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Original Article Female solo song and duetting are associated with different territoriality in songbirds

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Recently, there has been an increased effort to unravel selective factors behind female song evolution in songbirds. Female birds which produce songs may sing either solo or in duets; although the 2 vocal performances likely evolved through different selection forces and mechanisms, the majority of large-scale studies to date have focused only on duetting or female song in general (pooling female solo song and duetting into a single category). Hence, here we estimate the effect of behavioral life-history traits (territoriality, social bonds, and cooperative breeding) and environmental productivity on the occurrence of female solo song and duetting separately in songbirds of South Africa and Lesotho. The focal region is characterized by subtropical/tropical climate, clear spatial environmental productivity gradient, and detailed knowledge on avian species distribution and behavioral life-history traits. Phylogenetically informed comparative analyses revealed that species where females produce only solo songs exhibited higher levels of territoriality than species with nonsinging females (in an univariable model) but, simultaneously, lower levels than duetting species. Although both species with female solo song and duetting establish mainly long-term social bonds, the former defend their territories seasonally while the latter exhibit mainly year-round territoriality. Cooperative breeding and environmental productivity were not associated with the distribution of female solo song and duetting in any model. Our results indicate that when exploring female song ecology and evolution, female solo song and duetting are likely to be distinct song categories associated with different levels of territoriality.

Lay Summary: Female birds produce songs either solo or in duets. Although large-scale relationships between duetting and social or environmental factors have been studied intensively, such associations remain largely unexplored for female solo song. We found that species with female solo song are less territorial than duetting species and both groups are simultaneously more territorial than species where female song is absent. Hence, female solo song and duetting may represent distinct song categories associated with different levels of territoriality.

Key words: behavioral life-history traits, macroecology, normalized difference vegetation index, phylogenetic comparative analyses.

INTRODUCTION

The complex song of songbirds (Passeriformes: Passeri) has long been attributed to males only, with the assumption that it evolved through sexual selection via male–male competition and female choice (Darwin 1871; Catchpole 1987). Present opinion is that female song is ancestral to songbirds and that it is phylogenetically widespread and occurs in species inhabiting a range of climatic zones (Garamszegi et al. 2007; Odom et al. 2014). In general, females may sing either independently of males, that is, emitting solo songs, or in duets, that is, coordinated with the mate. For species in which both sexes sing, the prevailing view is that females sing for similar reasons as males (but the distribution of functions of female song could to be more variable than in males) (Langmore 1998; Hall 2004). In addition to intrapair contact (de Silva et al. 2004) and coordination of breeding activities (Gilbert and Carroll 1999), female singing may also be associated with mate attraction, mate guarding, and defense of territories (Langmore 1998; Hall 2004, 2009; Cain and Langmore 2015; Krieg and Getty 2016; Tobias et al. 2016). Although female solo song and duetting can

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share some similar functions, the 2 types of performances are not necessarily equivalent (Langmore 1998; Hall 2009; Odom et al. 2015; Tobias et al. 2016). Moreover, although duets are rare in temperate zone birds, female solo song occurs more often there than duetting (Garamszegi et al. 2007; Tobias et al. 2016). Differences in function and geographical distribution between these 2 types of vocal performance indicate that they likely evolved through different selection forces and mechanisms (Odom et al. 2015).

Previous studies have shown an association between the distribution of female song in general (involving both duetting and female solo song) and behavioral life-history traits such as the long-term territoriality (Robinson 1948; Benedict 2008), occurrence of social monogamy (Price 2009; Odom et al. 2015; but see Benedict 2008), absence of migration (Price 2009; Logue and Hall 2014; Odom et al. 2015), and convergent sex-roles (Slater and Mann 2004). A global synthesis on social and environmental factors behind the evolution of duetting revealed that duetting was, out of many factors evaluated, most strongly linked to year-round territoriality and stable social bonds (Tobias et al. 2016). Nevertheless, it is difficult to make a deeper insight into female solo song evolution from these studies, because results in female song studies might be largely driven by the inclusion of duetting species. Evolutionary and ecological factors driving the evolution of female solo song remain largely unexplored and large-scale studies on female solo song are, according to the best of our best knowledge, still missing. For instance, it is unclear which selective factors favor the evolution of female solo song and duetting with respect to each other.

Global variation in avian behavioral traits, as, for instance, territoriality (Maher and Lott 2000), breeding systems (Jetz and Rubenstein 2011), and migration (Alerstam et al. 2003), is largely determined by environmental conditions including those presumably associated with the distribution of female song evolution. Species with females that sing are predicted to inhabit regions with high-resource availability and little seasonal change. Such birds are expected to reside and breed over the prolonged season (Ricklefs 1969; Price et al. 2009) and experience increased pressure from both intra- and interspecific intruders (Ballance et al. 1997; Justino et al. 2012). In fact, predictable environments rich in food resources seem to favor birds exhibiting more sedentary lifestyles and longer-term partnerships, thus driving the evolution of singing in female birds (Logue and Hall 2014; Odom et al. 2015; Tobias et al. 2016). Indeed, species with females that sing have been found to be particularly common among highly productive tropical regions characterized by low levels of environmental seasonality (Morton 1996; Slater and Mann 2004; Price et al. 2009; Odom et al. 2014, 2015; Tobias et al. 2016).

In this study, we employed phylogenetic comparative analyses to explore interspecific variability in female solo song and duetting in association with important intrinsic (behavioral) and extrinsic (environmental productivity across species distribution range) traits in songbirds to determine whether both vocal performances are associated with the same or different selective factors. First, we explored variability in duetting, because a substantial body of theoretical and empirical work regarding female song ecology and evolution focuses on duetting, and predict that females that sing in duets belong mainly to species with year-round territoriality, establishing long-term social bonds as well as inhabiting more productive areas (Tobias et al. 2016). However, female solo song seems to be relatively more common than duetting in temperate zone species (Garamszegi et al. 2007; Odom et al. 2015) which exhibit different behavioral traits and face more variable environment; hence, we predict associations of female solo song with decreased level of

territoriality, shorter-term social bonds, and lower environmental productivity compared with duetting species. We tested these hypotheses on a sample of songbirds breeding in sub-Saharan Africa that is rarely studied in regard to avian female song. We specifically focused on South Africa and Lesotho, a region occupied by more than 350 songbird species of 39 families (Lepage 2018). The knowledge on species distribution, life-histories, and environmental conditions is exceptionally detailed there (see METHODS), making the region very well suited for our research purposes. From a global perspective, South African songbirds typically exhibit slow ("tropical") pace of life (Jetz et al. 2008), but on regional scale these traits tend to vary across species, and species in the region significantly differ in production of female song (Hockey et al. 2005). Furthermore, although the climate is generally subtropical to tropical, key environmental conditions in the region show a clear longitudinal trend (driven by a longitudinal precipitation gradient), from dry and unproductive desert in the west to moist and productive woodland in the east (Hořák et al. 2015).

METHODS

Data collection

Species distribution data

Comprehensive data on the distribution of songbird species across South Africa and Lesotho were obtained from the Southern African Bird Atlas Project (SABAP) (Harrison et al. 1997), which surveyed all birds living in this region between 1987 and 1992. Each set of songbird species recorded within a fine $\sim 25 \times 25$ km grid cell (0.25° spatial resolution) was considered as a local assemblage (the region covered by 1,858 grid cells/assemblages in total).

Female song data collection

Song was defined as primary long-range complex acoustic vocalization used by birds mainly during the breeding season. In accordance with this definition, information on the presence or absence of female song in South African songbirds was primarily obtained from data compiled for global assessments, with further relevant data taken from other literature sources (see below for further details). Species producing only simple call-like vocalization (e.g., some corvids) were omitted from the analyses because the lack of song in both sexes might be because of different selection pressures than in species with male song only. Similarly, species for which relevant information on vocalization was lacking were omitted from further analyses.

Duetting was defined as coordinated or alternated long-range vocalization that is performed communally by two bird individuals (usually the members of a mated pair) (Tobias et al. 2016). This working definition harbors duets as generally understood, but excludes simple vocalizations such as different types of calls. Following suggestions by Logue and Hall (2014) and Tobias et al. (2016), duetting species were pooled together with chorusing species (involving 3 or more individuals), because both types of signalizations are similar in structure and function (Logue and Hall 2014). It is thus often difficult to distinguish between them (e.g., many duetting species were observed chorusing and vice versa) and, moreover, duets and choruses are thought to have evolved under similar selection pressures (e.g., Seddon and Tobias 2003; Tobias et al. 2016).

Because information that females of particular species sing only solo songs is rarely explicitly stated in literature, we have to extract such information by focusing on indirect evidence. Firstly, we prepared a female song dataset where we combined data on presence/ absence of female song in general provided by Webb et al. (2016), then Hockey et al. (2005), which directly focus on birds of South Africa and Lesotho, and finally continuously updated online edition of "Handbook of the Birds of the World Alive" (del Hoyo et al. 2015). In general, female song was scored as present when females were reported as singing or where species accounts stated that song is persistent in both sexes. Female song was scored as absent when production of song was reported by males only, or when female produced only simple calls. Finally, scores on female solo song distribution among species were obtained by combination of data included in female song and duetting data set. We considered that a given species only has a female solo song if female song was scored as present for that species in the female song data set and simultaneously the exhaustive update on duetting distribution across world birds by Tobias et al. (2016) stated that females of this species do not sing in duets or choruses.

After excluding temperate zone migrants (13 species) and species lacking information on all traits (nine species), of the 278 songbird species for which we had breeding distributional data, we were able to obtain information on presence or absence of duetting for 269 species (out of these 52 species produce duets) and presence or absence of female song for 163 species (out of these 30 species produce female solo song).

Behavioral life-history traits

We collected data on several key behavioral life-history traits hypothesized to play a role in the evolution of song production in female songbirds, including the level of territoriality, stability of social bonds, and cooperative breeding (Logue and Hall 2014; Najar and Benedict 2015; Odom et al. 2015; Tobias et al. 2016). Information on these traits for species breeding in South Africa and Lesotho were obtained from recent large-data compilations by Tobias et al. (2016) (territoriality and social bond type) and Dale et al. (2015) (cooperative breeding). Tobias et al. (2016) also scored data according to the level of quality (i.e., uncertainty of classification assignment). The majority of data on territoriality and social bond for birds of South Africa were of high quality; we thus decided to omit quality scores from the analysis. Because definitions and categories in some traits change from source to source, we provide definitions as used in data-source studies.

Territoriality. Species were scored following definitions provided by Tobias et al (2016) as follows: 1) nonterritorial that do not defend territories, or defend only very small areas around nest sites, or species where males defend song or display posts only; 2) seasonally or weakly territorial, having home ranges that largely overlap, or that usually join mixed flocks with poorly defined spatial ranges; and 3) year-round territorial that defend territories all year (for further details see Tobias et al. 2016).

Social bonds. Species were scored as 1) solitary if they do not form pairs, or form them only for a short time during the courtship period, 2) having short-term pair/group bonds if they establish only seasonal partnership and change it in subsequent breeding attempts (low partner fidelity and >50% divorce rate per year), and 3) having long-term pair/group bonds if pair/group members establish yearround partnership or their seasonal pair/group lasts toward subsequent breeding attempts (high partner fidelity and <50% divorce rate per year) (for further details see Tobias et al. 2016).

Cooperative breeding. Species were classified in the following way: 1) noncooperative; species with no more than 2 adult birds caring

for the offspring, and 2) cooperative; species with more than 2 birds taking care for the offspring (for further details see Dale et al. 2015).

Environmental productivity

We obtained the "normalized difference vegetation index" (hereafter NDVI), an estimate of environmental productivity based on the spectral properties of vegetation, for each grid cell from the data set provided by the U.S. Geological Survey (http://iridl.ldeo.columbia.edu/SOURCES/.USGS/.ADDS). Maximum NDVI values (hereafter NDVI_{max}), represented by the average NDVI value of the month with the highest NDVI (available for 1981-2008), were chosen as a proxy of environmental productivity. As the NDVI describes the "greenness" of vegetation and is closely correlated with rainfall, total green biomass, and net primary productivity (Goward and Dye 1987; Chong et al. 1993; Paruelo et al. 1997; Schmidt and Karnieli 2002), it is expected to reflect food availability to songbirds. This assumption is supported by the findings of Lassau and Hochuli (2008) and Lafage et al. (2014, who found a positive correlation between the amount of food available (e.g., arthropod abundance) in the breeding season and NDVI. For subsequent statistical analyses concerning individual species, we calculated the average values of NDVI_{max} across all cells occupied by given species. We used $NDVI_{max}$ because we expected that the analyzed traits could play an important role during a breeding period, typically a period of the year when birds can potentially obtain the maximum amount of food resources from the environment.

Phylogenetic tree construction

A phylogenetic tree of South African songbirds was constructed using the avian phylogenetic tool available at http://birdtree.org/ (Jetz et al. 2012). The maximum credibility tree was built from 1000 randomly generated trees based on a Hackett backbone (Hackett et al. 2008). Moreover, for subsequent analyses, we also used 100 randomly selected phylogenetic trees. The maximum clade credibility tree was then determined using the TreeAnnotator tool v. 1.8.2 in the BEAST software package v. 1.8.2 (Drummond and Rambaut 2007).

Statistical analyses

As phylogenetically related taxa have a higher probability of sharing characteristics from a common ancestor, phylogenetic relatedness of species could affect presence of duetting and female solo song. Therefore, we modeled associations between variables, including nonindependence in species data, using phylogenetic generalized linear mixed-effect models (PGLMM) (Ives and Helmus 2011). We produced models containing all behavioral life-history traits and environmental productivity as explanatory variables, and with duetting and female solo song as response variables. Duetting, female solo song, and cooperative breeding were used as binary (presence/absence) variables, whereas environmental productivity was used as a continuous variable. We decided to use territoriality and social bonds as continuous rather than categorical variables in the analyses because there is a gradient in the levels of these variables, which means that the cutoff criteria for their categorization into distinct categories were somewhat arbitrary. Moreover, models with continuous variables are less sensitive to available sample size and the symmetry of the observations for each category. It should be noted, however, that inclusion of territoriality and social bonds as categorical explanatory variables did not change the overall conclusions (see below).

We performed four comparisons contrasting: 1) duetting species and nonduetting species (with either nonsinging or solo singing females), 2) duetting species and species with nonsinging females, 3) species with females producing solo song and duetting species, and 4) species with females producing solo song and species with nonsinging females. First, we conducted a multivariable model and subsequently univariable models for each explanatory variable separately (for univariable models, see Supplementary Table S1). We used species-level phylogeny; to enhance the informative value of results, we used 2 ways how to deal with phylogenetic uncertainty. In one case, we performed a model with single maximum credibility phylogenetic tree, and in the second case, we used 100 randomly selected phylogenetic trees and combined the outputs as the average values of the posterior outcomes (Supplementary Table S2). These 2 approaches were applied for both multivariable and univariable models, respectively, and showed the same results; hence, in the main text, we report only models using single maximum credibility phylogenetic tree. However, because every species was represented by only one sample in our data set, the random effect of the species could potentially be confounded with the residuals (Hadfield 2010a). To avoid this obstacle and test the robustness of these results, we also performed the same models with different parameterization using family-level phylogeny (Supplementary Tables S3–S5); importantly, both approaches gave identical results.

We performed PGLMM by Bayesian inference using the Markov chain Monte Carlo technique (MCMCglmm; Hadfield 2010b). This approach allowed us to control for phylogenetic co-variation among species by including phylogenetic distance into the model as a random variable (Hadfield and Nakagawa 2010). We used the inverse-gamma prior for random effects and an uninformative prior for the residual variance in all MCMCglmms. The choice of priors was determined by the character of our data, sometimes containing a small number of samples for some variable categories. All models were run for 1,000,000 iterations with elimination of the first 20,000 iterations as a burn-in period and thinning to every 100th iteration. All binary variables were centered by subtracting their mean and the numeric variables were centered and standardized on the same scale (range 1) to improve interpretability. For models with a maximum credibility phylogenetic tree, we used the Gelman-Rubin statistic to check convergence of multiple MCMC chains runs in parallel. This compares within-chain variance with between-chain variance and calculates the potential scale reduction factor (Gelman and Rubin 1992). The iteration chains mixed well, exhibiting no observable autocorrelation. The Gelman-Rubin statistic threshold for models with a maximum credibility phylogenetic tree was < 1.05 in all models. Posterior fixed effect distribution was examined for overlap with zero (as the significance test), using 95% highest posterior density as a credible interval. We also calculated phylogenetic signal as an estimate of the proportion of variance in duetting and female solo song after conditioning on explanatory variables explained by the effect of phylogenetic relatedness. All data were processed and statistically analyzed using R 3.3.1 (R Development Team 2013).

RESULTS

We found that in the first 2 comparisons, that is, duetting species versus nonducting species, and duetting species versus species with nonsinging females, the strongest predictors of duetting distribution were the level of territoriality and length of social bonds. However, it was not possible to test the effect of social bonds in these contrasts as it was not possible to estimate the posteriors for this parameter. This was because all species singing in duets fall into one category of social bonds (long-term). This, however, indicates that the 325

association of duetting song with the long-term social bonds is indeed strong. Univariable models lead to the same results (Figure 1, Table 1, see also Supplementary Tables S1 and S2). Species where females sing in duets maintain longer-term territoriality and social bonds when compared with relatively shorter-term territoriality and social bonds in species where females produce no duets and no female song, respectively. However, when contrasting species with females singing solo songs and duetting species, the only statistically significant association in both multivariable and univariable models was with the level of territoriality such that the level of territoriality increases toward duetting species (Figure 1, Table 1, see also Supplementary Tables S1 and S2). Finally, when contrasting species with female solo song and species with nonsinging females, no significant predictor was identified in multivariable models. However, univariable models revealed association with the level of territoriality; species wherein females produce solo songs exhibited higher level of territoriality than species with no female song (Figure 1, Table 1, see also Supplementary Tables S1 and S2). In all contrasts, cooperative breeding and the environmental variable, NDVI_{max}, did not explain the presence of any singing characteristic.

To test robustness of these results, we also prepared models where territoriality and social bonds were coded as categorical variables (results are summarized in Supplementary Tables S6 and S7). Duetting species exhibited significantly more often year-round territoriality than seasonal or weak territoriality when compared with nonduetting species and species with no female song. Furthermore, species with solo singing females were significantly more often seasonally territorial when compared with mainly year-round territorial duetting species but exhibited lower proportion of weak territoriality than species with no female song.

The above results are nicely supported by spatial geographical patterns. There was a clear spatial pattern in duetting distribution across the study region (Figure 2a, b), where regions with a high proportion of duetting songbirds strongly overlapped spatially with regions with high proportion of year-round territorial species (Supplementary Figure S1). At the same time, the association between the proportion of duetting and environment (NDVImax) was less clear; however, higher proportion of duetting species was partially recorded in humid and highly productive areas (Supplementary Figure S1), including savannahs, woodlands, and forests in eastern and north-eastern South Africa, as well as areas along the Indian Ocean coastline. A low proportion (occasionally approaching zero) of duetting species was detected in central, higher elevated grasslands, and in Succulent Karoo, Nama Karoo, and Kalahari and Namib Deserts in western South Africa. When contrasting species with the presence of female solo song against species with the presence of duetting, the proportion of female solo song was highest in central parts of South Africa (Figure 2c), copying geographical trends in the distribution of seasonal territoriality; these areas were also characterized by less productive environments (Supplementary Figure S1). Finally, when contrasting species with the presence of female solo song against species without female song, areas with the high proportion of species with female solo song geographically coincide with areas with the high proportion of year-round territorial species, similarly to the first 2 previous contrasts (duetting vs. non-duetting and duetting vs. no female song; Figure 2d, Supplementary Figure S1).

DISCUSSION

We found high variation among South African songbirds with regard to the presence of female singing. It is worth noting that



Figure 1

Associations between female song categories (duetting, female solo song, no duetting, and no female song) and the level of (a) territoriality (weak, seasonal, year-round) and (b) social bonds (solitary, short-term, long-term). Each barplot represents different female song category and the height of differently colored bars within each category refers to the proportion of species associated with different levels of territoriality and social bonds. The number N represents the number of species in each group.

species involved in our study exhibit slow pace of life from a global perspective (Jetz et al. 2008), and inhabit subtropical to tropical environments, where singing females are often reported (Tobias et al. 2016). Although both duetting species and species with female solo song establish mainly long-term social bonds, female solo song-duetting comparison revealed a negative association between presence of female solo song and territoriality. Subsequent analysis found that duetting species exhibited mainly the year-round territoriality while female solo song predominated in species that are territorial only seasonally although the proportion of yearround territorial species was still relatively high (>20%) in latter group. Species wherein females do not produce song exhibited on average lower level of territoriality than species with solo singing (in univariable model only) and duetting females. Interestingly, neither in multivariable models nor in univariable models cooperative breeding and environmental productivity was associated with the distribution of duetting and female solo song. Hence, level of territoriality rather than other social and environmental factors is the immediate driver affecting the distribution of female song performances in our sample of subtropical to tropical birds.

We found that female solo song emerged mainly in species exhibiting seasonal territoriality while duetting species were characterized by the presence of year-round territoriality. This indicates that the 2 vocal performances probably evolved in association with different selection pressures or different levels of the selection factors (Langmore 1998). Price (2015) suggested that sexual dimorphism in singing is often the result of losses in females rather than gains in males. Then, instead of being an evolutionary precursor of duetting, presence of female solo song may also emerge in bird lineages which expanded to areas where year-round territoriality is costly, for example, from tropical to temperate zones. However, further studies are needed to focus in greater detail on factors and large-scale patterns of female solo song in birds. Either way, despite the fact that duetting and female solo song are often clumped together under the "female song" category in multitaxonomic studies (e.g., Najar and Benedict 2015; Webb et al. 2016), our results suggest that the 2 vocal performances should be considered as independent composites of female song (also see Odom et al. 2015).

Although it is difficult to disentangle effects of territoriality and social bonds on duetting, it seems that the presence of duetting is more closely associated with presence of year-round territoriality than presence of long-term social bonds (though this was not explicitly tested; also see Tobias et al. 2016). We argue that although the presence of duetting is slightly better predicted by long-term social bonds than year-round territoriality, absence of duetting was almost always linked to the loss of year-round territoriality while majority of nonduetting species still establish long-term social bonds. For instance, duets were completely lacking in some of species-rich families inhabiting South Africa such as old-world buntings (Emberizidae), finches (Fringillidae), swallows and martins (Hirundinidae), and pipits and wagtails (Motacillidae) with no

Table 1

Results of multivariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with species-level phylogeny (the maximum credibility phylogenetic tree) as a random effect for (a) duetting (vs. no duetting, i.e., no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as response variables and life-history traits (territoriality, social bonds, and cooperative breeding) and an environmental variable (NDVI_{max}) as explanatory variables in songbirds of the South Africa and Lesotho

Predictor	Posterior mean	95% CI	Lambda	pMCMC
(a)				
Territoriality	455.42	231.16-701.29	0.645	< 0.001
Social bonds ^a				
Cooperative breeding	31.09	-111.77 - 173.11		0.653
NDVI _{max}	120.66	-154.84 - 402.10		0.376
(b)				
Territoriality	412.89	203.70-625.62	0.815	<0.001
Social bonds ^a				
Cooperative breeding	58.35	-102.72 - 211.62		0.458
NDVI _{max}	225.80	-45.11 - 506.46		0.087
(c)				
Territoriality	-273.22	-517.45 - 56.75	0.997	0.006
Social bonds	-59.93	-211.85 - 109.18		0.439
Cooperative breeding	-28.33	-266.44 - 204.10		0.821
NDVI _{max}	-42.06	-427.07 - 398.03		0.823
(d)				
Territoriality	186.50	-63.04 - 435.89	0.755	0.110
Social bonds	126.81	-131.47 - 405.33		0.321
Cooperative breeding	84.92	-236.30 - 390.08		0.550
NDVI _{max}	310.73	-186.44-881.82		0.212

Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda), and pMCMC values are reported. Statistically significant results are highlighted by bold.

^aBecause all species singing in duets belonged to one social-bond (long-term) category, it was not possible to establish social bonds as an explanatory variable.



Figure 2

Geographical patterns in the proportion of species having (a) duets vs. no duets (N = 269 species), (b) duets vs. no female song (N = 133 species), (c) female solo song vs. duetting (N = 82 species), and (d) female solo song vs. no female song (N = 111 species).

year-round territorial species, whereas all batises and wattle-eyes (Platysteiridae) together with bush-shrikes (Malaconotidae) defend their territories year-round and also sing in duets. This close duetting-year-round territoriality association suggests that, similarly to findings of Tobias et al. (2016) on a global scale, variation in duetting among songbirds of South Africa could be explained by uneven taxonomic and geographical distribution of year-round territoriality rather than by other factors.

We found no direct association between distribution of any of female song composites and environmental productivity. Although South Africa represents a relatively small area in terms of a global perspective, the local productivity shows a clear and strong gradient with huge regional differences in NDVI_{max}; hence, the lack of this association should not be attributed to only low variation in the environmental variable evaluated. However, social behavior of birds has inevitably evolved in accordance with environmental conditions. For instance, distribution of year-round territoriality coincides to some level with the distribution of highly productive areas in South Africa (Supplementary Figure S1). Similarly, an inverse association between NDVI and clutch sizes indicates that South African songbirds inhabiting more productive areas exhibit slower pace of life (Hořák et al. 2015). In productive and relatively stable environments, species can reside and breed over the prolonged season as they are not forced to migrate, promoting sedentary lifestyles and affecting also birds' willingness to defend their territories over long periods (Ricklefs 1969; Price et al. 2009; Odom et al. 2015; Tobias et al. 2016). Under such conditions, source and mate defense may become too demanding, thus promoting singing in both partners (Tobias et al. 2016). Taken from the opposite side, these premises indicate that species inhabiting less productive and more variable environment are expected to exhibit lower levels of territoriality, favoring the presence of female solo song or no song in female birds over duetting. It is also possible that some other unmeasured environmental factor, or more probably a combination of several of them, forms specific conditions facilitating the emergence of duetting. Altogether, our results indicate that the strength of selection favoring year-round territoriality may be spatially variable also within tropical and subtropical regions, such as over the territory of South Africa.

Both female solo song and duetting are associated with higher levels of territoriality and long-term social bonds, suggesting that they may have evolved as byproduct of cooperative breeding (Seddon and Tobias 2003). However, we did not find any effect of cooperative breeding neither on female solo song nor on duetting. This may indicate that, at least in our sample of species, the evolution of singing in females and cooperative breeding is independent. Other possibility is that the absence of such association in South African species could be linked to low variability in this trait and presence of cooperative breeding only in few avian clades in the area.

In conclusion, our study finds some evidence that species of South Africa and Lesotho wherein female birds produce solo song exhibited, on average, a lower level of territoriality than duetting species but, simultaneously, a higher level of territoriality than species with nonsinging females. Hence, we suggest that female solo song and duetting may represent independent composites of female song whose evolution is driven by different levels of the territoriality. We propose that the actual value of individual territory, and consequently a bird's willingness to defend these territories, is the primary driver of the evolution of female solo song and duetting in South African songbirds. Although our study focuses on a restricted region and limited set of species, our results may have implications for furthering understanding of bird song evolution in general, and female solo song in particular. For instance, it may help us to explain why female solo song is more common than duetting in nontropical (e.g., temperate zone) songbird species.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Mikula et al. (2019).

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