RESEARCH PAPER

Scale effects on the body size frequency distributions of African birds: patterns and potential mechanisms

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ABSTRACT

Aim To describe and analyse the body size frequency distributions (BSFDs) of avian assemblages at several spatial scales in the Afrotropics. We also tested if the variation in median body size across assemblages at different spatial scales was related to environmental variables and whether purely stochastic processes could explain BSFDs.

Location The Afrotropical biogeographic realm.

Methods Avian body masses for 1960 species where analysed at continental, biome, ecoregion and local spatial scales with standard metrics. Variation in median assemblage body size was modelled as a function of environmental and spatial explanatory variables to assess non-random assemblage structure. We tested if BSFDs of smaller spatial scale distributions are random subsets of the larger spatial scale assemblages in which they are embedded, and used three different null model randomizations to investigate the influence of stochastic processes on BSFDs.

Results The African avifauna's continental BSFD is unimodal and right-skewed. BSFDs generally become less skewed and less modal with decreasing spatial scale. The best-fit model explained 71% of median body size values at the ecoregion scale as a function of latitude, latitude^2, longitude, species richness and species range size. BSFDs at smaller scales show non-random assembly from larger scale BSFDs distributions.

Main conclusion African avifaunal BSFDs are quantitatively dissimilar to African mammal BSFDs, which are bimodal at all spatial scales. Much of the change in median body size with spatial scale can be captured by a range-weighted null model, suggesting that differential turnover between smaller- and larger-bodied species might explain the shift in the central tendency of the BSFD. At the local scale, energy may well contribute to structuring BSFDs, but this pattern is less pronounced at larger spatial scales.

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INTRODUCTION

Body size is one of the most striking attributes of an organism. It affects many physiological and ecological traits (Gaston & Blackburn, 2000), including species home range size (Haskell *et al.*, 2002), species abundances (Lewis *et al.*, 2008), geographic range size (Gaston & Blackburn, 1996) life-history strategies (Rohwer *et al.*, 2009) and can mediate invasions (Roy *et al.*, 2002). Species extinction probabilities are also linked to body size (Gaston & Blackburn, 1995, 1996; Fritz *et al.*, 2009). Therefore, investigations of spatial variation in body size have provided important insights into the ecological and evolutionary processes structuring biological assemblages, with considerable implications for conservation (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Roy *et al.*, 2001; Gaston *et al.*, 2008; Meiri *et al.*, 2009).

Species body size frequency distributions (BSFDs) form a significant means of understanding spatial variation in body size

(Gaston & Blackburn, 2000). Thus, determining the generality of BSFDs across taxa, regions and spatial scales, and the mechanisms underlying deviations from general patterns are fundamental questions in macroecology (Gaston & Blackburn, 2000). Although much is now known about general patterns in BSFDs at the broadest spatial scales (Blackburn & Gaston, 1994; Roy et al., 2000; Smith et al., 2004), at smaller spatial scales the nature of variation in BSFDs and the mechanisms underlying this variation are not as comprehensively understood. At the regional to global scale, BSFDs for birds, mammals, lizards, bivalves and most insects are generally strongly right-skewed on a logarithmic scale (Brown & Nicoletto, 1991; Gaston & Blackburn, 2000; Roy et al., 2000; Meiri, 2008; Chown & Gaston, 2010), but bimodal for North American squamates (Cox et al., 2011) and not skewed in snakes (Boback & Guyer, 2003), some beetles (Dixon & Hemptinne, 2001), or squamates generally (Reed & Boback, 2002). At smaller spatial scales BSFDs can also be highly variable, ranging between right-skewed (Gaston et al., 2001), less strongly right-skewed (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Smith et al., 2004; Greve et al., 2008; Chown & Gaston, 2010), flat (indistinguishable from log-uniform) (Marquet & Cofré, 1999), or even multimodal (Chown & Gaston, 1997; Raffaelli et al., 2000; Kelt & Meyer, 2009; Cox et al., 2011).

For smaller spatial scales, a key question is whether BSFDs are merely random subsets from the larger spatial scale assemblages in which they are embedded. If they are not, then some factor must be invoked at that scale to explain observed BSFDs (Gaston & Blackburn, 2000). In North and South American mammals, smaller spatial scale BSFDs are not random subsets of the larger scale BSFDs (Brown & Nicoletto, 1991; Bakker & Kelt, 2000). BSFDs of North American mammals are modal and right-skewed, show non-random assembly, and decrease in skewness in assemblages at progressively finer spatial scales. Brown & Nicoletto (1991) ascribed this pattern to three main mechanisms: (1) competition for limited resources means local faunas contain fewer modal-sized species; (2) large species with small geographic ranges are more extinction prone; and (3) allometric constraints on physiology lead to greater specialization of modal-sized species. However, Cox et al. (2011) argued that these mechanisms may be of less importance for the squamates of North America, with deep phylogenetic differences among component taxa being more significant. The BSFDs of South American mammals in general are similar to those of North American mammals in showing non-random assembly, but they are multimodal at all spatial scales and do not become indistinguishable from log-normal at the smallest spatial scales (Marquet & Cofré, 1999). The additional mode persists at smaller spatial scales, and could be due to habitat specialization (Bakker & Kelt, 2000). The BSFDs of African mammal assemblages are multimodal at all spatial scales. Kelt & Meyer (2009) suggested that the secondary mode could be a consequence of the assemblage not being as adversely affected by anthropogenic Pleistocene extinctions as in other regions, but they did not test if local assemblages were random subsets from the larger species pool.

The global bird BSFD is right-skewed (Blackburn & Gaston, 1994), just as in the Americas (Cardillo, 2002). South African birds also have right-skewed BSFDs, and much of the variation in median body size can be predicted by randomly drawing species from the regional distribution (Greve et al., 2008). Therefore, purely stochastic processes also need to be taken into account when explaining BSFDs as they can contribute to observed patterns (Meiri & Thomas, 2007). Blackburn & Gaston (2001) showed that in a local assemblage of birds in Britain, a random draw model from the regional bird assemblage accurately predicts most descriptive statistics if the probability that a species is selected is weighted by its geographic range size. However it is unclear how ubiquitous right-skewed BSFDs are for birds, whether BSFDs at smaller scales are indeed non-random subsets of larger scale distributions, and what mechanisms might underlie the scaling effects on BSFDs.

Here, we therefore analyse the BSFDs of avian assemblages at several spatial scales across the Afrotropics. We test whether the variation in median body size across assemblages at different spatial scales was related to energy, species richness and range size, all variables which are known to correlate with the median body size of birds globally (Olson et al., 2009). We also test whether smaller spatial scale distributions are random subsets of the larger spatial scale assemblages in which they are embedded. The influence of stochastic processes on BSFDs is further investigated by comparing observed distributions to three types of null distributions generated by randomly resampling the continental avifauna. Finally, we determine whether energy, species richness and range size could explain the deviation of the model null distributions from the median observed data, at the local scale.

METHODS

Species distribution data

We used the WWF Wildfinder database (Olson et al., 2001) at the ecoregions scale as a template for collating data on all bird species in the Afrotropical bioregion, excluding offshore islands, the Arabian Peninsula and Madagascar. Ecoregions are spatially discrete units that contain geographically distinct assemblages of natural communities that share a large majority of their species, ecological dynamics and similar environmental conditions (Olson et al., 2001). The taxonomy and distribution of species was comprehensively updated from Sinclair & Ryan (2003). The ranges of species absent from the Wildfinder database (mainly due to taxonomic changes and errors) were digitized in ESRI ArcGIS 9.3 (2011) at the ecoregion scale from Sinclair & Ryan (2003). This study focuses on terrestrial species, excluding vagrants, introduced species and offshore-nesting seabirds. We included migrant species here as their inclusion or exclusion had no significant effect on the BSFD of the South African avifauna (Greve et al., 2008). While in polar and temperate regions small-bodied migratory species are significantly overrepresented (Olson et al., 2009), our study area is not in these regions, further motivating the inclusion of migrants.

Species were assigned to a continental species list, biome species lists, ecoregion species lists and local scale lists. Species lists were generated from the continental species lists for the seven major biomes of sub-Saharan Africa (Deserts and Xeric Scrubland, Mediterranean, Grasslands, Savanna, Flooded Savanna, Moist Broadleaf Rainforests, and Dry Broadleaf Rainforests following Olson *et al.,* 2001). A total of 86 ecoregions were used, excluding mangroves. Local lists were compiled for sites that were historically undisturbed (preferably Protected Areas), and had been surveyed in at least two seasons or years using multiple techniques. Local scale sites varied in size but averaged approximately 25 km^2. A total of 23 local scale lists were used for analysis, with representation from all biomes (see Supporting Information Appendix S1 and a map of the study region in Appendix S2).

Body size data

Body mass data for all species was primarily obtained from Dunning (2008), and supplemented with data from Hockey *et al.* (2005) and Fry *et al.* (1988) where needed. We accounted for different reporting standards in the data (such as masses for one sex only, masses for few individuals, and masses from different locations) using the methods of Greve *et al.* (2008). Where races differed in body size (as reported in Dunning, 2008), but were treated as one species in Sinclair & Ryan (2003), the mean body size across races was used. Since the masses of 10% of species (200/1967) could not be obtained from the literature, we divided the database into two sets. First, we used all the species with mass data obtained from the literature ($n = 1767$). Second, we estimated the mass of species lacking data by averaging the masses of all congeners ($n = 1967$). For seven of these species in monotypic genera body masses could not be estimated by this method and these species were omitted from this study (*Coccycolius iris*, *Dryotriorchis spectabilis*, *Pseudoalcippe abyssinica*, *Pseudochelidon eurystomina*, *Tigriornis leucolophus*, *Todirhamphus chloris* and *Zavattariornis stresemanni*). The distribution of bird body sizes from the two datasets did not differ significantly (Kolmogorov–Smirnov (KS) test, $D = 0.0211$, $P > 0.99$) and did not lead to different interpretations from the BSFDs (data not shown) and, therefore, we only report results further including the data calculated from congeners ($n = 1960$). Both the common and Somali ostriches (*Struthio camelus* and *S. molybdophanes*, respectively) may be outliers in the dataset due to their very large body mass (*c.* 70 kg), but omitting them had a negligible impact when comparing the distributions of the two datasets (KS test, $D = 0.0004$; $P > 0.99$), or when interpreting BSFDs histograms (data not shown), so we retained these species at all scales where applicable.

Statistical analysis

General

The preliminary analyses broadly followed the methods of others (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Cardillo,

2002; Greve *et al.,* 2008; Kelt & Meyer, 2009). All body masses were converted to log$_2$ units to reduce heteroscedasticity and for ease of representation. Histograms were used to assess qualitatively the frequency distributions at all spatial scales. Because the analysis of BSFD can be affected by the position of frequency bins, we calculated the BSFD from the mean of three bracketed bins, at 0.5, 1 and 1.5 log$_2$, respectively, following Kelt & Meyer (2009). Since body size distributions are typically skewed, median body size is a more appropriate measure for analysing body size data of assemblages than the mean (see Meiri & Thomas, 2007).

Body size distributions were described using standard metrics: median body size, interquartile range, kurtosis and skew. To test the significance of differences in frequency distributions between successively smaller spatial scales, a Kolmogorov–Smirnoff goodness-of-fit test was used to compare all distributions and the larger spatial scale assemblages in which they are embedded (e.g. continental BSFD with all biomes' BSFDs and biomes with all their constituent ecoregions). To test if the observed distributions differed significantly from a log-uniform distribution (e.g. Bakker & Kelt, 2000), we compared every site to the average of 1000 randomly generated log-uniform distributions with the same number of species and statistical range of masses as in that site. Since all sites differed highly significantly from a log-uniform distribution at all spatial scales (data not shown), we repeated the test using a random uniform distribution, especially given that the expectation is for such a distribution at the finest spatial scales (Bakker & Kelt, 2000).

We also tested if the body masses of species assemblages at smaller scales are a random sub-sample from larger BSFDs. For each of the smaller scale assemblages we randomly drew, without replacement, species' body masses from the larger spatial scale assemblages, drawing the same number of species as was observed at that smaller scale site. Resampling was repeated 10,000 times, after which the median of each resampling was compared with the observed median for that particular site, and the proportion of simulated medians less than or greater than the observed median calculated (following Brown & Nicoletto, 1991). Where the proportion of simulations meeting these criteria was less than 0.025 or greater than 0.975 (i.e. a two-tailed test), the result indicated a significant difference, and therefore non-random local scale assemblage, at the alpha = 0.05 level.

Generalized linear models

The relationship between the median body size and environmental and spatial explanatory variables was examined at ecoregion and local spatial scales using generalized linear models (GLMs; assuming a Gaussian distribution with a log-link function). We did not conduct this analysis at the biome scale due to a small sample size and high collinearity between explanatory variables. For each site, at ecoregion and local scales, explanatory variables were species richness, the mean range size of all species in each site in km^2 of ecoregion area occupied, latitude, longitude and seasonality in primary productivity (as estimated by

the absolute difference between January and July NDVI values from 2004–2009, using the SPOT imagery at a 1 km × 1 km spatial resolution; http://www.devcocast.eu). The centroids of all sites were calculated with XTOOLs (http://www.xtoolspro.com) in ESRI ArcGIS 9.3 (2011) for the latitude and longitude coordinates. A small positive constant was added to response variables prior to analyses to ensure that only non-negative values were subject to the log-link function. To account for potential non-linear relationships the quadratic forms of all variables were also included in the models. To avoid multicollinearity among predictor variables, we deleted variables with high collinearity (measured as a Variance Inflation Factor > 10; Quinn & Keough, 2002) in a stepwise manner until collinearity was minimal (the Variance Inflation Factor < 10 for all variables included in the model; following Zuur *et al.,* 2010). A best subsets regression approach was implemented using the 'bestglm' package in R (McLeod & Xu, 2010), with all permutations of explanatory variables considered. The models were then ranked by Akaike Information Criterion (AIC) values, with the lowest AIC value indicating the best-fit model (Johnson & Omland, 2004; McLeod & Xu, 2010).

Null models

Null models are pattern-generating models based on random sampling from a known distribution (Gotelli & Graves, 1996). Three kinds of null models were produced to investigate whether stochastic processes contribute to observed patterns (Meiri & Thomas, 2007), and to investigate the influence of geographic range size (Blackburn & Gaston, 2001) and energy (Aava, 2001; Huston & Wolverton, 2009) on structuring BSFDs. First, to assess whether observed BSFDs could be explained by purely random assembly an 'unweighted null model' was produced, where for each site the same numbers of species as occurring at that site were randomly drawn without replacement from the continental species pool, the median body mass calculated across the randomly sampled species, and the resampling process repeated 10,000 times. For this model all species have an equal probability of being sampled. Second, to account for wide-ranging species being more likely to occur at more sites, a 'range-weighted null model' was produced. For this null model the random draw procedure was repeated, but the probability of a species selection from the continental pool was positively weighted proportional to its range across all ecoregions (in km²). Thus species with large ranges have a higher probability of being drawn. Third, to assess whether primary productivity structures BSFDs (see Aava, 2001 and Huston & Wolverton, 2009), a 'NDVI-weighted null model' was created by weighting a species probability of selection from the continental pool by the mean NDVI value across its range. We compared each of the three null models calculated medians for each site at all scales to the actual observed median body mass values at that site with a Mann–Whitney *U*-test (Quinn & Keough, 2002).

All analyses were conducted in R (R Development Core Team, 2010) and Microsoft Excel, Microsoft Access and ESRI ArcGIS 9.3 (2011) were used for data curation.
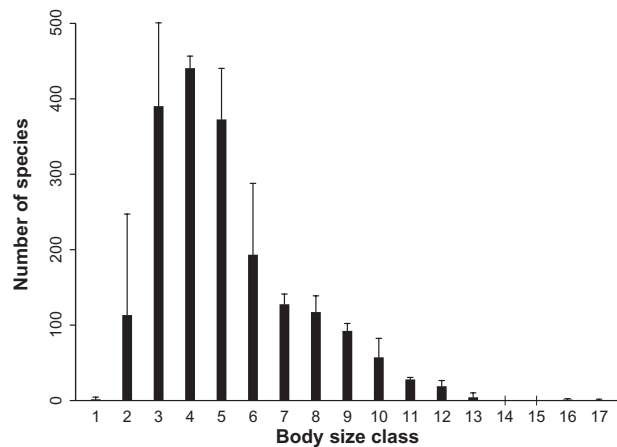

Figure 1 Body size frequency distribution for the avifauna of the continental Afrotropical biogeographic realm (*n* = 1960). Avian body masses were log₂ transformed and span body size classes from size class 1 (4.1 g) to 17 (*c.* 111 kg). Error bars indicate one standard deviation, as calculated across three size class bins.

RESULTS

The African continental avian BSFD is unimodal and significantly right-skewed (Fig. 1; Skew = 1.14; *P* < 0.0001) with a mode in size class 3–5 (5.7–45.3 g). BSFDs generally became less skewed and less modal with decreasing spatial scale of the analysis (Figs 2 & 3e; Appendix S3). At successively smaller spatial scales, the mean, median and interquartile range of body mass generally increases and the distribution's skew and kurtosis decreases (Appendix S3). Across all the BSFDs from all the three scales investigated, only the Mt Kupe and the Kibale Forest local scale assemblage were more strongly skewed than the continental BSFD (Appendix S3). Most distributions (95%; 112/117) are significantly right-skewed (skew for 112 distributions: 0.31–1.26; *P* < 0.05), apart from three ecoregions and two local scale distributions which show approximately symmetric distributions (East African montane moorlands, Ethiopian montane moorlands, Eritrean coastal desert, Seekoeivlei, Topoa Region; Appendix S3). Nearly all (97%; 112/116) of the BSFDs showed a decrease in kurtosis by comparison with the continental assemblage (Appendix S3).

The majority of distributions (98%; 115/117) differed significantly from a random uniform distribution (means of 1000 iterations; KS tests 0.152 < *D* < 0.450; and *P* < 0.04; Appendix S4). Only two distributions, the East African montane moorlands ecoregion and the Seekoeivlei local scale assemblage, did not differ significantly from a random uniform distribution (means of 1000 iterations; KS tests *D* = 0.154, *P* = 0.185 and *D* = 0.152, *P* = 0.258, respectively, Appendix S4).

The majority of smaller scale distributions are significantly different from their larger scale BSFDs (69%; 80/116; all 81 comparisons: KS tests 0.07 < *D* < 0.25; *P* < 0.05; Appendix S5). The Moist Forest and Savanna biomes do not differ significantly from the Continental distributions (KS tests *D* = 0.02, *P* = 0.7 and *D* = 0.310, *P* = 0.3, respectively) and neither do 22 ecore-
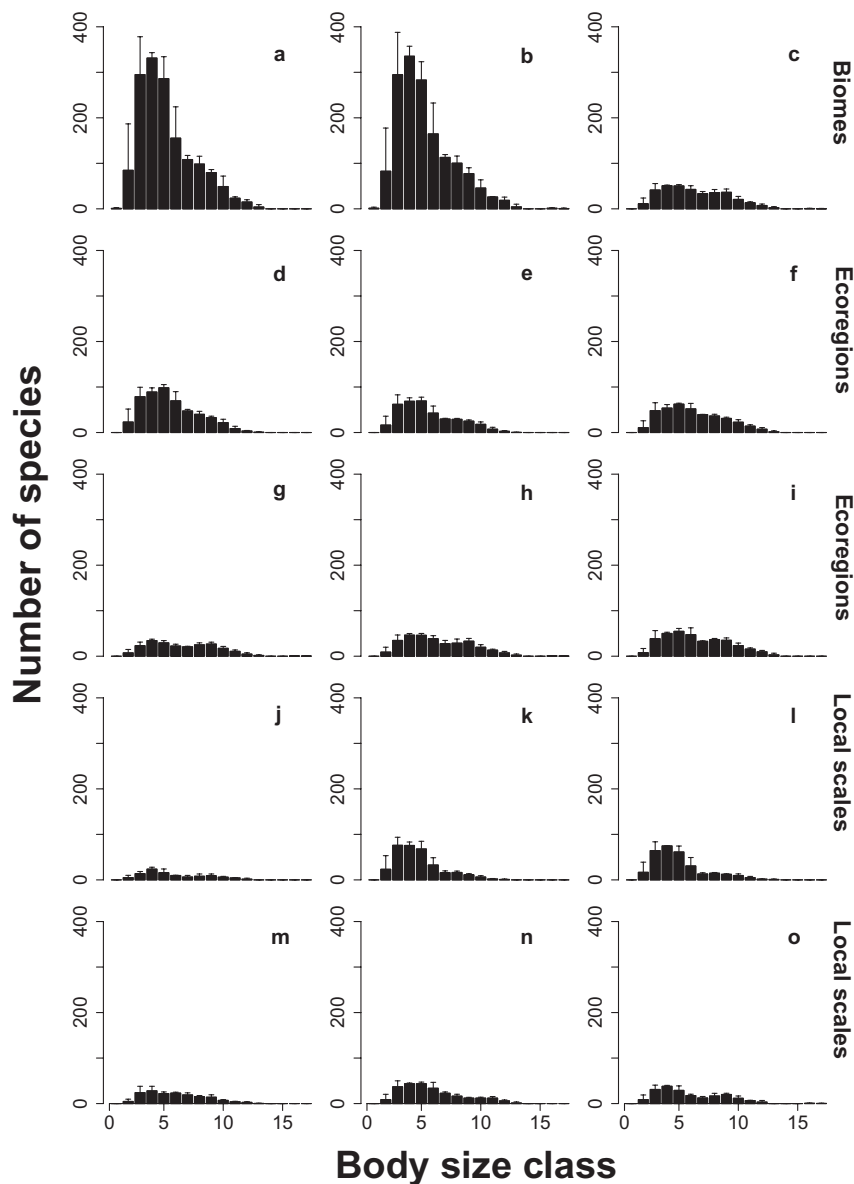
Figure 2 Body size frequency distributions from representative biome (top row), ecoregions (rows 2–3) and local scale sites (rows 4–5). Avian body masses were log$_2$ transformed and span body size classes from size class 1 (4.1 g) to size class 17 (*c.* 111 kg), with the primary mode generally in size class 3–5. Error bars indicate one standard deviation. See Appendix S1 for details of all biomes, ecoregions and local sites, and Appendix S2 for a map of the study region. (a = Moist Forest; b = Savanna; c = Fynbos; d = Eastern Guinean Forests; e = Cross-Niger Transition Forests; f = Western Zambezian Grasslands; g = Succulent Karoo; h = Montane Fynbos and Renosterveld; i = Maputaland-Pondoland Bushland and Thickets; j = Skilpadvlei Nature Reserve; k = Mt Kupe; l = Kibale Forrest; m = Bagarinnaye and Maïjémo; n = Hans Merensky Nature Reserve; o = Vrolijkheid Nature Reserve).

gions and nine local scale distributions differ significantly from the larger scale BSFDs distributions (Appendix S5). The median body mass of the majority of sites (84%; 97/116) differs significantly from distribution of medians generated through random selection of species from the larger spatial scale assemblages in which they are embedded (Appendix S6). Most sites have significantly higher body mass than expected by chance (71%; 82/116), although 13% of sites have a significantly lower mass than expected (15/116) and some are not significantly different (16%; 19/116; Appendix S6). These results in general are indicative of the non-random assembly of BSFDs at successively smaller spatial scales.

The best-fit GLM model explained 70.82% of the variation in median body mass values at the ecoregion scale and included latitude, latitude^2, longitude, species richness and species range size as significant explanatory variables (Table 1). At the local

scale the best-fit model explained 84.98% of variation in median body mass as a function of NDVI, species richness^2 and range (Table 1).

At all spatial scales the median body sizes from all of the three null models were higher than the observed continental median (Fig. 3a–d; Mann–Whitney *U*-test, all significantly different; $49 < W < 10{,}211$; $P < 0.05$). The body size predicted by the null models was generally lower than the observed median values at the biome and ecoregions scales, although this was reversed at the local scales (Fig. 3a–d; Appendix S7). Compared with observed data, the unweighted null model produced median masses that are significantly lower at the biome and ecoregion scales, but higher at the local scales. This finding reaffirms that random processes alone cannot explain observed body size frequency distributions (Fig. 3b; Appendix S7). The biome and ecoregion scale range-weighted null model medians did not

Table 1 Best fit multivariate generalised linear models of median body mass in relation to environmental variables.

Predictor variable	Ecoregion scale			Local scale		
	Slope	SE	P	Slope	SE	P
AIC	51.316			5.821		
AIC weight	0.53			0.39		
N	86			23		
Deviance explained	70.82%			84.98%		
Intercept	1.485	0.057	****	1.305	0.056	****
Latitude	0.002	0.001	**	n.s.		
Latitude^2	0.001	0.001	****	n.a.		
Longitude	0.002	0.001	****	n.a.		
Longtitude^2	n.a.			n.s.		
NDVI	n.a.			0.001	0.000	***
NDVI^2	0.001	0.001		n.a.		
Species Richness	0.001	0.001	****	n.a.		
Species Richness^2	n.a.			0.000	0.000	
Range	0.442	0.0645	****	0.615	0.072	****
Range^2	n.a.			n.a.		

Significance codes: ****$P < 0.0001$, ***$P < 0.001$, **$P < 0.01$, n.s. = not significant; n.a. = not applicable (variable with high multicollinearity and was not used; see text for details).

differ significantly from the observed median (Fig. 3c; Mann–Whitney U-test, $30 < W < 6421$; $P > 0.3$), although at the local scale there was a significant difference. Compared to observed data, the NDVI-weighted null model produced median masses that were significantly lower than expected at the biome and ecoregion scales, but higher at the local scales (Fig. 3d; Mann–Whitney U-test, all significantly different Mann–Whitney U-test; $30 < W < 6341.5$; $P < 0.01$). The skew of all null models at all scales was lower than the observed continental skew, and significantly different at all scales from the observed data (Fig. 3e–h; Mann–Whitney U-test; $47 < W < 7332$; $P < 0.002$).

While the range-weighted null model provided an indication of the process underlying the observed BSFDs especially at broader scales (see Discussion), none of the null models showed median body masses or distribution skews similar to the local scale observed BSFDs (Fig. 3). To test if the difference between observed median and null-modelled medians at the local scale (hereafter termed the null model residuals) could be explained, we used the same generalised linear modelling approach and identical variables as detailed in the above, for analysing the local scale data. Best fit models to explain the null model residuals at the local scale all had significant terms for space (latitude or longitude), NDVI and range, but not for species richness. Deviance explained for the unweighted null model, range-weighted null model, and NDVI-weighted null model, was 76.70%, 81.04% and 75.90%, respectively (Table 2).

DISCUSSION

The continental African avifaunal body size frequency distribution (BSFD) is predominantly right-skewed and unimodal,

similar in general to the BSFDs found for many vertebrates (e.g. Brown & Nicoletto, 1991; Greenwood et al., 1996; Arita & Figueroa, 1999; Polo & Carrascal, 1999; Bakker & Kelt, 2000; Knouft & Page, 2003; Meiri, 2008; Griffiths, 2011; but see Reed & Boback, 2002; Boback & Guyer, 2003; Olden et al., 2007; Cox et al., 2011; Hu et al., 2011), for birds in the New World (Cardillo, 2002) and for the global avifaunal distribution (Olson et al., 2009). Indeed, this pattern seems general (Gaston & Blackburn, 2000; Chown & Gaston, 2010; but see Roy & Martien, 2001; Boback & Guyer, 2003; Ulrich & Fiera, 2010). Although the median mass of African birds (33.5 g) is only slightly lower than that of global avifauna (37.6 g; Blackburn & Gaston, 1994), the BSFDs for the African avifauna generally become less skewed and less modal with decreasing spatial scale of the analysis, as has been found for mammals elsewhere (e.g. Brown & Nicoletto, 1991; Marquet & Cofré, 1999; Bakker & Kelt, 2000; Smith et al., 2004; Kelt & Meyer, 2009). Surprisingly, the change in shape and central position of the BSFD has not been as widely characterized at a variety of spatial scales for birds, as it has been for mammals or reptiles (Cox et al., 2011). Indeed, formal, quantitative investigation of change in the BSFD with spatial scale for birds is typically limited to investigations of two spatial scales (e.g. Blackburn & Gaston, 2001; Greve et al., 2008). In consequence, an understanding of the generality of the patterns found here across multiple spatial scales for a major continental landmass must rely on work done mostly on mammals.

Unlike African mammals, the African avifaunal BSFDs are not bimodal at all spatial scales (Kelt & Meyer, 2009). Kelt & Meyer (2009) argued that large mammals in Africa coevolved with proto-human hunters and so predominantly escaped the mass extinctions typical of other regions. For birds at least, our data does not support this interpretation, mainly because it requires the presence of an additional mode to vindicate it, and the effect of proto-human hunters in structuring bird assemblages in any case is unclear. Rather, we suggest the difference in BSFDs between African mammals and birds points to substantial differences in various life history traits, body shape, foraging ecology, body architecture and macroecological features among these major taxa (Silva et al., 1997; Speakman, 2005; Melo et al., 2009). Such consistent, among-clade trait variation potentially accounts for observed differences in the BSFDs of other taxa, such as the squamate reptiles (Boback & Guyer, 2008; Cox et al., 2011). From the perspective of changes in BSFDs with spatial scale, the implications of these differences warrant further analysis. The pronounced additional mode at smaller spatial scales found in South American mammals is also absent in the African avifauna. Bakker & Kelt (2000) posited that Neotropical arboreal mammal species are of a smaller body size and can co-exist due to the addition of the rain forest canopy habitat which contains more and typically larger species, thus inflating local scale species richness and so increasing the number of low to medium mass species in the assemblages (Bakker & Kelt, 2000, and see Marquet & Cofré, 1999; Polo & Carrascal, 1999). Again that interpretation does not seem to apply here, mainly since it requires the addition of a second mode in BSFDs at smaller spatial scales (e.g. in Fig. 2; Appendix S3). Nonetheless, a
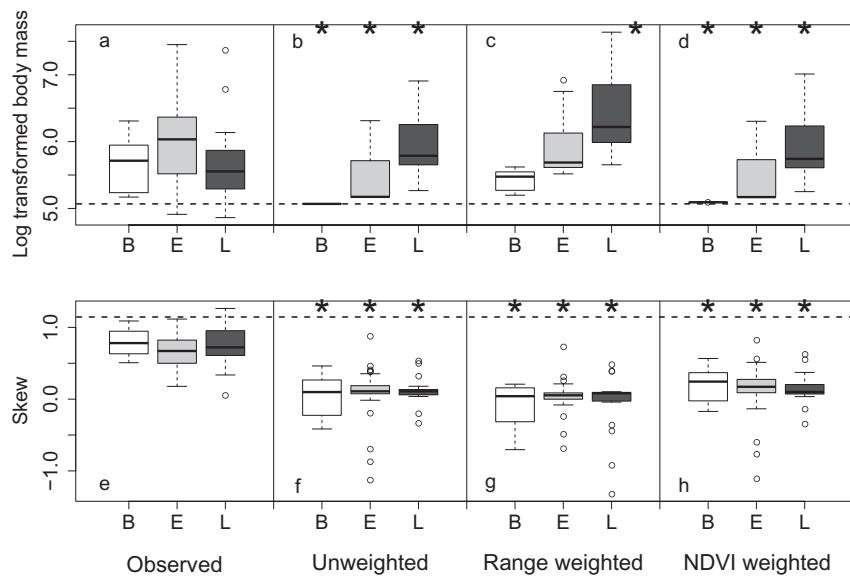
Figure 3 Median body mass and skew for observed data (a,e), the unweighted null model (b,f), the range-weighted null model (c,g), and the NDVI-weighted null model (d,h), at biome, ecoregion and local scales respectively. Dashed lines indicate the observed median body mass (5.07; top row of panels) and observed skew (1.14; bottom panels) at the continental scale. Thick lines indicate median values, boxes indicate the interquartile range, whiskers indicate the non-outlier range, and empty circles indicate outlier values (values more than 1.5 times the interquartile range) across sites at that scale. B = biome scale; E = ecoregion scale; L = local scale. Null models marked with an asterisk differ significantly from the observed median at that scale (Mann–Whitney *U*-test; $30 < W < 6341.5$; $P < 0.01$). All skew values differ significantly from observed skew (Mann–Whitney *U*-test; $47 < W < 7332$; $P < 0.002$).

Table 2 Best fit multivariate generalised linear models of unweighted, range-weighted and NDVI-weighted null model residuals (observed median minus calculated null model median), in relation to explanatory environmental variables at the local scale.

	Unweighted			Range-weighted			NDVI-weighted		
AIC	20.745			20.735			22.333		
AIC weight	0.43			0.54			0.42		
N	23			23			23		
Deviance explained	76.70%			81.04%			75.90%		
Predictor variable	Slope	SE	*P*	Slope	SE	*P*	Slope	SE	*P*
Intercept	−1.340	0.270	***	−1.140	0.267	***	−0.773	0.202	**
Latitude	0.085	0.004	*	n.a.			n.a.		
Latitude^2	n.a.			−0.001	0.001	***	n.s.		
Longitude	n.a.			n.a.			n.a.		
Longtitude^2	0.001	0.001		n.s.			0.001	0.001	*
NDVI	0.009	0.002	***	n.a.			0.008	0.008	***
NDVI^2	n.a.			0.001	0.001	***	n.a.		
Species Richness	n.s.			n.a.			n.a.		
Species Richness^2	n.a.			n.s.			n.s.		
Range	n.a.			2.250	0.347	***	n.a.		
Range^2	1.855	0.355	***	n.a.			1.712	0.295	***

Significance codes: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, n.s. = not significant; n.a. = not applicable (variable with high multicollinearity and was not used; see text for details)

similar mechanism may well apply at local spatial scales (see Gómez de Silva & Medellín, 2002). Despite these differences with mammalian assemblages, the change in BSFDs from the continental to local scale found here is similar to the limited work on birds (Gaston & Blackburn, 2000; Blackburn & Gaston, 2001; Cardillo, 2002; Greve *et al.*, 2008), suggesting that patterns

found here likely hold for birds generally, as they seem to for many other taxa (e.g. Chown & Gaston, 2010), although not for North American squamates (Cox *et al.*, 2011).

In keeping with work on mammals (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Smith *et al.*, 2004; Rodríguez *et al.*, 2006) and birds (Blackburn & Gaston, 2001; Greve *et al.*, 2008),

Afrotropical avian BSFDs at a range of spatial scales show non-random assembly from larger scale assemblages. Several explanations could account for this pattern. First, it has been suggested (Meiri & Thomas, 2007) and demonstrated (Greve *et al.*, 2008) that richness is likely to have a substantive effect on assemblage median mass, especially since in low richness sites the modal size is likely to be higher for reasons of sampling alone (Gaston & Blackburn, 2000; Meiri & Thomas, 2007). Although we found that richness was a significant explanatory variable for median mass at the ecoregion scale, when richness was accounted for in the unweighted null model, it failed to simulate the observed median body size. In consequence, some other mechanistic process must be responsible for the differences between the null and observed assemblages. Two of the primary contenders are energy, given its role in affecting size and size distributions (reviewed most recently by Huston & Wolverton, 2011), and range size, given that smaller-bodied species tend to have higher spatial turnover than larger-bodied ones (Brown & Nicoletto, 1991; Brown & Lomolino, 1998; Melo *et al.*, 2009; Chown & Gaston, 2010), leading to the accumulation of more small-bodied species in BSFDs compiled at larger spatial extents.

Median body mass of assemblages in the NDVI-weighted null models differed significantly from the observed values at all spatial scales, and NDVI likewise did not enter as an explanatory variable in the generalized linear models except at the local scale. In consequence, at least at the biome and ecoregion scales variation in energy availability is unlikely a contender for explaining variation in BSFDs. By contrast, not only did range size enter the generalized linear models as a significant term, but at the biome and ecoregion scales, median body mass of the range-weighted null assemblages did not differ significantly from the observed values. In consequence, it appears that, at least at these scales, the change in central tendency of the BSFDs is well-explained by differences in turnover rate among smaller- and larger-bodied species, with the former tending to have the largest turnover rates (as suggested by a triangular range-size body size relationship; Appendix S8 and see Brown & Lomolino, 1998; Fernández & Vrba, 2005; Melo *et al.*, 2009). While it does not seem to apply to squamates (Cox *et al.,* 2011), this explanation for differences in BSFDs at different spatial scales has been mooted for both birds and mammals (Brown & Nicoletto, 1991; Blackburn & Gaston, 2001), and our work provides further evidence for it.

Although not adequately captured in our null models, energy may still structure BSFDs especially at local scales, as indicated by differences between the NDVI-weighted null model median and observed median and that the observed data at this scale continue to be related to NDVI. While our measure of energy may be too coarse and should have rather been eNPP (Ecologically relevant Net Primary Productivity, defined as net primary production during the growing season; Huston & Wolverton, 2011), it is clear that some other process is likely also involved because our models inevitably failed to capture the skew in the observed data. This unexplained mechanism may well be the optimization of size based on the size-dependence of production rates (the difference between energy assimilation and respiration) and mortality rates (Kozłowski & Gawelczyk, 2002).

Production rates are directly related to energy availability, while mortality may be indirectly related in the sense that mortality from predators, parasites or competitors is likely to increase as diversity increases, which is in turn related to energy availability (Hawkins *et al.*, 2003; Currie *et al.*, 2004). Such varying size optimization, an essentially evolutionary mechanism, is a key process that leads to positively skewed frequency distributions, but one that is not captured by any of the null models here. At larger spatial scales, size-based variation in diversification rates (Maurer *et al.*, 1992; Gaston & Chown, 1999; Kozłowski & Gawelczyk, 2002), accompanied by variation in dispersal rates, which have a large influence on clade diversity (Phillimore *et al.*, 2006), may be key in determining skewness. The role of productivity therefore clearly deserves further attention for the explanation of changes in size distributions with changing spatial scale.

Several caveats need to be taken into consideration in interpreting our results. First, in common with many other studies of BSFD variation, we were not always able to assess the effects of spatial autocorrelation, and future studies should take the potential effects thereof into consideration (see, e.g., Bahn *et al.*, 2006), although given the strength of the results here we do not think that the outcomes will be much affected (see also Bini *et al.*, 2009). Second, due to the lack of an appropriate and well resolved molecular phylogeny for the species in our study area, we could not incorporate phylogenetic affects, and future work incorporating such an approach, especially examining the evolutionary mechanisms underlying the patterns we document, would likely account for much of the unexplained variation. Finally, there is much variation in the actual size of areas within the ecoregion and local scales. The continued presence of modes in body sizes at especially local scales (i.e. Mt Kupe; Fig. 2k) might indicate that our sites are too large or heterogeneous to effectively capture the change in BSFDs with scale. However, there is a consistent dampening of BSFDs across scales (Appendix S3), a consistent low kurtosis of BSFDs *within* local scales (Appendix S3) and the majority of smaller scale distributions differ from the larger scale distributions within which they are embedded (Appendix S5). Consequently, regardless of the effective area of our sites, it appears that the observed patterns are consistent.

In conclusion, here we have shown that on log scales, the BSFDs in Afrotropical birds are unimodal, right-skewed and become less skewed and less modal with the decreasing spatial scale of the analysis, in keeping with patterns found in other taxa. Much of the pattern in median body size change with spatial scale can be captured by a range-weighted null model, suggesting that differential turnover between smaller- and larger-bodied species might explain the shift in the central tendency of the BSFD. However, at smaller spatial scales energy availability may be the most significant determinant of median size, and energy may also play a role in determining the substantial skew of distributions at all spatial scales through species-level optimization of size and the processes that lead to size-biased diversification. Exactly how diversity, size and diversification interact to produce BSFDs across spatial scales

remains one of macroecology's largest challenges (see Allen *et al.*, 2006; Smith & Lyons, 2011).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Size, centroid coordinates and origin of all sites analysed.

Appendix S2 Map of the study area.

Appendix S3 Summary statistics for all sites analysed.

Appendix S4 Kolmogorov–Smirnoff tests between random uniform distributions and observed data.

Appendix S5 Kolmogorov–Smirnoff tests between all nested distributions at all scales.

Appendix S6 Simulations and statistics of body size frequency distributions drawn from the larger spatial scale assemblages in which they are embedded.

Appendix S7 Percentage of all null models greater than, less than, or equal to observed.

Appendix S8 Range size and body mass relationship for 1960 African birds.

BIOSKETCHES

Bernard W.T. Coetzee has a range of interests in biogeography and conservation science, with a focus on Protected Areas and global change drivers. He is also interested in science policy and science–public interfaces.

Peter C. le Roux is interested in the determinants of species ranges and the influence of biotic interactions on the ecological consequences of climate change.

Steven L. Chown works in the fields of ecology and physiology, and their integration. He has a long-standing interest in the ecology, physiology and evolution of the biotas of the islands of the Southern Ocean.

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