital scales (Ohaus Scout). For each species, the time of year was classified into four seasons estimated from the approximate start and finish of the rains: end of dry season (February–April), start of wet season (May–July), end of wet season (August–October) and start of dry season (November–January). Seasonal rainfall at the site was estimated from monthly rainfall summaries from Jos Airport (09°52'N, 08°53'E), which is located in the centre of Jos Plateau and 26 km from Amurum Forest Reserve. Each species was assigned a residency status on the basis of seasonal variation in capture rates. Migratory status was assigned to any species that had > 50% reduction in capture rate between the end of the wet season and the end of the dry season CES (Table 1). A species was considered sedentary if there was a < 50% variation in catching totals between CESs. Species were assigned to feeding guilds according to diet (Elgood *et al.* 1994, Urban *et al.* 1997, Fry *et al.* 2004).

Variables and statistical analysis

We adopted the information-theoretic statistical approach to test for the relative importance of six parameters on mass variation in each species (Akaike's information criterion, AICc, Burnham & Anderson 2002). Parameters included in the model were season (S), year (Y), variation in the annual timing of mass variation (S*Y), age, seasonal rainfall (mm), sex (where sexes could be reliably distinguished in the hand) and wing length (as an index of overall size, in mm). We included the interaction (S*Y) to test whether seasonal patterns were consistent between years. If S*Y was not

significant ($n = 40$ species), we reran the model excluding this interaction. If $S*Y$ was significant ($n = 7$ species), we ran separate models for every year and averaged effect size across years.

The mass of a species for a particular season was calculated from the parameter estimates (for example, $\text{mass} = \text{intercept} + (\text{mean wing} * \text{wing estimate}) + \text{year estimate} + (\text{total rain} * \text{rain estimate}) + \text{age estimate for adults} + \text{sex estimate (if included)} + \text{season estimate}$). The predicted mass of a species in the lightest and heaviest season within a year was calculated by using the season with the lowest and highest parameter estimate, respectively. The proportional difference in predicted mass between the lightest and heaviest season was then calculated $((\text{mass in the heaviest season} - \text{mass in the lightest season}) / \text{mass in the lightest season})$. To standardize effects across species, the estimate for year was arbitrarily set for 2006 (the year of largest sample size and mid-point of the study) for species with models that did not show a significant interaction of season with year ($S*Y$). For species where this interaction was significant, we simply averaged effect sizes across the models from different years.

The best models were then evaluated using AICc to calculate the Akaike weight (W_1) of the top model. W_1 converts the deviance of all possible models to a scale of zero to one. Each weight then represents the likeliness that that model is the best model. We also calculated the number of models which showed equal support for the top model ($\Delta < 2$; Burnham & Anderson 2002, Richards 2005). We recorded which variables were represented in models where $\Delta < 2$ (Table 1, Fig. 1) before model averaging all possible models to obtain relative variable weights. There was a positive relationship between sample size and the weight of the top model and a negative relationship between sample size and the number of models where $\Delta < 2$. Analysis was conducted using the MuMIn and lme4 packages in R 2.13.0 (R Development Core Team 2011).

We examined to what extent the range of species in our sample was phylogenetically representative of West African savannah birds. Although we sampled reasonably randomly with respect to species that might show seasonal mass variation (any species caught in sufficient numbers by mist-netting was included here), any overall estimate of the proportion of species showing seasonal mass gain may be confounded if some genera (or

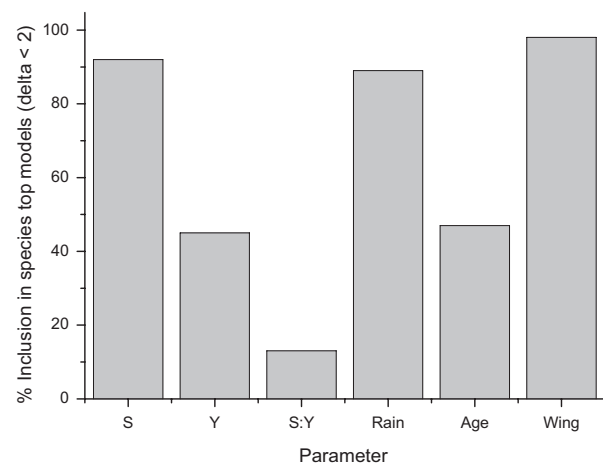


Figure 1. Proportional representation in top models of species ($\Delta < 2$) of the effect on bird mass of the parameters: season (S), year (Y), variation in seasonal mass change pattern ($S*Y$), rain, age and wing (sex not shown because it was not tested for every species).

families, or orders) were sampled more frequently with respect to proportion of species than others, and some taxa are more likely to show seasonal mass change than others. We adjusted for any such effects of uneven sampling across species by multiplying the total number of species within genera (or within families, or within order) available at the study site by the proportion of species sampled within that genera (or family, or order) that showed seasonal mass change. We then averaged this true estimate of the number of species within genera across all genera present at the study sites (or species within families across all families present at the study sites, or species within an order across all orders present at the study sites) showing seasonal mass change.

Time of day was not included in the analysis because these data were missing in many cases and including it would have reduced our sample sizes greatly. Inclusion of time of day to the nearest hour in the best model for each species did not significantly affect seasonal and annual parameter estimates except as might be expected by a reduction in sample size ($n = 9010$, species = 38). The lack of effect of time of day on seasonal results was expected because data were almost always collected between 06:30 and 10:30 h (and most commonly between 07:00 and 09:00 h), and any effects acted in an unbiased way across seasons.

Ethical note: although the research work described here does not require any licences within

Nigeria, all ringing was directly carried out and supervised by British Trust for Ornithology (BTO) 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.

RESULTS

There was strong evidence for consistent seasonal mass variation linked to rainfall variation in most species. Season was included as a parameter in at least one of the top models for 43 species (91%, Table 1, Fig. 1). All four species that did not include season in their top models had significantly different seasonal catching totals and small sample sizes (Table 1), suggesting that seasonal mass variation may have been detected in these species with a larger or more seasonally uniform dataset. The timing of the seasonal mass change varied across years for six species (13%, Table 1). Year was included as a parameter in at least one of the top models for 21 species (45%, Table 1). Rainfall was included as a parameter in at least one of the top models for 42 species (89%, Table 1). Examples of a species showing predictable seasonal variation in mass (African Thrush *Turdus pelios*) and a species showing variation in the seasonal pattern of mass change dependent on year (Northern Red Bishop *Euplectes franciscanus*) are illustrated in Figure 2.

Seasonal mass change was on average 12.6% (± 1.6) across the 47 species. Most species had their highest mean mass at the end of the wet season and start of the dry season, but there was no clear season in which most species were lightest (Table 1, Fig. 3). There was no significant difference in the frequency of the season with the lowest mass ($\chi^2_3 = 0.3$, $P = 0.96$) or highest mass ($\chi^2_3 = 0.5$, $P = 0.93$) according to resident or transient status (Table 1). The effects of the predictor variables were fairly consistent regardless of feeding guild, and there was no significant difference in the frequency of the season of lowest mass ($\chi^2_9 = 9.8$, $P = 0.37$) or highest mass ($\chi^2_9 = 15.8$, $P = 0.07$) according to guild (Table 2). There was no significant variation in percentage mass change by either residency status ($F_{1,41} = 0.03$, $P = 0.86$) or guild ($F_{3,41} = 0.3$, $P = 0.80$) controlling for overall mass ($F_{1,41} = 0.4$, $P = 0.53$).

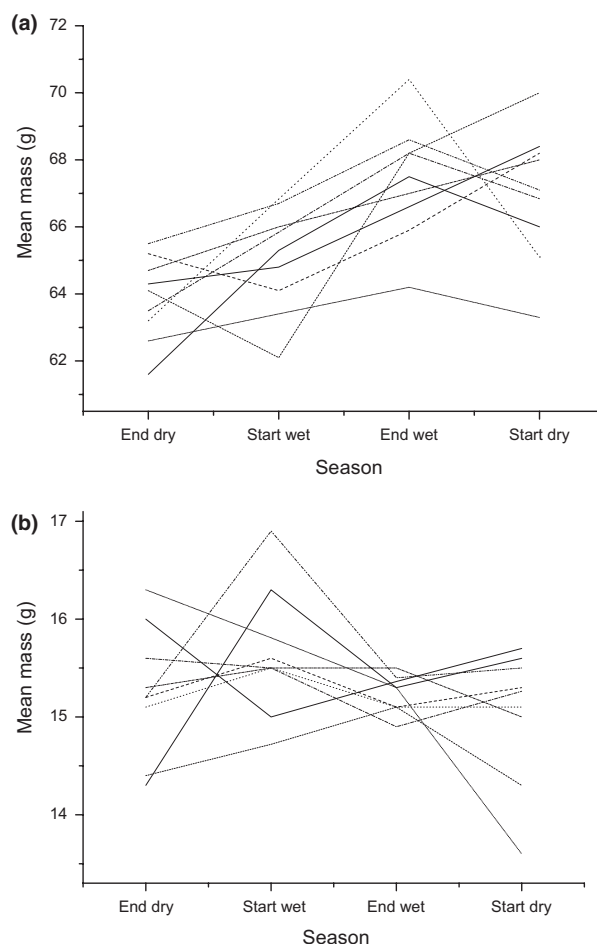


Figure 2. Species which displayed mass variation were found either to: (a) vary their mass in a clear annual pattern that was consistent across the years ($n = 37$) or (b) vary their mass differently in different seasons across years ($n = 6$). We present the mean mass of two case study species by season and year: individual lines represent different years. (a) African Thrush ($n = 516$), which is heaviest at the end of the wet season (69.7 g, $n = 89$) and lightest at the end of the dry season (64.5 g, $n = 324$), resulting in an 8% annual change in mean mass. (b) Northern Red Bishop ($n = 1762$), which is on average heaviest at the end of the wet season (15.2 g, $n = 511$) and lightest at the end of the dry season (14.7 g, $n = 391$), resulting in a 5% annual change in mean mass.

Of the 194 possible species caught during mist-netting at Amurum and Yankari, 47 (24.2%) provided mass data sufficient for meaningful analysis and 43 showed seasonal mass variation in their top models. Unbiased estimates of occurrence of seasonal mass change were high at all taxonomic levels. Seasonal mass change was estimated to occur in 91.9% (± 4.4) of species within genera averaged across all genera present at the sites

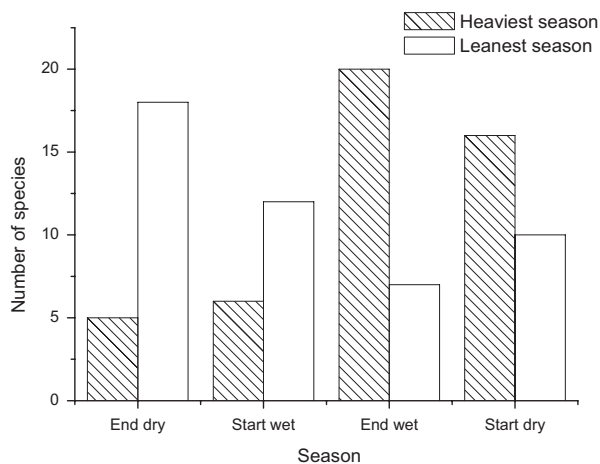


Figure 3. Season of the highest and lowest mass for 47 species of tropical savannah bird, from data pooled across years. Most species were heaviest at the end of the wet season or start of the dry season ($\chi^2_3 = 14.0$, $P = 0.003$), whereas there was no season in which most species were lightest ($\chi^2_3 = 5.5$, $P = 0.14$).

($n = 79$ possible species in the 32 genera caught), in 90.8% (± 5.5) of species within family averaged

across all families present at the sites ($n = 118$ possible species in the 20 families caught), and in 97.9% (± 2.0) of species within order averaged across all orders present at the sites ($n = 163$ possible species in the five orders caught).

DISCUSSION

Our study showed that the mass of about 91% of tropical savannah species was affected by season grouped into wet and dry periods. Rainfall was in the top models for 89% of these species and in all top models for species where the seasonal timing of mass varied significantly between years, suggesting that the annual variation in the arrival of the rains is important as well as its variability. There were no clear differences in seasonal mass patterns with migratory status or foraging guild, again suggesting a reasonable consistency of selection for mass regulation in response to rainfall across species.

The magnitude of seasonal mass gain was of the order of 12.6%. Six species showed relatively high

Table 2. Important parameters affecting mass in 47 species of West African tropical bird, summarized across four feeding guilds (mean values and percentage inclusions were calculated from Table 1, see also Table 1 for variable explanations).

	Frugivores	Insectivores	Nectivores	Granivores	All species
No. species	6	14	4	23	47
Migratory status					
Transient	2	8	2	14	26
Resident	4	6	2	9	21
Mean W_1	0.35	0.35	0.47	0.47	0.38
Mean Δ	4	3.5	3	3	3.4
%inclusion of each variable in the top models ($\Delta < 2$)					
S	100	86	75	96	92
Y	50	29	50	52	47
S*Y	33	0	0	17	13
Rain	100	86	100	87	89
Age	66	57	100	35	47
Wing	100	100	100	96	98
Mean Σ of predictor variables					
S	0.6	0.53	0.7	0.68	0.63
Y	0.4	0.21	0.42	0.43	0.37
Season of minimum mass					
1	1	8	0	9	18
2	1	3	1	7	12
3	1	2	1	3	7
4	3	1	2	4	10
Season of maximum mass					
1	0	4	1	0	5
2	2	3	0	1	6
3	2	3	2	13	20
4	2	4	1	9	16

variation in seasonal mass ($> 25\%$), but their analyses were probably less reliable because of small sample sizes ($n < 200$). After controlling for sample size (by including only species where $n > 200$) the maximum average degree of seasonal mass change in tropical species ($8 \pm 4.1\%$, species = 21) was comparable with both northern temperate (maximum of 12%, Baldwin & Kendeigh 1938; 2–8%, September–December only, Haftorn 1989) and southern temperate species (8–14%, Rozman *et al.* 2003). Even the four species (9%) which did not have season in their top models showed a comparable variation range in mass gain (9%).

That variation in the timing and amount of rainfall results in consistent mass variation across many bird species is perhaps not surprising. There is strong seasonality in the tropics brought about by the arrival of the rains, which causes a profound increase in primary productivity and the availability of standing water (Dingle & Khamala 1972, Wolda 1978, Poulin *et al.* 1992). Species were generally heaviest during the late wet season, which probably coincided with high vertebrate populations (Dingle & Khamala 1972), or at the start of the dry season, when seed availability is most abundant (Crowley & Garnett 1999, Brandt & Cresswell 2009). This also coincided with the peak of breeding for many species (unpublished data from the occurrence of brood patches during the CES). We conclude that although there is no 'winter' period with a particularly high starvation risk, the arrival of the rains and the subsequent increase in resources changes the predictability of the foraging environment for many species, causing variation in fat reserves.

That mass reserves *peak* with favourable foraging conditions in tropical savannah birds presents an apparent conflict when considering the northern hemisphere paradigm of *low* fat reserves being associated with favourable foraging conditions. However, under increasingly favourable foraging conditions and constraints to foraging time such as high predation risk, an increase in resource availability may result in a shift from a mass-dependent predation risk response (where birds lose mass) to an interrupted foraging response (where birds increase in mass; Lima 1986, Houston & McNamara 1993, Houston *et al.* 1993). This is because overall mass levels are affected not only by foraging unpredictability as a direct consequence of environmental factors (such as temperature) but also by conflicts with foraging such as avoiding

predators. For example, when prey avoid predators, both in time and space, the prey's foraging options are reduced and this may then lead to mass increases as insurance against the increased unpredictability in foraging (Lilliendahl 1998, Gentle & Gosler 2001, Rands & Cuthill 2001). However, interrupted foraging occurs only if foraging conditions are sufficiently good to allow long-term energy budgets to be met in the remaining time and space available after birds have avoided predators (Brodin 2007). Although it is well established that reduction in foraging predictability directly from the environment leads to high total body mass (e.g. Rogers 1987, Bednekoff *et al.* 1994, Gosler *et al.* 1995, Cresswell 1998), these studies are all associated with northern temperate winters, when environmental effects on foraging predictability are likely to be very severe. In tropical areas, the effects of behaviours that conflict with foraging may be relatively more important because baseline foraging certainty is always relatively high and so mass response by birds may be largely concerned with interrupted foraging responses. Such situations are possible even in northern temperate species, as demonstrated by a range of species (MacLeod *et al.* 2007), particularly by Great Tits *Parus major* (Cresswell *et al.* 2009).

Overall, our results of lowest mass, on average, in the non-breeding season suggest that foraging predictability in the tropics (and possibly in the southern hemisphere; Rozman *et al.* 2003) remains high, probably because of relatively high temperatures and relatively little shortening of day length. Consequently, birds can minimize mass to avoid mass-dependent costs. In contrast, in the northern temperate non-breeding season, much greater unpredictable foraging associated with very long nights followed by freezing days, when foraging is impossible, causes birds to increase fat reserves. Temperate species therefore accept a higher maintenance cost and a higher predation risk in the non-breeding season, which may account for some of the lower survival rates reported on average for temperate vs. tropical species (McGregor *et al.* 2007). Furthermore, we suggest that a seasonal breeding period in both temperate and tropical areas is associated with increased mass because the constraints of breeding reduce foraging predictability in terms of self-maintenance for an adult bird. In other words, breeding season priorities such as feeding chicks, singing, territory maintenance, mate

guarding and nest building conflict with foraging, but increased mass reserves allow self-maintenance to be scheduled between these activities rather than always taking priority. Consequently, we see an interrupted foraging response associated with the breeding season because many breeding activities conflict with foraging for self-maintenance. However, in temperate areas this mass increase is not apparent because it is always measured relative to the greater mass increase in the non-breeding season preceding it. It is interesting to note that in temperate species, where annual mass variation has been analysed in detail, minimum annual mass occurs immediately after breeding, before moult (e.g. Macleod *et al.* 2005). This relatively brief period of long day length and favourable temperatures where only self-maintenance is required, is perhaps then equivalent to the non-breeding season in tropical areas.

We could find little evidence for the effects of seasonal mass gain associated with migrants. We suggest that many transient species only travel relatively short distances within Africa, and do not need to cross barriers, so they may be able to forage each day while they migrate in short daily legs (Elgood *et al.* 1973, Payne 1980). We also found little evidence for any effects of potential changes in density associated with some species migrating, despite major changes in abundance of many species across seasons. For example, resident populations of species such as the Northern Red Bishop show increased population density during the rains as transient populations converge at breeding locations (Craig 1980). However, our study was not designed to test these hypotheses specifically and it seems likely that true migratory fattening occurs in long distance intra-African migrants and as a result of competition. Further research is needed at sites which have greater variation in both these variables than we could measure.

Overall, our results show that approximately nine of 10 tropical savannah species from West Africa vary their mass seasonally and we provide evidence that this is most likely in response to rainfall seasonality. We suggest that these birds vary their mass in response to a variation in resource availability and foraging constraint as in temperate birds, but the season with the maximum mass is that with the highest resource availability as a consequence of the interrupted foraging response and relatively high foraging predictability during the rest of the year.

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