Large-scale assessment of commensalistic–mutualistic interactions between African birds and megafauna using internet images (#20913)

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Large-scale assessment of commensalistic–mutualistic interactions between African birds and megafauna using internet images

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The savannah has been recognized as an important ecological background for several well-studied co-evolutionary events. A visible, yet quite neglected, aspect is the commensalistic–mutualistic interaction including birds sitting, perching or feeding on live large African mammals (megafauna). Here, we investigate general patterns in such relationships at large spatial and taxonomic scales. To obtain large-scale data, an extensive internet-based search for photos was carried out on Google Images. We found that interaction web structure was only weakly nested for African birds and mammals. Regression models corrected for phylogeny showed that the best predictors of patterns of bird–mammal interactions were mammal body size, herd size, and habitat openness. We found that larger mammals hosted more individual birds and a higher mass of birds than smaller ones. A significantly higher bird mass was also associated with mammals in open areas and near waterbodies. Furthermore, mammal herd size was positively correlated with bird species richness as well as with bird mass. *Buphagus* spp. were most often associated with larger-bodied mammals but we did not found any significant association between their mass hosted by mammals and any mammal or environmental characteristics. This suggests that their host selection could follow an optimal foraging approach, since larger mammals have more ectoparasites but the birds visit mammals in groups of uniform size. We also identified some new or rare associations between birds and mammals but, on the other hand, we failed to find several previously described associations. Our results provide evidence that patterns of bird–mammal interactions may be determined by simple predictions, raising the importance of megafauna for conservation of the diversity of bird–mammal interactions and highlighting the potential role of information technologies and new media in further studies of ecology and evolution. However, further study would be needed to get proper insight into both, biological and

methodological processes standing behind observed patterns.

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Short title: African birds and megafauna

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Introduction

The savannah has been recognized as an important ecological template for several well-studied evolutionary events including interactions between various groups of organisms such as trees and grass (Scholes & Archer 1997), plants and ants (Byk & Del-Claro 2011) and herbivores (Stebbins 1981), respectively, and even between humans and, scavenging birds and mammals (Moleón et al. 2014; Morelli et al. 2015). Another widespread, but quite neglected interaction is that of the interspecific commensalistic–mutualistic relationship of savannah birds with large African terrestrial mammals, the latter known as megafauna (Dean & MacDonald 1981). Africa is home to very diverse communities of large mammals for which only limited equivalence can currently be found on other continents (Ripple et al. 2015). Furthermore, savannahs can have outstanding bird species richness (Hawkins et al. 2007) and levels of endemism (Orme et al. 2005). Thus the savannah provides an excellent study system for extending our knowledge of bird–mammal relationships. However, savannahs look not the same across the whole range of distribution of the biome, because of local climatic conditions and land-use by human or other organisms. For instance, savannahs differ in the particular species distribution, their abundances and habitat structure (Shorrocks & Bates 2015) which, in turn, have presumably strong effect of observed bird–mammal interactions. Hence, large-scale and multitaxonomical approach is useful when investigating patterns in bird–mammal interactions to avoid problems with interpretation and generalization of relationships which may be area or taxa specific. Still, majority of previous studies investigating patterns in commensalistic–mutualistic interactions between African birds and megafauna focus only on single or a small number of species (Hart, Hart, & Mooring 1990; Koenig 1997; Nunn et al. 2011; Ndlovu & Combrink 2015; Kioko et al. 2016) and no wide-scale study of patterns in bird–mammal interactions has been done on African fauna.

Many birds of the African savannah ecosystem use larger-bodied mammal hosts as perches and sometimes even as food sources, gleaning parasites and blood from the host (Dean & MacDonald 1981; Ruggiero & Eves 1988; Sazima et al. 2012; Ndlovu & Combrink 2015). The African megafauna is composed of many phylogenetic lineages with diverse body sizes and a tendency to form herds (Smith et al. 2004; Kingdon 2015), which makes them a moving system of islands and archipelagos across African savannahs. The number of birds directly interacting with mammals could be influenced by extrinsic factors, including host body size and herd size, mainly due to limited space available for hosting birds and the carrying capacity of mammal species. Moreover, larger mammals or mammals living in larger herds could be more visible to birds or disturb more insects or other small animals and subsequently may attract a wider or more abundant community of birds looking for food (Mooring & Mundy 1996; Nunn et al. 2011; Kioko et al. 2016). Environmental factors such as elevation and vegetation structure have also been shown to have an effect on species richness, distribution (James & Wamer 1982; Rahbek 1995; McCain 2004; Tews et al. 2004; Jankowski et al. 2013) and abundance (Terborgh 1977; James & Wamer 1982; Ferenc et al. 2016) of birds and mammals, potentially shaping interactions between birds and megafauna (Hart, Hart & Mooring 1990; Kioko et al. 2016).

The classical examples of birds interacting with mammals are the oxpeckers: the small-bodied passerines *Buphagus africanus* and *B. erythrorhynchus* (family Buphagidae). Here, the species interaction may differ from other birds since *Buphagus* spp. are exclusively obligate mutualists with African megafauna and their presence on host species has been found to be strongly correlated with the character of host infestation by ectoparasites (Hart, Hart & Mooring 1990; Nunn et al. 2011). Mammal species and individuals differ significantly in tick infestation (Gallivan and Horak 1997); the distribution of *Buphagus* spp. can thus potentially follow optimal foraging patches (Charnov 1976) rather than mammal body and herd size *per se*. For instance, *Buphagus* spp. may prefer to visit mammal species or individuals inhabiting woody and scrubby areas with reportedly higher tick density than open grassland areas (Semtner & Hair 1973; Carroll & Schmidtmann 1996), larger mammals supporting higher tick abundance compared to smaller ones (Koenig 1997; Nunn et al. 2011) or, smaller mammals with a higher tick number to body mass ratio (Hart, Hart, & Mooring 1990). In addition, a preference for mammals living in larger herds could be adaptive for oxpeckers since the decreasing distance between host individuals makes feeding more efficient (Mooring and Mundy 1996).

Nowadays, human activity in natural habitats is more and more tangible with a generally negative effect on the savannah biome. Savannahs are one of the most threatened world ecosystems due to extensive habitat loss and poor protection (Hoekstra et al. 2005). It is mainly human-induced pressure that causes populations of many large-bodied mammal species to decline (Ripple et al. 2015). Sharp population decline or even extinction of megafauna in many world regions disrupts and reshapes present ecological interactions, with a likely negative effect on megafauna associated organisms, including birds (Galetti et al. 2017). This may cause that several bird–mammal interactions have been lost over time, resulting in decreased diversity of mutual interactions. On the other side, it is possible that other species which used to interact with megafauna establish new interactions with still common mammals (Galetti et al. 2017). To investigate current large-scale web-structure of bird–mammal interactions, extensive data collection from free available online sources may be useful.

During last decade, engagement of citizen volunteers in scientific projects, so called citizen science, ranging from the collection of Internet data uploaded by public to investigate various scientific tasks to active participation and collaboration of public with community scientists (e.g.

via online platforms) on range-wide projects, has became an integral part of current ecological and evolutionary research (Bonney et al. 2009; Silvertown 2009; Dickinson, Zuckerberg & Bonter 2010). Rapid technological development and still expanding access of public to the Internet and recording devices, such as cameras or smartphones, around the world have increased the accessibility, immediacy and extent of data sharing. Online data collected by public can represent a useful tool for expansion of science knowledge on rare or not well-studied phenomena (e.g. Mikula et al. 2016) but facilitate cost-effective and rapid large-scale data mining which may supplement or even challenge conventional practises in science (Leighton et al. 2016; Dylewski et al. 2017). Despite boom of such studies, material uploaded on the Internet by public is still an underexploited data source for studies in ecology and evolution.

Here, we used public photos collected using web-based searching engine Google Images to investigate some aspects of commensalistic–mutualistic interactions between African birds and mammal megafauna. In contrast to the majority of previous field studies focusing only on spatially and taxonomically restricted systems (e.g. Ndlovu & Combrink 2015; Kioko et al. 2016) or did not quantify these relationships (Dean & MacDonald 1981), we provide the first comprehensive investigation of patterns in bird–mammal interactions at large spatial and taxonomic scales. Firstly, the structure of the interaction web between birds and mammals was analysed. We then employed phylogenetically-informed comparative analysis to explore whether patterns in bird visitation of mammals follows simple rules, i.e. are determined by a combination of host mammal body and herd size. Additionally, we included two environmental variables, elevation and habitat openness, to investigate their potential effect on the character of bird–mammal interactions.

Materials and Methods

Data searching

To collect a large dataset of spatially and taxonomically distributed data on bird–mammal interactions, we did an extensive Internet search for photos on Google Images. Jarić et al. (2016) pointed out that Internet searching based on English common names produced more results than when scientific names were used. Moreover, since results of searches using English and scientific names were highly correlated, we decided to search only for English names of birds and mammals. However, we are aware of the fact that this could restrict geographical coverage and decrease the use of records from countries with a different language background, such as Mozambique or Angola. Our searching phrase typically contained the name of each species or genus of larger-bodied African mammal herbivores (>10 kg) (for the full index see S1 Appendix) combined with the name of the bird taxon that we expected to be most probably involved in this relationship (based mainly on reports reviewed by Dean & MacDonald 1981; for the full index see S1 Appendix). When no relevant results were found by this method, we replaced the bird name by the more general phrases "bird" or "birds". We sampled each potential association between bird and mammal species with equal effort, i.e. the Google search for photos for each combination of bird and mammal taxa was conducted separately and for each combination we collected as many photos as possible until the search produced only a small proportion of photos with relevant content. For common species it is virtually impossible to collect all available photos so this solution represented a trade-off between the number of available relevant photos and time spent searching for new photos. This procedure standardized our data for analysis and may have removed biases in measurements resulting mainly from variations in animal abundance and/or extent of spatial distribution. To investigate patterns of "sitting" interactions between birds and mammals, only interactions with birds observed directly upon the bodies of host mammals were analysed; cases where birds were feeding or flying around them were not included (for the full list of photo references see S2 Appendix).

We focused only on wild living, non-domesticated mammal species in sub-Saharan Africa. We thus excluded 32 cases of domesticated mammals recorded as bird hosts. Interestingly, almost 60% of records for domestic mammals originated in West Africa where native megafauna was largely hunted out as bushmeat (Brashares et al. 2004; Fa & Brown 2009), whereas West African records for native megafauna represented only <1% of all records. We also excluded photos where birds were observed on non domestic African mammals kept in captivity outside Africa (e.g. zoos).

When searching on the Internet, we found that several photos were also part of larger photo series, quite often containing more images of the same bird–mammal interaction event. In such cases, we chose the one photo showing the highest number of birds/mammals interacting with each other. Paintings and images which were suspected to be photomontages were ignored (<1% of all photos). To limit other sources of bias, photos suspected to be shared by multiple sources were briefly checked to see whether they had already been included (all photos were collected exclusively by one author, PM, enabling us to do this consistently). We were particularly careful when working with odd photos that people might prefer to share, e.g. a mammal individual covered by a large number of birds or "cute" or interesting animal species and scenes. However, it is still possible that a small number of duplicates remained undetected because we did not cross-check all possible combinations of photos. On the other hand, we noted that such cases were quite rare and it seems that online sharing of photos does not substantially bias results obtained from a Google search compared to field data. For instance, Leighton et al. (2016) found that the proportion of black colour morphs in black bear subspecies collected from a Google search was highly correlated with that from fieldwork, suggesting that online photos do not over-represent bears with atypical colouration in particular subspecies.

Finally, we are aware of the fact that there could be an inherent bias toward photos with larger numbers of birds on mammals caused by a preference by photographers to publish mammal photos with a larger number of birds. If true, we would expect that Internet photos for all species portrayed the maximum number of observed birds and this should not have an impact on relative differences in patterns of bird–mammal interactions. Similarly, in the case that only some photographers did this, we again do not expect any consistent bias in our data because photos originated from numerous authors. Further, probability to photograph a bird on a mammal may be related to the habitat structure (e.g. dense versus open habitats) and we recognise that this may under-estimate involvement of species living in more closed habitats in our dataset, Here, we note that substantial part of photos came from amateur photographs and tourists where lower bias toward odd photo presentation (e.g. over-representation of rare species) is expected when compared with professionals or researchers (see also Dylewski et al. 2017).

Bird and mammal characteristics

Each individual host mammal with birds observed on it represents a basic unit which was assessed separately. First, we counted the number of individual birds on each individual mammal. We also collected information on the total number of bird species on each mammal species across the entire pool of photos used to assess overall bird species richness hosted by them. Moreover, we collected information on mean herd size for mammal species; herd size was estimated as the number of mammal individuals (conspecific or heterospecific) in each analysed photo.

Furthermore, information on body mass of mammal species was taken from the online "Encyclopedia of Life" (http://www.eol.org/; accessed on 10 April 2016). The mean weights of bird species was obtained from the online edition of "Handbook of the Birds of the World" (http://www.hbw.com/; accessed on 9 April 2016). We used mean weights for nominate subspecies; we did not distinguish between sexes (where weights were given for both sexes separately, we calculated an mean value for the species) although sexual dimorphism in body size was present in some cases. Since mammals were considered as islands, and in the following analyses were treated for phylogenetic relationships, we accepted only records determined to species level. However, to minimize losses of information, we also accepted observations for birds which were indistinguishable between two possible species; in these cases body mass was calculated as the mean weight of both species.

Geographic location and environmental characteristics

To investigate the spatial patterns in our dataset, we included only photos with the location given to at least country level. Geographically unspecified records were excluded. For each record, we specified the geographical location as accurately as possible. When the location was only at the country level, coordinates were taken as the centre of the mammal and/or bird species distribution in that country (accessed on www.iucnredlist.org and http://www.hbw.com/). Elevation for each record was collected in a similar manner (accessed on https://www.daftlogic.com/sandbox-google-maps-find-altitude.htm).

Finally, photos were divided into four main categories according to the shown habitat structure as follows: (1) near water (e.g. swamps, lakes and other water sources), (2) open habitats (e.g. grassland, semi-deserts, and cases where only dry soil was visible), (3) higher mosaic vegetation cover (savannah, scrubland and bush) and (4) higher dense vegetation cover (open-forest and forest). To avoid a high inaccuracy in determination of the habitat from very magnified (zoomed) photos, these were not scored. To use habitat structure as a proxy for the level of habitat openness, each of habitats was scored from 1 for most open habitats (i.e. waterbodies) to 4 very closed habitats (i.e. forest).

Statistical analysis

Bird–mammal interaction web

In bird–mammal interaction web analyses, we included only interactions where both mammals and birds were determined to species level. Our basic unit for analysis was the number of cases and not the number of individuals, i.e. if several birds were observed on one mammal individual we considered this as one case. Because all associations were sampled with equal effort, we minimized biases in measures of specificity resulting mainly from variation in species abundance and extent of spatial distribution. The final standardized dataset contained 2,147 bird–mammal interactions. The bird–mammal interaction network for each species was visualized by the "plotweb" function and the network was analysed using the "bipartite" package (Dormann et al. 2009). Bascompte et al. (2003) suggested that mutualistic networks are nested. Even though later studies suggested that different measures of nestedness should be used (Ulrich, Almeida-Neto & Gotelli 2009) and results should be compared with a null model which is able to eliminate the effect of abundance inequality (Vázquez et al. 2007), it still seems that mutualistic networks, including those between birds and their mammal hosts (Sazima et al. 2012), have a nested structure (Joppa et al. 2010). To test whether such a nested structure exists for interactions between African birds and mammals, we calculated nestedness of the bird–mammal interaction network using quantitative NODF (Nestedness metric based on Overlap and Decreasing Fill) (Almeida-Neto & Ulrich 2011). We tested whether our network was significantly nested by comparing our network weighted NODF with a weighted NODF of 1000 networks generated randomly using a null model in "swap.web" (Dormann et al. 2009). Values of NODF range from zero in a non-nested web to 100 in a perfectly nested web (Almeida-Neto et al. 2008).

Several previous studies focusing on bird–mammal interactions (especially those including *Buphagus* spp.) characterized them by calculating host preference indices such as "preference index" *sensu* Grobler & Charsley (Grobler & Charsley 1978) or Jacobs index (Jacobs 1974; Mooring & Mundy 1996; Koenig 1997; Ndlovu & Combrink 2015; Kioko et al. 2016). Both these commonly used indices, however, work with real abundances of mammal species and their relative availability for birds. We did not use them because our dataset was compiled from the Internet, making it impossible to obtain information on actual species abundances in the proximity of each photo.

Photo zoom

Because we used several variables which were expected to be strongly influenced by photo zoom, all analyzed photos were scored according to their zoom on a three-point scale: (1) very zoomed photos (only part of mammal body was visible, e.g. head or hind legs with part of the belly), (2) medium zoomed photos (complete or almost complete mammal body was visible and free space on the photo constituted less than one mammal body length on each side), and (3) unzoomed photos (complete mammal body was visible and free space of more than one body length was present). More detailed photos could cause bias in estimation of mammal herd size because some individuals could be omitted from the photo. This, however, was not the case in our dataset because subsequent analyses revealed that species-specific herd size estimated from only unzoomed photos closely followed those from all photos (Pearson correlation r = 0.852, p = 0.002, N = 10 species; only species with a minimum of three unzoomed photos taken, data ln-transformed before analysis). Furthermore, photos depicting only part of the mammal body might underestimate the actual number of birds present on the mammal body because other individual birds can occupy unshown parts of the body at the same time. When several photos of the same scene were available, we tried to eradicate this issue by using the photo with the maximum number of interacting birds and mammals. More importantly, records where all or almost all of the mammal body was visible represented ~65% of all our records and we found that bird number and bird mass estimated from very zoomed photos was again strongly correlated with overall estimates (Pearson correlation r = 0.61, p = 0.012 and r = 0.719, p = 0.002, respectively, N = 16 species; species with minimum of three estimates, data ln-transformed before analyses).

Finally, to ensure that zooming really did not bias the observed patterns, the character of bird–mammal interactions was explored using generalized linear models (GLM). GLM analyses revealed no differences between results obtained for the full set of observations and for middle zoomed and unzoomed photos; in subsequent analyses we thus used data from the full dataset (for detail description of analyses see S3 Appendix).

Phylogenetic generalized least-squares (PGLS)

Although both generalist and specialized species can feed from the surface of the mammals (Dean & MacDonald 1981; Sazima et al. 2012; Ndlovu & Combrink 2015), due to the strong association of *Buphagus* spp. with this interaction, we decided to make analyses for the full dataset of species and also only for the subset of *Buphagus* spp. We preferred to use full set of species over separate set of birds that only perch on mammals for resting and increasing food detection because inclusion of two *Buphagus* species will add only two additional points in regression analysis (see results section for the number of used species), presumably having only small effect on results.

We further used phylogenetic generalized least-squares (PGLS) regressions using Pagel's lambda transformation of a correlation structure to estimate the effects of mammal and environmental characteristics on bird-associated characteristics after controlling for phylogenetic relatedness of mammal species. Animal characteristics, such as body size and behavioural patterns including social and feeding behaviour, have been found to be influenced by shared ancestry (Smith et al. 2004; Kappeler et al. 2013; Lefebvre, Ducatez & Audet 2016); identified patterns may be determined by a phylogenetically non-random set of species since phylogenetically related taxa thus have a higher probability of sharing characteristics from a common ancestor than do distant ones. The PGLS approach represents an extension of GLMs, accounting for the statistical non-independence of data points as a result of common ancestry of species (Pagel 1999; Freckleton, Harvey & Pagel 2002) and allows the estimation (via maximum likelihood) of the phylogenetic scaling parameter lambda (λ). A high value of lambda (i.e., $\lambda = 1$)

indicates strong phylogenetic dependence whereas λ = 0 indicate no phylogenetic relatedness. The maximum likelihood estimate of λ thus provides a measure of the importance of phylogenetic relationships on the association between studied variables.

We built multi-predictor models where the response variable was bird characteristics (mean bird mass and number of individuals and total species richness) and predictors were mammal (body and herd size) and environmental (elevation and habitat openness) characteristics. For the subset of *Buphagus* spp. we used only mean mass of birds as this family consists of only two species of similar weights. Both predictor and response variables were ln-transformed prior to analyses. However, for a few species, some data, mainly on habitat openness, were missing; to avoid loss of such species from analyses we added missing values by two different methods: (a) for the set of all species, missing values were calculated as family averages and (b) for *Buphagus* spp., visiting only 60% of the mammal species, missing values were taken from the full set of species (although *Buphagus* spp. could potentially use mammal individuals moving in habitats with different habitat openness and vegetation cover than other birds, we predict that habitat selection is done primarily by mammals and could be considered as "species-specific"). To evaluate the robustness of the obtained results, we made an additional analysis including only species with at least 10 photos. As suggested by Forstmeier & Schielzelt (2011) we present the full models because they clearly show the range of predictors included plus a balanced representation of non-significant results.

Reconstruction of the phylogenetic tree of African mammals was based on recent extensive data published by Hedges et al. (2015) (available online at http://www.biodiversitycenter.org/ttol). Normality of regression residuals after fitting the full models was again checked using Shapiro-Wilk test, revealing no violation of the assumptions of normality. The only exception was the model for *Buphagus* spp. with estimates based on at least 10 photos; in this case, the use of raw untransformed variables resulted in normal distribution of model residuals. PGLS regressions were performed using the "nlme" and "ape" package (Pinheiro et al. 2014; Paradis, Claude & Strimmer 2015). All data were statistically analysed in R v. 3.0.2 (R Development Core Team 2013).

Results

Taxonomic diversity and spatial distribution of bird–mammal interactions

In total, we collected information on 2,169 interactions of 4,840 individual birds, belonging to at least 48 bird species of 21 families, with 31 species of wild living African mammals of seven families. This dataset contains records from regions across sub-Saharan Africa with the majority of records from open and relatively well studied areas of East and Southern Africa (Fig. 1). Only a small number of records came from West and Central Africa (<2%).

Bird–mammal interaction web

2,147 interactions where both bird and mammal interactors were identified to species level were included in web analyses (data in S4 Appendix). Of these, 672 cases (31.3%) were represented by birds other than *Buphagus* spp., detected on 18 species of mammals (Fig. 2a). Of these, the most prevalent bird species associated with mammals were *Bubulcus ibis* (51.5% of non-*Buphagus* spp. cases), *Creatophora cinerea* (8.9%) and *Ptilostomus afer* (4.6%). Of all records, the most visited mammals were *Hippopotamus amphibius* (31.0%), followed by *Equus quagga*

(13.1%) and *Loxodonta africana* (11.5%). From interaction web visualization it is apparent that almost all bird species associated with waterbodies were detected on *H. amphibius* (Fig. 2a).

In *Buphagus* spp., *B. africanus* (407 cases, 27.5% of *Buphagus* spp. records) was observed on 16 mammal species whereas *B. erythrorhynchus* (1068 cases, 72.4%) was observed on 24 species of mammals (Fig. 2b). *B. africanus* was most often associated with larger-bodied mammals such as *Syncerus cafer* (35.9% of all species-specific cases), *Giraffa camelopardalis* (13.5%) and *H. amphibius* (11.3%). Mammal species most often visited by *B. erythrorhynchus* were *Aepyceros melampus* (18.6%), followed by *G. camelopardalis* (13.9%) and *Ceratotherium simum* (13.3%). In contrast to *B. africanus*, *B. erythrorhynchus* did not avoid very small mammal species (Fig. 2b).

When all species were analysed together, we found that the interaction web between birds and their mammal hosts had rather low level of nestedness (NODF = 24.655) and did not differ significantly from values expected under the null model (p = 0.774). When separate analyses for *Buphagus* spp. and for the remaining species were carried out, we found that web nestedness was higher in *Buphagus* spp. than in the other species (NODF = 32.551 and 10.634, respectively). The level of nestedness differed significantly from the null model only for *Buphagus* spp. (p = 0.017); the difference was not significant for the other species (p = 0.999).

Relationship between bird, mammal and environmental characteristics

The PGLS model analysing relationships between mean bird mass per mammal species and mammal and environmental characteristics revealed a strong positive relationship with mammal body size and a negative relationship with habitat openness (full model statistics: Log Likelihood

= -27.095, λ = 0.099) (for full results see Table 1; data in S5 Appendix). The number of birds positively correlated only with mammal body size (Log Likelihood = -16.188, λ = 0.335). Bird species richness was strongly positively correlated only with mammal herd size (Log Likelihood = -31.768, λ = 0.299). In *Buphagus* spp., however, no significant relationship was found with any mammal or environmental characteristics (Log Likelihood = -13.989, λ = 0.513).

The PGLS models including only species based on at least 10 photos had similar results (N = 15 mammal species for all species and N = 14 for *Buphagus* spp.). Again, bird mass was positively correlated with mammal body size and habitat openness but also with mammal herd size (Log Likelihood = 1.910, λ = 0.037) (Table 1). However, the relationship between the number of birds and mammal body size in this restricted set of species was non-significant, but we found a weak positive correlation with mammal herd size (Log Likelihood = 0.636, λ = 0.486). Results for bird species richness and members of *Buphagus* spp. remained similar to the larger dataset (Log Likelihood = -11.752, λ = 1.053 and Log Likelihood = -59.741, λ = -0.990, respectively).

Discussion

African savannahs are inhabited by some of the most diverse bird and mammal communities among the world's ecosystems (Hawkins et al. 2007, 2012). This region also probably harbours the world's most species-rich commensalistic–mutualistic interactions between birds and larger-bodied mammals (Dean & MacDonald 1981; Ruggiero & Eves 1988), enabling us to look at general patterns in such interactions. On the large set of photos collected from Google Images, we showed that the most important factors shaping bird–mammal interactions were mammal body and herd size and habitat-openness. We found that larger mammals supported higher bird mass and more individual birds. Furthermore, we revealed a strong association between mammal herd size and total bird species richness found on particular mammal species. Of the environmental factors, vegetation cover but not altitude influenced patterns of commensalistic–mutualistic interactions between birds and mammals with a mean mass of birds sitting on mammals higher in more open habitats. On the other hand, for *Buphagus* spp., we did not find any significant relationship between their mass on mammals and mammal and environmental characteristics.

When analysing the same relationships using the restricted dataset (mammal species with at least available 10 photos) the majority of results were similar. However, few differences did occur: (1) the relationship between bird mass and mammal herd size which was slightly non-significant for the full set of species was significant in the restricted dataset, (2) the weak significant correlation between number of birds and mammal body size was not detected in the restricted set of species but a weak significant relationship was found with mammal herd size. Data quality could be higher in the restricted dataset, but the restriction reduced the species pool used in analyses, causing problems with data generalization. However, collectively the results support a view that patterns in visitation to mammals by birds are linked mainly by mammal body, herd size and vegetation cover.

We found that larger bird mass was associated with larger-mammal species and probably also species living in larger herds and inhabiting open habitats. This pattern could be driven by the fact that the majority of larger-bodied birds in our dataset were waterbirds and the areas with the most open habitats were waterbodies and open savannahs where some mammals aggregate in large numbers. Because more than 60% of all bird species from our dataset were associated with water ecosystems (and half of all bird species was associated exclusively with *H. amphibius*), these habitats seem to be important in the conservation of many birds forming associations with mammals. Although living near large mammals might be sometimes costly since raptors were also recorded hunting alongside them (Dean & MacDonald 1981), in general associations with large mammals seems to be very advantageous. For instance, mammal-associated birds improve their foraging efficiency, receive more food and expend less energy than non-associated birds (Heatwole 1965; Smith 1971; Ruggiero & Eves 1988); some authors have even suggested that such an association might be protective against predators for both the birds and the host mammals (Ruggiero & Eves 1988; Koenig 1997).

One possible explanation for the observed patterns in bird–mammal interactions is the classical island biogeography theory, which represents a commonly used framework applied to a wide range of spatially heterogeneous ecological and evolutionary systems (MacArthur & Wilson 1963, 1967). In brief, model of island biogeography predicts species richness to be a dynamic equilibrium between immigration and extinction and rates of both variables are linked to island size and its isolation from the source mainland population. In result, larger islands and islands closer to mainland support higher species richness (MacArthur & Wilson 1963, 1967). For instance, "islands" have been reported as fragments of habitats (Saunders, Hobbs & Margules 1991), isolated lakes (Magnuson et al. 1998) and mountains tops (Sklenář, Hedberg & Cleef 2014) but their predictive capability also works well on much smaller scales, e.g. between cattle droppings and host organisms (Mohr 1943), host animals in relation to their parasites (Kuris, Blaustein & Alio 1980), and organic debris and aquatic microbial pathogens (Lyons et al. 2010). However, one could then also expect a correlation between bird species richness and mammal size since small mammals could serve as hosts for mainly smaller bird species while larger mammals host both smaller and larger birds. However, we found a correlation between bird species richness and mammal herd size but not with mammal size. At least in a case of our dataset, it seems that the basic unit acting as an "island" when focusing on bird species richness is at a higher level than the individual mammal, i.e. it is the size of the mammal herd. However, we were unable to control for distance between mammal individuals and herds which is an important component theory of island biogeography framework, and, hence, further research using more appropriate data is required.

In agreement with previous field studies, analysis of Internet photos showed that *Buphagus* spp. were very often associated with larger-bodied mammals (with exception of common association of *B. erythrorhynchus* with *A. melampus*) (Mooring & Mundy 1996; Koenig 1997; Nunn et al. 2011; Ndlovu & Combrink 2015). Despite the fact that smaller mammals have a higher tick number to body mass ratio (Hart, Hart & Mooring 1990), potentially increasing the efficiency of tick harvesting, it seems that the absolute number of ticks and their abundance play a more important role (Mooring & Mundy 1996; Koenig 1997; Nunn et al. 2011). *Buphagus* spp. were identified as very effective tick removers from body parts that are inaccessible to self-grooming by host mammals, suggesting that they should play an important role in tick control in visited mammals (Mooring et al. 2000; Bezuidenhout & Stutterheim 2009; Nunn et al. 2011; Ndlovu & Combrink 2015). Further, Ndlovu & Combrink (2015) suggested that *Buphagus* spp. may prefer larger-bodied ungulates possibly because larger mammals can provide a more stable platform upon which to forage, or are just large enough to support simultaneous feeding of more *Buphagus* spp. individuals. According to our results, the last explanation seems to be less probable as we were unable to find any significant relationship between the average number of *Buphagus* spp. individuals on particular mammal species and body mass of those mammals. This could be due to the fact that *Buphagus* spp. live in small groups (van Someren 1951), the majority of which may be of quite uniform size. It is also possible that members of such groups might prevent access to the host by other unfamiliar individuals or groups. However, we were not able to find any observational or experimental study dealing with this issue.

The nested structure of mutualistic networks is usually interpreted as asymmetric specialization (i.e., specialists are rather specialized to generalists than to other specialists). This concept of nestedness has important consequences for ecological (Bastolla et al. 2009) and evolutionary (Bascompte et al. 2003) principles of biodiversity maintenance. In contrast to earlier results on a similar system in a Neotropical region (Sazima et al. 2012), we found only a weak nested web structure for African birds and mammals caught on Internet photos. A relatively weak nested web structure even for *Buphagus* spp. could be due to the fact that only a limited diversity of large herbivores is available in Neotropical regions compared to Africa (Dean & MacDonald 1981; Sazima et al. 2012; Ripple et al. 2015). However, except for *Buphagus* spp., nestedness did not differ significantly from a null model indicating that birds do not prefer mammal species which are visited by a large number of bird species. In *Buphagus* spp., however, this suggests that a nested structure is not the result of a random assignment of birds to their mammal hosts. Because only two species of extant *Buphagus* spp. are known, our results indicate that *B. africanus* is more specialized, using a subset of hosts used by the less specialized *B. erythrorhynchus*. This is in agreement with field studies showing that even on localities where distribution of both species overlaps (i.e. spectrum of potential mammal hosts should be the same for both species), *B. erythrorhynchus* has a wider range of hosts (Ndlovu & Combrink 2015).

We also highlight the potential role of information technologies and new media, such as Internet search engines, for further studies in ecology and evolution. Google Images represent one such resource that could facilitate a rapid collection of information on various aspects of ecological systems at large spatial and taxonomical scales. As Leighton et al. (2016) pointed out, results obtained from the analysis of Internet images can be in good agreement with data from fieldwork and such an approach could therefore, at least in some cases, supplement or replace less effective and time- and money-consuming fieldwork. For instance, our approach identifies new associations, e.g. that *B. erythrorhynchus* feeds from time to time on much smaller hosts than previously reported (including *Eudorcas thomsonii* weighting ~20 kg) (Dean & MacDonald 1981; Hart, Hart & Mooring 1990; Feare & Craig 2010; Ndlovu & Combrink 2015). On the other hand, we were not able to find any evidence for several previously described associations. This may indicate that that several bird–mammal interactions may have been lost over time thus having potential implications for wildlife conservation. Mammal megafauna is typically at a higher extinction risk than smaller mammals (Cardillo et al. 2005) and extinctions of the world's megafauna are now mainly occurring in sub-Saharan Africa and Southeast Asia, with 60% of the largest herbivore species threatened with extinction (Ripple et al. 2015). Loss of megafauna could thus cause an impoverished diversity of mutual interactions. Alternatively, this may indicate limitations of our approach which may be the result of species-specific public attention paid particularly to common or "charismatic" species of birds and mammals (Clucas, McHugh & Caro 2008; Troudet et al. 2017). A strong association with larger-bodied mammals also raises a question whether the rapid loss of African megafauna could have a negative impact on the survival of *Buphagus* spp. Although it seems that *Buphagus* spp. are able to behave plastically and can shift their host selection to other available herbivores, including domestic mammals in regions where they are common (Dale 1992; Feare & Craig 2010), this issue needs to be investigated in future studies.

Conclusions

In summary, we showed that using internet sources gives us an opportunity to access big amount of data on the bird–mammal commensalistic–mutualistic system, which was not studied in such wide perspective before. We found several interesting patterns in these data and we propose some biological explanations on these patterns. However, we are aware of several limitations of used approach and, hence, interpretations and extrapolations of our results on real biological systems must be careful. Hence, our arguments should be understood in the context of method we used.

We found support for the idea that patterns of interactions between birds and large African megafauna can be shaped by simple mechanisms including mammal species body mass, herd size and habitat openness. We also found that *Buphagus* spp. tended to visit mainly larger-body mammals, however, we did not find any significant association between their number and mammal and environmental characteristics. This suggests that their host selection could target an optimal foraging patch since larger mammals could support more ectoparasites, but they can behave territorially on host animals preventing the entry of other unfamiliar *Buphagus* spp. individuals or groups. Sitting, perching or feeding interactions between African birds and megafauna in savannahs are only one aspect of commensalistic–mutualistic interactions between birds and mammals. Similar interspecific relationships have also convergently evolved between birds and, for instance, larger-bodied terrestrial mammals in Neotropical regions (Sazima et al. 2012), monkeys (Boinski & Scott 1988), otters (D'Angelo & Sazima 2014), dolphins (Bräger 1998), and domestic animals such as cattle which replaced native megafauna in many world regions (Lyons et al. 2010; Kioko et al. 2016; Galetti et al. 2017). Our results could thus also bring new insights on the complexity of bird–mammal interactions in other world regions and systems including different animal taxa but further comparison with *in situ* observations of commensalistic–mutualistic systems to check for potential biases is required.

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Table 1(on next page)

Relationships between bird, mammal and environmental characteristics

Relationships between bird, mammal and environmental characteristics for (a) the full set of species and (b) species based on at least 10 photos, after correcting for phylogenetic relationships of the mammal species using phylogenetic generalized least square regression (PGLS). Statistically significant relationships are highlighted in bold.

Model	(a) Slope	SE	t-value	p-value	(b) Slope	SE	t-value	p-value
ALL SPECIES								
Mean bird mass								
Intercept	0.041	0.694	0.059	0.954	2.638	1.427	1.843	0.095
Mammal mass	4.836	0.085	2.897	**0.008**	0.254	0.044	5.717	**<0.001**
Herd size	0.247	0.200	2.047	0.051	0.364	0.094	3.861	**0.003**
Elevation	-0.105	0.121	-0.866	0.395	0.230	0.212	1.085	0.303
Vegetation cover	-0.773	0.341	-2.269	**0.032**	-0.762	0.231	-3.300	**0.008**
Mean bird number								
Intercept	4.836	1.006	4.808	<0.001	-0.584	1.030	-0.567	0.583
Mammal mass	0.155	0.061	2.569	**0.016**	0.078	0.037	2.072	0.065
Herd size	-0.035	0.132	-0.265	0.793	-0.165	0.071	-2.307	**0.044**
Elevation	-0.033	0.078	-0.429	0.672	0.143	0.151	0.947	0.366
Vegetation cover	-0.107	0.229	-0.470	0.642	0.013	0.182	0.070	0.946
Total species richness								
Intercept	-1.441	1.256	-1.147	0.262	3.401	2.368	1.436	0.182
Mammal mass	0.192	0.109	1.757	0.091	0.011	0.117	0.098	0.924
Herd size	0.911	0.241	3.782	**<0.001**	1.208	0.168	7.176	**<0.001**
Elevation	0.185	0.142	1.303	0.204	-0.328	0.325	-1.009	0.337
Vegetation cover	-0.235	0.415	-0.566	0.577	-0.292	0.757	-0.386	0.707
Buphagus spp.								
Mean bird mass								
Intercept	4.990	0.784	6.366	<0.001	96.084	49.502	1.941	0.084

Mammal mass	0.106	0.069	1.544	0.138	0.014	0.007	1.940	0.084
Herd size	0.316	0.263	1.203	0.242	5.567	10.378	0.536	0.605
Elevation	-0.139	0.080	-1.735	0.097	0.029	0.028	1.041	0.325
Vegetation cover	-0.274	0.249	-1.099	0.284	1.389	13.352	0.104	0.919

1

Figure 1

Geographical distribution of recorded bird–mammal interactions.

Geographical distribution of recorded bird–mammal interactions. Most records are distributed in East and Southern Africa whereas only restricted numbers of records originate from Central and West Africa.

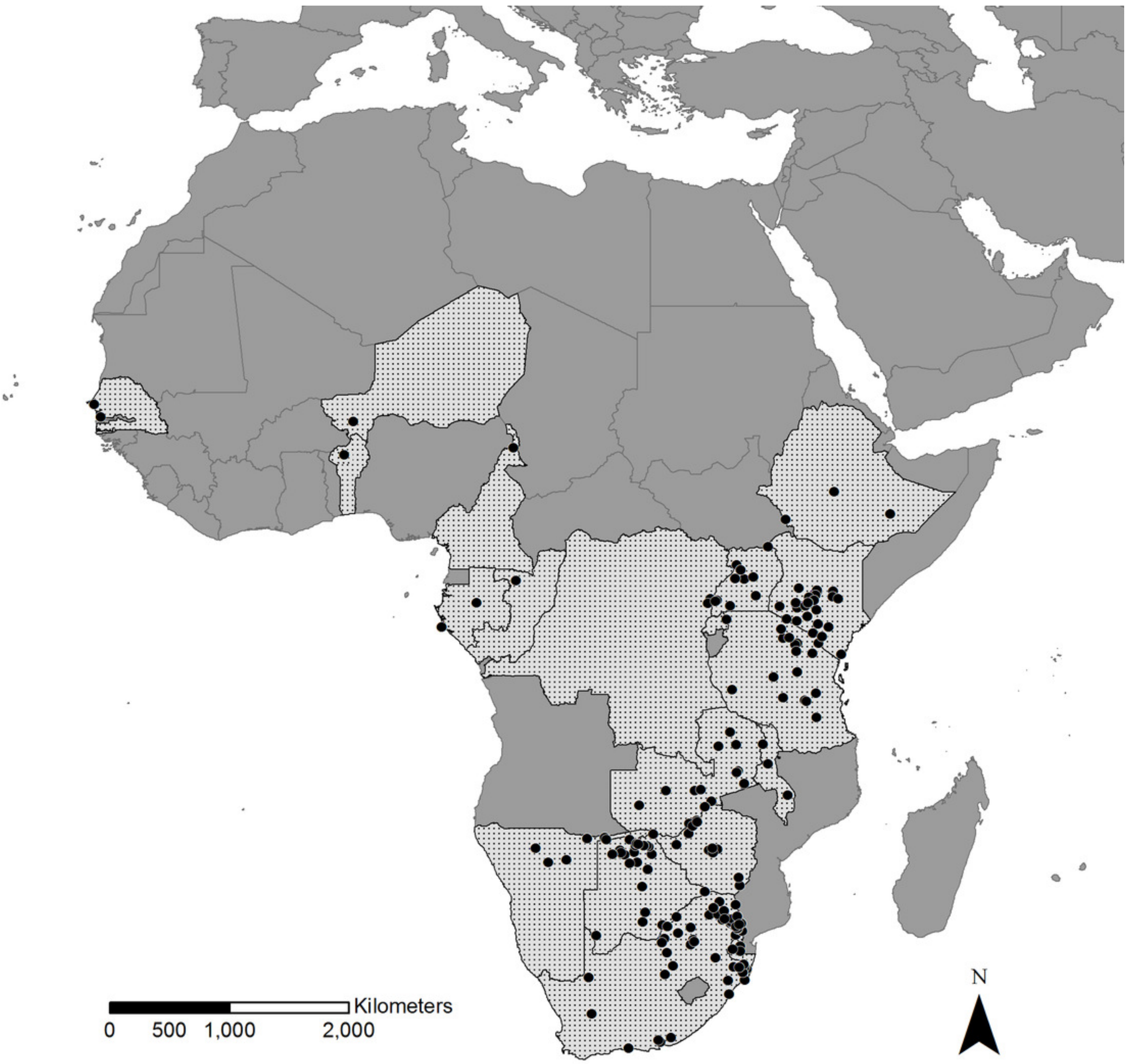
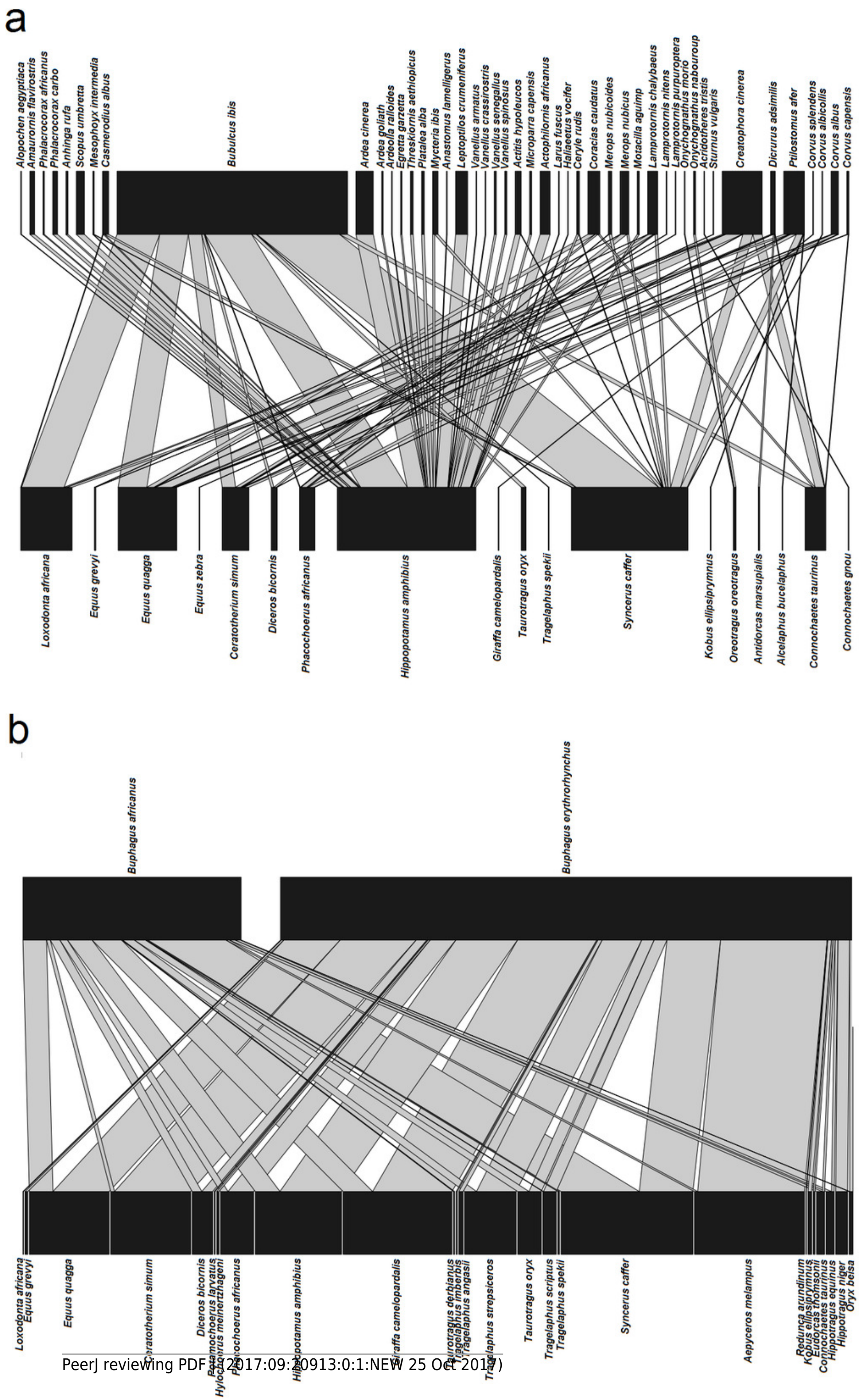


Figure 2

Quantitative bird–mammal interaction webs for all bird species without *Buphagus* spp. and *Buphagus* spp. only.

Quantitative bird–mammal interaction webs for all bird species without *Buphagus* spp. and *Buphagus* spp. only. For each web, the lower bars represent the frequency with which each mammal species is visited by birds, and upper bars represent the number of interactions for each bird species. Interactions for all mammal and bird species were sampled with equal effort and are ordered according to phylogenetic relationships among mammals and birds, respectively.


a
Alopochen aegyptiaca
Amaurornis flavirostris
Phalacrocorax africanus
Phalacrocorax carbo
Anhinga rufa
Scopus umbretta
Mesophoyx intermedia
Casmerodius albus
Bubulcus ibis
Ardea cinerea
Ardea goliath
Ardeola ralloides
Egretta garzetta
Threskiornis aethiopicus
Platalea alba
Mycteria ibis
Anastomus lamelligerus
Leptoptilos crumeniferus
Vanellus armatus
Vanellus crassirostris
Vanellus senegallus
Vanellus spinosus
Actitis hypoleucos
Microparra capensis
Actophilornis africanus
Larus fuscus
Haliaeetus vocifer
Ceryle rudis
Coracias caudatus
Merops nubicoides
Merops nubicus
Motacilla aguimp
Lamprotornis chalybaeus
Lamprotornis nitens
Lamprotornis purpuroptera
Onychognathus morio
Onychognathus nabouroup
Acridotheres tristis
Sturnus vulgaris
Creatophora cinerea
Dicrurus adsimilis
Ptilostomus afer
Corvus splendens
Corvus albicollis
Corvus albus
Corvus capensis
Loxodonta africana
Equus grevyi
Equus quagga
Equus zebra
Ceratotherium simum
Diceros bicornis
Phacochoerus africanus
Hippopotamus amphibius
Giraffa camelopardalis
Taurotragus oryx
Tragelaphus spekii
Syncerus caffer
Kobus ellipsiprymnus
Oreotragus oreotragus
Antidorcas marsupialis
Alcelaphus bucelaphus
Connochaetes taurinus
Connochaetes gnou
b
Buphagus africanus
Buphagus erythrorhynchus
Loxodonta africana
Equus grevyi
Equus quagga
Ceratotherium simum
Diceros bicornis
Potamochoerus larvatus
Hylochoerus meinertzhageni
Phacochoerus africanus
Hippopotamus amphibius
Giraffa camelopardalis
Taurotragus derbianus
Tragelaphus imberbis
Tragelaphus angasii
Tragelaphus strepsiceros
Taurotragus oryx
Tragelaphus scriptus
Tragelaphus spekii
Syncerus caffer
Aepyceros melampus
Redunca arundinum
Kobus ellipsiprymnus
Eudorcas thomsonii
Connochaetes taurinus
Hippotragus equinus
Hippotragus niger
Oryx beisa