Evolution of Phenotypic Sex Differences in Cooperative Species: is Competition an Opposing Force?

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Abstract. Sexual selection is generally thought to be weak in cooperative breeding species, largely because polygamous mating patterns that drive sexual selection can erode the kin-selected benefits of cooperation. Social selection, on the other hand, is expected to be strong among cooperative species especially because of the intense competition over status and resource access. In support of this view, several studies have shown monogamous mating and little sex difference in cooperative species. However, most previous studies have focused on species with relatively simple social systems and few studies have examined how mating patterns, social organization and ecological attributes have influenced the evolution of ornamentation in cooperative species. Here I used secondary data to examine several hypotheses and shed some light on how social and sexual selection influenced the evolution of phenotypic sex traits in cooperatively breeding birds. Despite the broad assumption that cooperative breeding species are monomorphic, results demonstrate that sex differences and the presence of ornamentation are widely spread in the group. Stable environments with higher precipitation are associated to the strongest differences between sexes. Results indicate that although extrapair matings and environment attributes are determinant to the evolution of sex differences, males and females of cooperative species seem to be more alike than their non-cooperative counterparts. The extent of mutual ornamentation found in cooperative species indicates that the combination of both sexual and social selection are imperative to determine how evolution has shaped phenotypic attributes in cooperative species.

Key words: dimorphism, dichromatism, epigamic selection, joint-nesting, mutual ornamentation, ornaments

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INTRODUCTION

Sexual reproduction and its inevitable dilution of relatedness between parent and offspring sets the stage for genetic conflicts of interest among interacting individuals, which led Wilson (1975) to assert that "sex is an antisocial force in evolution". Accordingly, animal societies represent a balance between competition and cooperation influenced by underlying genetic conflicts of interest (Emlen 1982). Social competition is likely to be particularly acute in cooperative breeding species, as in such species some individuals invest in raising offspring that are not their own (Grinsted & Bilde 2013, Lutermann et al. 2013, Nelson-Flower & Ridley 2015). The study of cooperative species therefore has been a focal point of interest for behavioral ecologists since the late 1950s and early 1960s (e.g., Skutch 1959, 1961, Orians 1961, Brown 1963, Rowley 1965, 1968), and these first case studies were associated with early theoretical models

of inclusive fitness theory that attempted to explain helping behavior in animals as a result of kin selection (Hamilton 1964).

Species that breed cooperatively are taxonomically diverse, exhibit different mating and social systems (Ligon 1999). Among them, cooperative breeding birds are particularly well studied (Emlen 1991, Mumme 1992, Arnold & Owens 1998, Blackmore & Heinsohn 2008, Preston et al. 2016). Yet most such studies have focused on the costs and benefits of helping, both direct and indirect, to reproducers and helpers alike (Russell 2001, McGowan et al. 2003, Dias et al. 2015), and relatively few studies have examined competition for mates (or resources needed for breeding) in such species (Brouwer et al. 2011, Cockburn et al. 2013, Aranzamendi et al. 2016). Particularly, in addition to mate choice, sexual selection was traditionally defined as an evolutionary force that derives explicitly from competition among individuals for mating access to individuals of the

opposite sex (Darwin 1859), and the mechanisms and operation of such competition remain poorly understood for cooperative breeding animals. In general, sexual selection is thought to be a weak force in cooperatively breeding species, partly because many such species are traditionally viewed as being reproductively monogamous (Pruett-Jones 2004). Moreover, the polygamous mating patterns that lead to strong sexual selection are likely to erode genetic relatedness within social groups, thus undermining the evolution of complex cooperative groups and vice-versa (Boomsma 2007, 2009, Cornwallis et al. 2010, Lukas & Clutton-Brock 2012).

The type of mating system has been frequently associated to phenotypic differences between sexes, with polygamous species presenting a higher divergence between males and females (Price & Eaton 2014, Ribeiro et al. 2015). Despite that, several studies have indicated that sexual differences may have arisen more commonly through changes in females (Burns 1998, Figuerola & Green 2000, Badyaev & Hill 2003, Dunn et al. 2015) due to natural selection (Amundsen 2000), social selection (West-Eberhard 1983), among other factors. Despite the expectations for coordination and collaboration, competition for breeding opportunities in cooperative breeders may be very intense leading to agonistic behaviors between group members (Williams 2004), and extreme behaviors such as egg destruction (Koenig et al. 1995) and infanticide (Macedo & Melo 1999).

Ecological factors such as climate stability and warmness, have been related to the evolution of cooperative breeding, because they may promote sedentariness leading to habitat saturation (Ligon & Burt 2004) and may also increase the number of social interactions all year round. Interestingly, those aspects have also been related to the variation of sexual selection (Garant et al. 2004, Cockburn et al. 2008) and also seem to be associated to evolutionary change potential (Charmantier & Garant 2005). Climate parameters may affect different aspects of animal reproduction such as migration patterns (García-Peńa et al. 2009), resources and mates availability (Emlen & Oring 1977, Ryder & Sillett 2016), duration of the breeding season (Møller et al. 2010), breeding synchrony (Williams et al. 2015), among others. Therefore, climate variation may help to determine the strength of selection. Considering that climate stability and warmness are typical from tropical zones and since most cooperative breeding birds are tropical, it may increase the opportunity for social and sexual selection to operate.

Although sexual selection appears to be weak in many cooperative species, a large number of exceptions to this pattern exist (e.g., Webster et al. 2007, Cockburn et al. 2009), and we currently lack a solid foundation for understanding why sexual selection might operate in some social species but not in others. Moreover, recent work has made it clear that sexual selection can operate on females as well as males (Amundsen 2000, Clutton-Brock 2007, 2009, Kraaijeveld et al. 2007, Rosvall 2011), and this might be particularly true in species that breed cooperatively. Some authors (e.g., Lyon & Montgomerie 2012, Tobias et al. 2012) have recently emphasized that sexual selection is a specialized case of the broader concept of social selection, as originally suggested by West-Eberhard (1983), and social selection might be a particularly potent force in cooperative species because there is (by definition) reproductive skew and competition among individuals for breeding opportunities. Competition for resources that directly affect dominance, parental favoritism and other non-sexual aspects may also be mediated by signals and weapons (Tanaka 1996, Lyon & Montgomerie 2012).

The main objective of this study is to improve the understanding of the evolution of phenotypic sex differences and ornamentation in cooperative breeding birds and evaluate how climate, sexual and social selection affected the evolution of phenotypic sex differences in these species. I also made inferences on the evolution of mating system and sex differences among cooperative species. Moreover, I hypothesized that (1) polygamous mating systems and the occurrence of extra-pair paternity may be associated with phenotypic sex differences among cooperative species due to a higher strength of epigamic selection; (2) the evolution of phenotypic sex differences may be correlated to the evolution of mating system complexity with the transition to different sexes associated with the transition to polygamous mating systems; (3) the level of sociality (coloniality and joint-nesting) may have negatively influenced the evolution of phenotypic sex differences through social selection, favoring the evolution of ornamentation in both sexes; (4) cooperative breeding may favor the evolution of ornamentation in both sexes as an effect of social selection, and (5) phenotypic differences between sexes is associated to climate stability in cooperative breeders due to higher opportunities for diversification and selection.

MATERIALS AND METHODS

Data gathering and general procedures

This study was based on a list of cooperative breeding birds (Ligon & Burt 2004) and also new records of cooperative breeders that were obtained through a literature search carried out using a commercial academic search engine ISI Web of Knowledge. The search at the database was conducted between May and July 2017. I used combinations of the terms cooper* breeding OR helper OR auxiliary, associated with (i.e. AND) the species scientific and common names. For each species accessed in this study, I registered information relative to their mean latitude of distribution, their mating system, whether or not the species is colonial, presence of specific reproductive strategy (joint-nesting, extrapair paternity) and occurrence of differences between sexes (more details below). Species ecological and behavioral information were obtained from papers, field guides and books. Following Brown (1987), I classified joint-nesters as those species where more than one female contributes with eggs to a nest and I classified as colonial those species where females nest under extremely close proximity (i.e. within meters of one another). Extrapair paternity (EPP) was categorized as present or absent. I included non-cooperative species of the same genus of their cooperative counterparts to investigate the role of cooperation in the evolution of sex differences (more details below). If it was not possible to identify and select at least one non-cooperative species, the genus was excluded from this specific analysis. Moreover, I included non-cooperative species in the correlated evolution analysis (more details below). Between one to five non-cooperative species, for each bird order, was used according to the information available in the literature for each species. Species classified as non-cooperative have published information on reproduction and parental care with no evidence of the presence of auxiliaries. Species distributions were obtained from Birdlife International dataset (www.birdlife.org) in shapefile format. I used the centroid of the distribution to estimate a mean latitude value for each species. Climate data was obtained from the WordClim dataset (www.worldclim.org) (Hijmans et al. 2005). Bioclimatic variables (BIOCLIN) that may better represent climate variation were chosen for the analysis (detailed below). The original data was in raster format (1 km^2 resolution).

Phenotypic sex differences assessment and mating system classification

I established a scale to classify the species according to their sex differences. The scale ranged from 0 (no perceptible difference) to 5 (sexes are completely different with the presence of elaborated sexual signals, Table 1). For those species where no perceptible difference was detected I also evaluated the presence of ornamentation in both sexes. For this analysis, to be conservative, only the presence of carotenoid-based coloration patches and modifications on bill (e.g. casque of Hornbills, Bucerotidae), tail (e.g. long tails of Mousebirds, Coliidae) and head (e.g. crest of Magpie-jays, Corvidae) structures were considered as ornamentation. I decided to be conservative in this case because it is known that human vision may not be able to detect sexual dichromacy in the same perspective as birds do (Eaton 2005). The figures of the Handbook of Birds of the Word Alive (www.hbw.com) were used in the classification process. To simplify the analysis, the mating system was organized in two larger groups: monogamous (including socially and genetically monogamous species) and polygamous (including polygynous, polyandrous and polygynandrous species). The same information about mating system and level of phenotypic sex differences were recorded for non-cooperative breeders.

Statistical analysis

All the analyses were performed using the software R (version 3.5.0, R Development Core Team 2018). Moran's I values were calculated using the package *ape* to examine the possibility of spatial autocorrelation. Except for the climate variables (which were incorporated in a Spatial Principal Component Analysis), all the other variables included in the analyses demonstrated to be spatially independent (Moran's I ≤ 0.028; p ≥ 0.146

Table 1. Categories to classify the phenotypic differences between sexes.

Category	Criteria
0	No perceived difference
1	Small difference in size (measurable perceived)
2	Presence of a patch in one sex but not in the other
3	Differences between the sexes easily perceived by the coloration, despite some shared traits.
4	Sexes are very different. However, they have no sexual signal such as modified feathers, bill, crest or tail structures.
5	Sexes are completely different and one sex exhibit ornaments such as modified feathers, bill, crest or tail structures

in all cases). The function "phyloglm" of the package *phylolm* were used to fit Phylogenetic Generalized Linear Models (PGLMs). PGLMs were fitted using Poisson (count response variable, Paradis & Claude 2002) error distribution to investigate the effects of the mating system (considering both social or genetic), joint-nesting (yes or no), coloniality (yes or no), latitude and climate (more details below) on the level of phenotypic differences between sexes in cooperative breeders. The Generalized Estimating Equations (GEE) for Poisson regression were used (Paradis & Claude 2002). The scale parameter of the function "phyloglm" was used to estimate the possibility of overdispersion in the fitted model. To evaluate the effects of the same variables on ornamentation (presence of absence) in both sexes, PGLMs fitted using binomial (binary response variable, Ives & Garland 2010) error distribution were applied using the "Logistic_MPLE" (Maximized Penalised Likelihood) method. For monomorphic species, the same variables were also used to access its effects on the evolution of ornamentation in both sexes. In addition, using a subset of the data for which molecular information was available on the original studies, I investigated the role of mating system and extrapair paternity (present or absent) on the level of sex differences. Moreover, including both cooperative and non-cooperative species, I evaluated the effects of mating system and cooperation (whether or not the species is cooperative) on the level of sex differences. Climate information was obtained using the function "extract" from the package *dismo*. Six bioclimatic variables were used to represent climatic stability. Each bioclimatic variable was averaged over each species distribution area. To summarize the bioclimatic variables a Spatial Principal Component Analysis (SPCA) were performed using the function "sPCA" of the package *adegenet* (Jombart 2008). The PC1 explained 81% of the data variation and was negatively loaded by temperature seasonality and positively loaded by precipitation of wettest quarter (Table 2). The latitude used in this study represents the centroid of the species distribution. The latitude was obtained by applying the function "gCentroid" of the package *rgeos* (Bivand et al. 2013).

The correlation between the evolution of mating system and phenotypic sex differences were analyzed following Pagel (1994) in the module DISCRETE from the program BayesTraitsV3. The method is based on a Markov transition rate model of trait evolution which depends on the

Table 2. Principal Component Analysis results of climate variation within the distribution of cooperative breeding species.

Variables	PC1
Mean Diurnal Range	-0.0052
Temperature Seasonality (standard deviation *100)	0.4530
Mean Temperature of Warmest Quarter	0.0014
Mean Temperature of Coldest Quarter	0.0130
Precipitation of Wettest Quarter	0.8685
Precipitation of Driest Quarter	0.2005
Explained variation (%)	81.45

current state only not on a set of ancestral values, avoiding problems relative to ancestral character reconstruction (Pagel 1997). The model assumes a constant probability of change throughout the tree. I ran the DISCRETE analysis with mating system as monogamous (0) or polygamous (1) and with sex differences as absent (0) or present (1). Both dependent and independent models were fitted and compared using the Bayes Factor (Pagel 1997, 1999).

To produce inferences about the evolution of sex differences and mating system within cooperative breeders I used a subset of 100 trees (with branch length present) based on the Hackett backbone (Hackett et al. 2008), obtained from the Birdtree project (http://birdtree.org, Jetz et al. 2012). The ancestral state of both mating system and whether the sexes were alike or not were estimated under "all-rates-different" (ARD) Markov model using the function "ace" of the package *ape* (Paradis 2006).

RESULTS

General patterns of mating system and breeding strategies in cooperative breeders

A total of 388 cooperative species were initially considered in the study, however, there was consistent information available in the literature for only 187 species (Appendix 1). Considering these species, as expected, the vast majority (89%) is exclusively tropical and/or subtropical and 20.2% are described as exhibiting more than one mating system. Around 80% of cooperative breeders exhibit social monogamy. Including those species that presents more than one mating system (N = 21), roughly 7% of the species are known to be polygynous, 7% are polyandrous and almost 10% are polygynandrous. Considering only those species with molecular data available (N = 67), data suggest that alternative mating strategies,

including extrapair paternity (70%) and intraspecific parasitism (6%), are fairly common among cooperative breeders. On average, 12% of the nestlings (range 0–63%) of cooperative species were the result of extrapair paternity. There was no effect of latitude on the level of extrapair paternity (Phylogenetic Linear Model; t = -0.340; p = 0.734). Despite that the level of extrapair paternity was 14.2 ± 16.7% (mean ± SD) for Tropical and Subtropical species and 2.7 ± 3.6% for the Temperate counterparts. Forced copulations are very uncommon within cooperative breeders (< 0.1%). Only 6% of the species are colonial or semi-colonial and 8% are joint-nesters.

Contrary to the broad assumption that cooperative breeding species are usually monomorphic, for half of the species, both sexes exhibit some degree of dimorphism. Of these, approximately 10% show extreme dimorphism in ornamentation and in 38% of the species both sexes are ornamented. Reversed sexual dimorphism has also been described for five taxonomically diverse species: Laughing Kookaburra *Dacelo novaeguineae*, Striped Kingfisher *Halcyon chelicuti*, Harris Hawk *Parabuteo unicinctus*, and the Spanish Imperial Eagle *Aquila adalberti*.

Ecological, reproductive and social influences on the evolution of sex differences

Analysis revealed that the level of sex differences (N = 187 species) was not influenced by latitude (Phylogenetic Generalized Linear Model Z = 0.295, p = 0.767, Table 3), mating system and coloniality (Table 3). However, presence of joint-nesting and the combination of temperature seasonality and precipitation of wettest quarter demonstrated to affect the level of differences between sexes (Table 3, Fig. 1). Sex differences are higher in joint-nesting species. In addition, more harsh
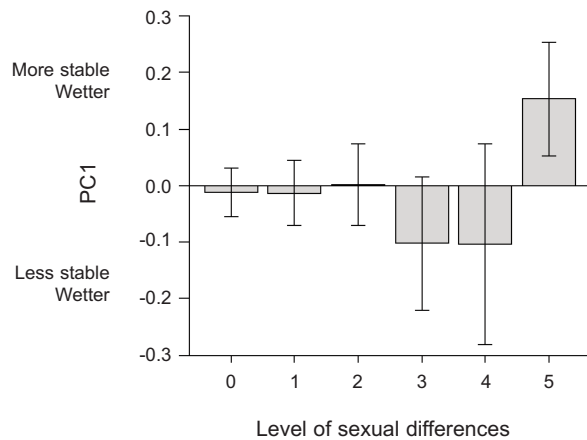

Fig. 1. Effects of climate stability on the level of phenotypic sex differences in cooperative breeding birds. Box represents the range of 50% of the scores, the thick line represents the median and whiskers are maximum and minimum values.

environments seem be associated to an increase in sexes differences, although species with the highest level of sex difference were associated to more stable environments. When considering only those species with molecular information available, there was no effect of the mating system on the level of sex differences (Z = -0.467, p = 0.640), but there was an effect of the occurrence of extrapair paternity (Z = 3.639, p < 0.001). The sexes in species with extrapair paternity were more different than those species that do not present extrapair paternity (Fig. 2).

Considering only those species that are phenotypically similar (e.g. no perceptible sex difference) or that shows a slight difference in size, the presence or absence of ornaments in both sexes were not explained by any of the evaluated variables: mating system, coloniality, joint-nesting, latitude or PC1 (Table 4).

Table 3. Summary of phylogenetic generalized linear models results from the effects on the level of phenotypic sex difference in cooperative species. The complete dataset was composed of 187 species. The restricted dataset considering only species with molecular information was composed of 67 species. The information in parenthesis represents the reference level for the dummy variables (sm — socially monogamous, gm — genetically monogamous).

| Models terms	Estimate	SE	Z	p
Level of sex difference (complete dataset)				
Latitude	0.000	0.001	0.295	0.767
Mating system (sm)	0.041	0.076	0.538	0.590
Coloniality (yes)	0.067	0.148	0.453	0.650
Joint nesting (yes)	0.301	0.137	2.183	0.029
Climate - PC1	-0.274	0.094	-2.906	0.003
Level of sex difference (restricted dataset)				
Mating system (gm)	-0.047	0.102	-0.467	0.640
Extra-pair paternity (yes)	0.668	0.183	3.639	< 0.001
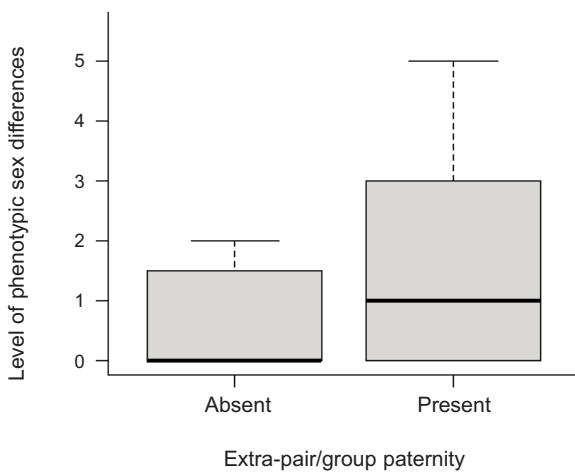
Fig. 2. Effects of extrapair paternity on the level of phenotypic sex differences in cooperative breeding birds based on studies with molecular information available. Box represents the range of 50% of the scores, the thick line represents the median and whiskers are maximum and minimum values.
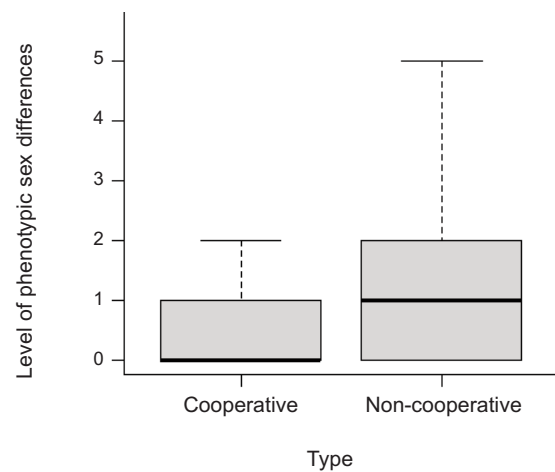
Fig. 3. Effects of cooperation on the level of phenotypic sex differences among same genus species. Box represents the range of 50% of the scores, the thick line represents the median and whiskers are maximum and minimum values.

Are there any effects of cooperation in the evolution of sex differences?

When I evaluated the effects of mating system and reproductive sociality (whether the species is cooperative or not) on the level of sex differences using a phylogenetic approach, it was possible to observe that both mating system ($Z = 5.287$, $p < 0.001$, Table 5) and reproductive sociality ($Z = 6.692$, $p < 0.001$, Fig. 3) significantly affected the level of differences observed. Sexes in cooperative species were more similar among themselves than their non-cooperative congeners.

Ancestral state reconstruction and correlated evolution

The DISCRETE module of BayesTraitsV3 was used to assess whether changes in the mating system were associated to the evolution of sex differences in cooperative species. There was a strong support for the independent model (mean $LL_{I\ (independent)}$ = -455.61 ± 0.01 s.e.m.; Fig. 4) over the dependent model (mean $LL_{D\ (dependent)}$ = -432.65 ± 0.01 s.e.m.; Bayes Factor = 45.92), supporting the hypothesis that mating system and sex differences did not coevolve in cooperative breeders. Based on the ADR model, transition rates from monogamy towards polygamy were much more common than the other way around. Transitions involving sex differences were not clearly characterized, demonstrating that traits involved in the processes are unstable (i.e. transitions to phenotypic sex differences and the other way around are random). The all-different rate model suggest that basal cooperatives were monogamous. However, the reconstruction considering the species as either "sexually alike" or "sexually different" provided equivocal support (Fig. 5).

Table 4. Summary of phylogenetic generalized linear models results from the effects on ornamentation (presence or absence) in both sexes of cooperative species where sexes are phenotypically similar. The dataset was composed of 71 species. The information in parenthesis represents the reference level for the dummy variables (sm — socially monogamous).

Models terms	Estimate	SE	Z	p
Ornamentation in both sexes				
Latitude	-0.021	0.013	-1.523	0.127
Mating system (sm)	0.205	0.413	0.495	0.620
Coloniality (yes)	0.759	0.707	1.073	0.283
Joint nesting (yes)	0.054	0.578	0.934	0.350
Climate - PC1	-0.000	0.000	-1.266	0.205

Table 5. Summary of phylogenetic generalized linear model results from the effects on the level of phenotypic sex difference in cooperative (77) and non-cooperative (66) species of the same genus. The information in parenthesis represents the reference level for the dummy variables (sm — socially monogamous, nc — non-cooperative).

Models terms	Estimate	SE	Z	p
Level of sex difference				
Mating system (sm)	0.670	0.126	5.287	< 0.001
Type (nc)	0.574	0.085	6.692	< 0.001

DISCUSSION

There is a wide diversity of social and genetic mating systems encompassed in cooperative breeding birds (Cockburn 2004), the breadth of which has progressively increased as more species have been studied over a broader geographic scale. In the current study, an analysis revealed that cooperative breeders seem to have an overall lower percentage of species exhibiting social monogamy (80%) compared with what is generally accepted for non-cooperative species (approximately 93%, Lack 1968). Moreover, the occurrence of multiple mating systems is common (around 11% of the species) and phenotypic sex differences were observed in 50% of the species, suggesting that social systems in cooperative species may be more complex than initially assumed. Different studies have demonstrated associations between mating system and sex dimorphism, suggesting that individuals exhibit greater variation in reproductive success under specific mating systems which may result in the evolution of sexually selected traits (Clutton-Brock et al. 1977, Kleiman 1977, Owens & Hartley 1998, Bro-Jorgensen 2007). Traditionally, the extent of sex differences exhibited by species was expected to be a clue to the strength of sexual selection (but see, Soulsbury et al. 2014). However, considering the methodological decisions made in this study (e.g. using an ordinal scale to score sex

differences), I found no effect of mating system on phenotypic sex differences in cooperative breeders. One explanation for this pattern may be the conflicts over access to resource among members of cooperative groups which could favor the evolution of signaling traits in both sexes associated with dominance status as possibly being the result of social selection (Lyon & Montgomerie 2012). For most species, it is expected that these conflicts should be common, since breeding opportunities are scarce due to ecological constraints (Ekman et al. 2004). Consequently, group members must compete with their relatives as well as unrelated individuals to inherit a territory, acquire social status and gain a reproductive position or even copulations. Different studies have demonstrated the existence of female competition for access to reproduction, mediated by their dominance status, which may be signaled through elaborate ornaments (Irwin 1994, Clutton-Brock 2007, Kraaijeveld et al. 2007, Murphy et al. 2009). Such competition may have important implications for the evolution of female traits, especially in cooperative species (Rubenstein & Lovette 2009).

Intense competition among females within cooperative groups, especially joint-nesting species with high levels of reproductive skew (Magrath et al. 2004), may be expected to favor the evolution of female ornamentation, weapons or aggressive behaviors. In such cases, similar patterns of coloration and ornaments/weapons could evolve and be maintained in both males and females (i.e., sexual monomorphism with both sexes being ornamented, Johnstone et al. 1996). For example, in the monomorphic Diamond Firetail *Stagonopleura guttata* white flank spots are determinant for feeding dominance in females, being associated with immune response (Crowhurst et al. 2012). Here, results demonstrated that ornamentation is widely found in both males and females of cooperative species. While coloniality seems to have not affected the evolution of phenotypic differences nor the occurrence of ornamentation among males and females in the
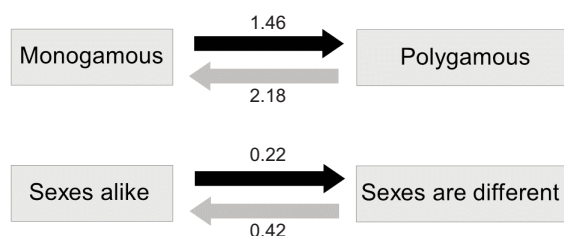
Fig. 4. Evolutionary transitions from independent evolution of mating system and phenotypic sex differences in cooperative species. Values represents estimated transition rate.
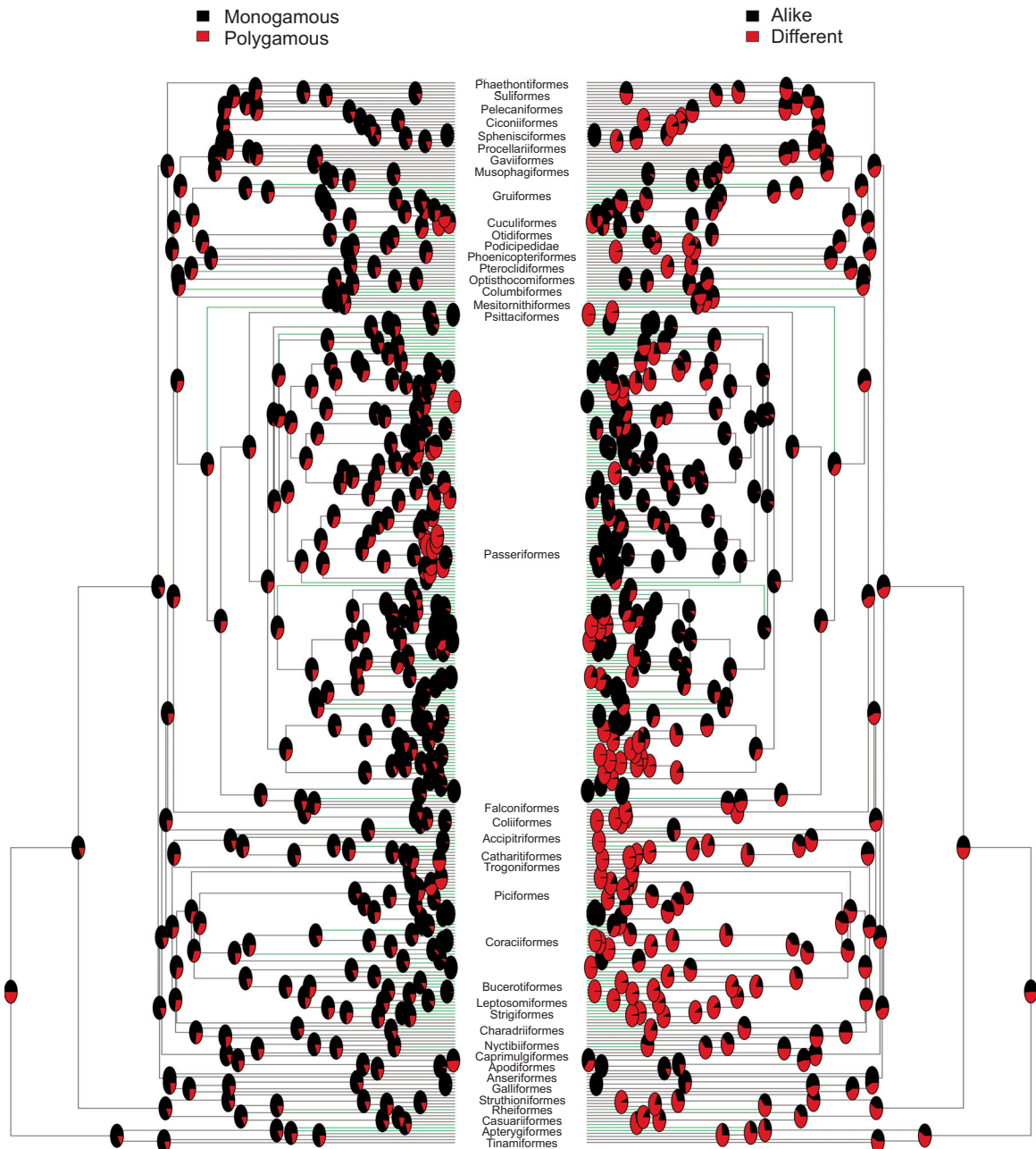
Fig. 5. Ancestral state reconstruction of mating system and phenotypic sex difference. All states were reconstructed using all-rates-different (ARD) Markov model. Taxon names as presented by the Birdtree project (http://birdtree.org). Species of the same genus presenting the same patterns of phenotypic sex difference and mating system were clustered by genus. Green clades represent cooperative breeders.

studied species, the presence of joint-nesting demonstrated to be responsible for the evolution of small differences between sexes. Different species may be used to illustrate these results, for example, male and female Acorn Wood-peckers *Melanerpes formicivorus*, compete within joint-nesting groups for reproduction, and outside

of their groups for breeding vacancies (Mumme et al. 1988, Koenig & Stacey 1990), and the sexes are barely size dimorphic with females presenting a slight difference on the extension of the red patch on the head. Similarly, recent comparative work on African starlings (Sturnidae) documented reductions in size dimorphism in cooperative

breeding species in contrast to non-cooperative starlings (Rubenstein & Lovette 2009). Conversely, we should consider that in the four tropical joint-nesting Crotophagine species, intense reproductive competition leads to specialized behaviors in females (and occasionally males) that include egg burial, egg ejection and infanticide (Vehrencamp 1977, Macedo 1992, Macedo & Melo 1999, Riehl & Jara 2009). In these species males and females are generally monomorphic in size, color and ornamentation (e.g., Guira Cuckoo *Guira guira* crests).

On the other hand, it is usually accepted that the loss of ornamentation in females, through natural selection due to predation during nesting, may be responsible for the evolution of sexual dichromatism (Badyaev & Hill 2003). In the case of cooperative breeders, the enhancement in vigilance and defense by auxiliaries may have not favored the evolution of a duller coloration in females. Moreover, when cooperative birds were compared with non-cooperative ones of the same genus it was possible to notice that non-cooperative species are more sexually different than their cooperative counterpart. Again, social selection may have played a role in the evolution of monomorphism/monochromatism in cooperative breeders.

In contrast to what was expected, results indicated that the evolution of mating system and phenotypic sex differences have occurred independently in cooperative breeders. Considering the evolution of sex differences, even though the transitions from different to similar sexes, and *vice versa*, have occurred many times in several cooperative taxa, it was not possible to identify a general pattern for the whole group of species. However, it is often assumed that sexual dichromatism is the ancestral state for birds (Badyaev & Hill 2003). In families, such as Icterids, the transition between dichromatism to monomorphism were a common evolutionary trend (Drury & Burroughs 2016). On the other hand, it is known that altriciality and life history traits such as the evolution of diets that facilitated female-only care (helping males to maximize reproductive efforts) played an important role on the transition between social monogamy to more complex mating systems (polygyny, polyandry, polygynandry) (Burley & Johnson 2002). As expected, the ancestral state for mating system on cooperative species was monogamy. This support the traditional view for the evolution of cooperative breeding from a familiar group within a saturated habitat, favoring

the postponement of reproduction, delayed dispersal and the promotion of kin selection (Ekman et al. 2004). Additionally, the presence of auxiliaries in cooperative species may have stimulated breeders to enhance the investment in reproductive activities favoring the evolution of mating systems that produce higher fitness and promote genetic diversity among the offspring.

The risk of incest and, consequently, inbreeding is expected to be a problem in cooperative breeders due to the typically high levels of relationship between group members. Therefore, alternative reproductive strategies may be important to avoid inbreeding depression and maintain genetic variation (Koenig & Haydock 2004, Aranzamendi et al. 2016). Extrapair paternity is widely observed in birds (Griffith et al. 2002, Westneat & Stewart 2003) being also prevalent in several cooperative species (Berg 2005, Blackmore & Heinsohn 2008, Colombelli-Négrel et al. 2009, Aranzamendi et al. 2016). Extrapair paternity is usually believed to be more common among Temperate than Tropical species (Stutchbury & Morton 2001). Notwithstanding, even though cooperative breeding is mainly a Tropical phenomenon it was not possible to detect any latitudinal effect on the level of extrapair paternity within cooperative breeders. Moreover, plumage-color dimorphism has already been demonstrated to be associated with the frequency of extrapair paternity (Owens & Hartley 1998) as well as the evolution of male ornamentation in several non-cooperative bird species such as Yellow Warblers *Setophaga petechia* (Yezerinac & Weatherhead 1997), Collared Flycatchers *Ficedula albicollis* (Sheldon & Ellegren 1999), Tuis *Prosthemadera novaeseelandiae* (Wells et al. 2015), Tree Swallows *Tachycineta bicolor* (Whittingham & Dunn 2016), among others. In this study, the level of extrapair paternity also seems to affect the differences between sexes of cooperative breeders. Species with young sired by extrapair matings also present more differences between sexes when compared to those where extrapair paternity was absent.

Historically, researchers have attempted to find ecological factors that may have promoted the evolution of cooperation, but have not been very successful in identifying factors that can predict the occurrence of cooperative breeding (Ligon & Burt 2004, but see Rubenstein & Lovette 2007). However, most research has confirmed that cooperative breeding is primarily observed in the Tropics, rarely evolving in Temperate zone species

(Mumme 1992, Cockburn 1996). Although largely ignored in sexual selection studies, climate condition has been demonstrated to affect sexually selected traits in different bird species (Garant et al. 2004, Møller & Szép 2005). Studies demonstrated that favorable conditions generate genetic variation and that evolutionary response in a given trait in these environments tends to be faster (Hoffmann & Merila 1999). In the cooperative breeder Superb Fairy-wren *Malurus cyaneus* favorable environment conditions such as years with high levels of rainfall increase the intensity of sexual selection due to anticipated molting of males (Cockburn et al. 2008). The present study has demonstrated that harsh environments may positively affect the level of phenotypic sex differences, especially for those species with intermediate or no sex differences. However, species occupying areas with lower seasonality and higher precipitation presented the strongest differences between sexes, suggesting that ecological factors alone may not be a good indicator of the levels of social and sexual selection.

Sexual selection is often invoked to explain sex differences in size, color, behavior or weaponry, and is usually discussed in non-familial settings and without regard to kinship patterns (Andersson 1994). In cooperative breeders, it seems that both sexual and social selection are equally important for the evolution of ornamentation and differences between sexes. The lower sex differences found in cooperative breeders may have resulted from simultaneous (or balanced) sexual selection, i.e., sexual selection acting equally strongly on males and females because some individuals of both sexes forgo or are prevented from breeding within groups (Hauber & Lacey 2005, Clutton-Brock et al. 2006, Rubenstein & Lovette 2009). Additionally, sexual selection seems to also work cryptically through extrapair matings. Conversely, social selection resulting from the competition between group members in non-sexual contexts, such as parental favoritism, competition for dominance, food, space or any other resource that influences fecundity and survival (West-Eberhard 1979, 1983) may have also favored the evolution of ornamentation in both sexes in many species. Finally, the importance of ecological factors on the emergence of sex differences has been traditionally overlooked despite being determinant for traits evolution, particularly through the reinforcement of sexual and social selection.

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STRESZCZENIE

[Ewolucja fenotypowych różnic pomiędzy płciami u gatunków gniazdujących kooperatywnie]
Uważa się, że dobór płciowy słabo oddziałuje w przypadku gatunków, u których występuje kooperacja rozrodcza, głównie dlatego, że poligamiczne systemy kojarzenia, które prowadzą do silnego doboru płciowego, mogą ograniczać korzyści wynikające ze współpracy spokrewnionych ze sobą osobników. Z drugiej strony oczekuje się, że wśród gatunków gniazdujących kooperatywnie istnieje silny dobór społeczny, zwłaszcza ze względu na intensywną konkurencję o status w grupie i dostęp do zasobów. Na poparcie tego poglądu, wiele badań wykazało, że u gatunków gniazdujących kooperatywnie występuje kojarzenie monogamiczne i niewielkie różnice fenotypowe pomiędzy płciami. Jednak większość wcześniejszych badań koncentrowała się na gatunkach o stosunkowo prostych systemach socjalnych, a niewiele badań dotyczyło tego, w jaki sposób system rozrodczy, organizacja socjalna czy warunki ekologiczne mogą wpływać na ewolucję ornamentów u gatunków gniazdujących kooperatywnie.

W badaniach wykorzystano istniejące dane literaturowe. Dla każdego gatunku uzyskano dane o systemie rozrodczym, strategii rozrodczej (występowanie zjawiska kojarzeń pozapartnerskich oraz wspólnego gniazdowania), występowaniu gniazdowania kolonijnego, a także oceniono różnice fenotypowe pomiędzy płciami wykorzystując pięciostopniową skalę (Tab. 1). W analizach uwzględniono zasięg występowania (wykorzystując średnią szerokość geograficzną zasięgu) i klimat panujący na obszarze zajmowanym przez dany gatunek (sześć zmiennych klimatycznych, przy użyciu analizy składowych głównych, Tab. 2). Analizy przeprowadzono dla pełnego zestawu 187 gatunków oraz wyselekcjonowanych 67 gatunków, dla których istniały dane molekularne dotyczące rodzicielstwa (Apendyks 1).

Większość (89%) gatunków gniazdujących kooperatywnie występuje w strefie klimatu tropikalnego i subtropikalnego, ok. 80% wykazuje socjalną monogamię. Tylko 6% gniazduje kolonijnie, a u 8% występuje zjawisko wspólnego gniazdowania. Pomimo generalnego założenia, że gatunki gniazdujące kooperatywnie są monomorficzne, wyniki wykazały, że różnice fenotypowe pomiędzy płciami oraz obecność ornamentów są szeroko rozpowszechnione w tej grupie — u połowy gatunków stwierdzono pewne różnice pomiędzy płciami, u 38% stwierdzono ornamenty u obu płci, zaś u 10% — bardzo duże różnice w ornamentach. Największe różnice pomiędzy płciami obserwuje się w stabilnych środowiskach, z mniejszymi wahaniami temperatur oraz z większymi opadami atmosferycznymi (Fig. 1). Rozpatrując tylko te gatunki, u których obie płcie są podobne, nie stwierdzono, aby obecność ornamentów (m.in. zmodyfikowanych piór, czubów na głowie, itd.) była związana z którymś z badanych elementów — systemem rozrodczym, gniazdowaniem kolonijnym, szerokością geograficzną czy warunkami klimatycznymi. Wyniki wskazują, że obecność kojarzeń pozapartnerskich oraz klimat mają silny związek z różnicami fenotypowymi pomiędzy płciami (Tab. 3, Fig. 2). Jednak samce i samice gatunków gniazdujących kooperatywnie są bardziej podobne do siebie niż ich krewniacy, u których podczas lęgów nie stwierdzono pomocników gniazdowych (Tab. 5, Fig 3). Analizy filogenetyczne wykazały, że systemy rozrodcze oraz zróżnicowanie fenotypowe pomiędzy płciami nie ewoluowały wspólnie (Fig. 4, 5).

Appendix 1. Cooperative breeding species used in the analysis. Geographical region abbreviations: Subtrop = Subtropical, Temp = Temperate, Trop = Tropical.

Order	Family/ Species name	Common name	Geographical region	Genetic information
Struthioniformes	Struthionidae			
	Struthio camelus	Common Ostrich	Subtrop	Yes
	Rheidae			
	Rhea americana	Greater Rhea	Trop/Subtrop	No
Galliformes	Phasianidae			
	Tetraophasis szechenyii	Buff-throated Partridge	Subtrop	No
Anseriformes	Anseranatidae			
	Anseranas semipalmata	Magpie Goose	Trop/Subtrop	No
Mesitornithiformes	Mesitornithidae			
	Monias benschi	Subdesert Mesite	Subtrop	Yes
Caprimulgiformes	Apodidae			
	Tachymarptis aequatorialis	Mottled Swift	Trop	No
	T. melba	Alpine Swift	Temp/Subtrop	No
Opisthocomiformes	Opisthocomidae			
	Opisthocomus hoazin	Hoatzin	Trop	No
Cuculiformes	Cuculidae			
	Crotophaga ani	Smooth-billed Ani	Trop/Subtrop	No
	C. major	Greater Ani	Trop/Subtrop	Yes
	Guira guira	Guira Cuckoo	Trop/Subtrop	Yes
Gruiformes	Rallidae			
	Amaurornis flavirostra	Black Crake	Trop/Subtrop	No
	Fulica cristata	Red-knobbed Coot	Trop/Subtrop	No
	F. gigantea	Giant Coot	Trop	No
	Gallinula chloropus	Common Moorhen	Trop/Subtrop/Temp	Yes
	G. tenebrosa	Dusky Moorhen	Trop/Subtrop	Yes
	Tribonyx mortierii	Tasmanian Native-hen	Subtrop	Yes
	Porphyrio martinicus	Purple Gallinule	Trop/Subtrop	No
	Porphyrio porphyrio	Purple Swamphen	Trop/Subtrop	Yes
	Psophiidae			
	Psophia leucoptera	White-winged Trumpeter	Trop	No
Charadriiformes	Charadriidae			
	Vanellus chilensis	Southern Lapwing	Trop/Subtrop	No
	Laridae			
	Sterna paradisaea	Arctic Tern	Temp	No
	Stercorariidae			
	Catharacta antarctica	Brown Skua	Temp	Yes
Strigiformes	Strigidae			
	Bubo lacteus	Verreaux's Eagle-owl	Trop/Subtrop	No
Accipitriformes	Accipitridae			
	Aquila adalberti	Spanish Imperial Eagle	Temp	No
	Buteo galapagoensis	Galapagos Hawk	Trop	No
	Ictinia mississippiensis	Mississippi Kite	Temp/Subtrop	Yes
	Melierax canorus	Pale Chanting-goshawk	Subtrop	No
Coliiformes	Coliidae			
	Colius striatus	Speckled Mousebird	Trop/Subtrop	No
Bucerotiformes	Bucerotidae			
	Anorrhinus galeritus	Bushy-crested Hornbill	Trop	No
	A. austeni	Austen's Brown Hornbill	Trop/Subtrop	No
	A. tickelli	Tickell's Brown Hornbill	Trop	No
	Bycanistes subcylindricus	Grey-cheeked Hornbill	Trop	No
	Bycanistes bucinator	Trumpeter Hornbill	Trop/Subtrop	No
	Ceratogymna atrata	Black-casqued Hornbill	Trop	No
	Buceros hydrocorax	Northern Rufous Hornbill	Trop	No
	B. rhinoceros	Rhinoceros Hornbill	Trop	No

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Order	Family/ Species name	Common name	Geographical region	Genetic information
	Lophoceros camurus	Dwarf Hornbill	Trop	No
	Berenicornis comatus	White-crowned Hornbill	Trop	No
	Rhabdotorrhinus exarhatus	Sulawesi Hornbill	Trop	No
	P. manillae	Luzon Hornbill	Trop	No
	P. panini	Visayan Hornbill	Trop	No
	Phoeniculidae			
	Phoeniculus purpureus	Green Woodhoopoe	Trop/Subtrop	No
	P. damarensis	Violet Woodhoopoe	Trop/Subtrop	No
	Upupidae			
	Upupa epops	Common Hoopoe	Trop/Subtrop	Yes
Coraciiformes	Alcedinidae			
	Ceryle rudis	Pied Kingfisher	Trop	No
	Dacelo leachii	Blue-winged Kookaburra	Trop/Subtrop	No
	D. novaeguineae	Laughing Kookaburra	Trop/Subtrop	Yes
	Halcyon chelicuti	Striped Kingfisher	Trop/Subtrop	No
	Tanysiptera sylvia	Buff-breasted Paradise-kingfisher	Trop	No
	Meropidae			
	Merops apiaster	European Bee-eater	Temp/Subtrop	Yes
	M. bulocki	Red-throated Bee-eater	Trop	No
	M. bollockoides	White-fronted Bee-eater	Trop/Subtrop	No
Piciformes	Lybiidae			
	Lybius vieilloti	Vieillot's Barbet	Trop	No
	Pogonornis bidentatus	Double-toothed Barbet	Trop	No
	Trachyphonus darnaudii	D'Arnaud's Barbet	Trop	No
	Tricholaema lacrymosa	Spot-flanked Barbet	Trop	No
	T. leucomelas	Acacia Pied Barbet	Subtrop	No
	T. melanocephala	Black-throated Barbet	Trop	No
	Picidae			
	Colaptes campestris	Campo Flicker	Trop/Subtrop	Yes
	Leuconotopicus borealis	Red-cockaded Woodpecker	Temp	Yes
	Melanerpes formicivorus	Acorn Woodpecker	Temp/Subtrop	Yes
	Ramphastidae			
	Pteroglossus frantzii	Fiery-billed Araçari	Trop	No
	Semnornithidae			
	Semnornis ramphastinus	Toucan Barbet	Trop	No
Falconiformes	Falconidae			
	Falco columbarius	Merlin	Temp/Subtrop	Yes
	F. peregrinus	Peregrine Falcon	Trop/Subtrop/Temp	Yes
Psittaciformes	Psittacidae			
	Cyanoramphus saisseti	Red-fronted Parakeet	Temp	Yes
Passeriformes	Acanthisittidae			
	Acanthisitta chloris	Rifleman	Temp	Yes
	Acanthizidae			
	Acanthiza chrysorrhoa	Yellow-rumped Thornbill	Subtrop	No
	A. lineata	Striated Thornbill	Subtrop	No
	A. nana	Yellow Thornbill	Subtrop	No
	Sericornis frontalis	White-browed Scrubwren	Subtrop	Yes
	Aegithalidae			
	Aegithalos caudatus	Long-tailed Tit	Temp	Yes
	Artamidae			
	Artamus cinereus	Black-faced Woodswallow	Trop/Subtrop	No
	A. cyanopterus	Dusky Woodswallow	Subtrop	No
	A. leucoryn	White-breasted Woodswallow	Trop/Subtrop	No
	A. minor	Little Woodswallow	Trop/Subtrop	No
	A. maximus	Great Woodswallow	Trop	No
	Climacteridae			
	Climacteris erythrops	Red-browed Treecreeper	Subtrop	No

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	C. picumnus	Brown Treecreeper	Subtrop	No
	C. rufus	Rufous Treecreeper	Subtrop	No
	Corvidae			
	Aphelocoma californica	Western Scrub-jay	Temp/Subtrop	No
	A. coerulescens	Florida Scrub-jay	Temp	No
	A. ultramarina	Mexican Jay	Subtrop	Yes
	Calocitta formosa	White-throated Magpie-jay	Trop	Yes
	Corvus brachyrhynchos	American Crow	Temp	Yes
	C. caurinus	Northwestern Crow	Temp	No
	C. corone	Carrion Crow	Temp	Yes
	Cyanocorax beecheii	Purplish-backed Jay	Subtrop	No
	C. dickeyi	Tufted Jay	Subtrop	No
	C. yucatanicus	Yucatan Jay	Trop	No
	Psilorhinus morio	Brown Jay	Trop	Yes
	Gymnorhinus cyanocephalus	Pinyon Jay	Temp	No
	Perisoreus canadensis	Grey Jay	Temp	No
	P. infaustus	Siberian Jay	Temp	Yes
	Urocissa caerulea	Taiwan Blue Magpie	Subtrop	No
	Zavattariornis stresemanni	Stresemann's Bushcrow	Trop	No
	Turdoides caudata	Common Babbler	Trop/Subtrop	No
	T. jardineii	Arrow-marked Babbler	Subtrop	No
	T. squamiceps	Arabian Babbler	Subtrop	No
	T. striata	Jungle Babbler	Trop/Subtrop	No
	T. bicolor	Southern Pied Babbler	Subtrop	Yes
	Cracticidae			
	Cracticus cassicus	Hooded Butcherbird	Trop	No
	C. torquatus	Grey Butcherbird	Trop/Subtrop	No
	C. tibicen	Australian Magpie	Trop/Subtrop	Yes
	Dicruridae			
	Dicrurus macrocercus	Black Drongo	Trop/Subtrop	No
	Emberezidae			
	Calcarius pictus	Smith's Longspur	Temp	Yes
	Epthianuridae			
	Epthianura albifrons	White-fronted Chat	Subtrop	No
	Furnariidae			
	Coryphistera alaudina	Lark-like Brushrunner	Subtrop	No
	Phacellodomus rufifrons	Rufous-fronted Thornbird	Trop/Subtrop	No
	Pseudoseisura cristata	Caatinga Cachalote	Trop/Subtrop	No
	Granllinidae			
	Grallina cyanoleuca	Magpie-lark	Trop/Subtrop	Yes
	Hirundinidae			
	Hirundo rustica	Barn Swallow	Temp	Yes
	Tachycineta bicolor		Temp	No
	Delichon urbicum	Northern House Martin	Temp	Yes
	Icteridae			
	Agelaioides badius	Greyish Baywing	Subtrop	No
	Curaeus curaeus	Austral Blackbird	Subtrop	No
	Dolichonyx oryzivorus	Bobolink	Temp	Yes
	Hypopyrrhus pyrohypogaster	Red-bellied Grackle	Trop	No
	Pseudoleistes virescens	Brown-and-yellow Marshbird	Subtrop	No
	P. guirahuro	Yellow-rumped Marshbird	Subtrop	No
	Maluridae			
	Malurus amabilis	Lovely Fairy-wren	Trop	No
	M. melanocephalus	Red-backed Fairy-wren	Trop/Subtrop	Yes
	M. coronatus	Purple-crowned Fairy-wren	Trop/Subtrop	Yes
	M. cyanocephalus	Emperor Fairy-wren	Trop	No
	M. cyaneus	Superb Fairy-wren	Subtrop	Yes

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Order	Family/ Species name	Common name	Geographical region	Genetic information
	M. elegans	Red-winged Fairy-wren	Subtrop	Yes
	M. lamberti	Variegated Fairy-wren	Trop/Subtrop	No
	M. leucopterus	White-winged Fairy-wren	Subtrop	No
	M. pulcherrimus	Blue-breasted Fairy-wren	Subtrop	No
	M. splendens	Splendid Fairy-wren	Subtrop	Yes
	Stipiturus malachurus	Southern Emu-wren	Subtrop	Yes
	Meliphagidae			
	Lichenostomus melanops	Yellow-tufted Honeyeater	Subtrop	No
	Manorina melanocephala	Noisy Miner	Subtrop	Yes
	M. melanophrys	Bell Miner	Subtrop	Yes
	Mimidae			
	Mimus gilvus	Trop Mockingbird	Trop/Subtrop	Yes
	Nesomimus parvulus	Galapagos Mockingbird	Trop	Yes
	Ramphocinclus brachyurus	White-breasted Thrasher	Trop	Yes
	Monarchidae			
	Terpsiphone viridis	African Paradise-flycatcher	Trop	No
	Motacillidae			
	Motacilla capensis	Cape Wagtail	Subtrop	No
	Muscicapidae			
	Bradornis pallidus	Pale Flycatcher	Subtrop	No
	Notiomystidae			
	Notiomystis cincta	Stitchbird	Temp	Yes
	Oriolidae			
	Sphecotheres viridis	Timor Figbird	Trop	No
	Pachycephalidae			
	Falcunculus frontatus	Shrike-tit	Subtrop	No
	Mohoua albicilla	Whitehead	Temp	No
	Paridae			
	Pseudopodoces humilis	Ground Tit	Temp	Yes
	Petroicidae			
	Eopsaltria australis	Eastern Yellow Robin	Subtrop	No
	E. georgiana	White-breasted Robin	Subtrop	No
	Melanodryas cucullata	Hooded Robin	Trop/Subtrop	No
	Ploceidae			
	Bubalornis niger	Red-billed Buffalo-weaver	Trop	No
	Philetairus socius	Sociable Weaver	Subtrop	Yes
	Plocepasser mahali	White-browed Sparrow-weaver	Trop/Subtrop	Yes
	Pseudonigrita arnaudi	Grey-headed Social-weaver	Trop	No
	Pomatostomidae			
	Pomatostomus halli	Hall's Babbler	Subtrop	No
	P. isidorei	New Guinea Babbler	Trop	No
	P. ruficeps	Chestnut-crowned Babbler	Subtrop	No
	P. superciliosus	White-browed Babbler	Subtrop	No
	P. temporalis	Grey-crowned Babbler	Trop/Subtrop	Yes
	Prunellidae			
	Prunella collaris	Alpine Accentor	Temp	Yes
	P. modularis	Dunnock	Temp	Yes
	Pycnonotidae			
	Alophoixus pallidus	Puff-throated Bulbul	Trop/Subtrop	No
	Sittidae			
	Sitta pusilla	Brown-headed Nuthatch	Temp	Yes
	S. pygmaea	Pygmy Nuthatch	Temp/Subtrop	No
	Struthideidae			
	Corcorax melanorhamphos	White-winged Chough	Subtrop	No
	Struthidea cinerea	Apostlebird	Subtrop	Yes
	Sturnidae			
	Lamprotornis superbus	Superb Starling	Trop	Yes

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	Sylviidae			
	Acrocephalus sechellensis	Seychelles Brush-warbler	Trop	Yes
	A. melanopogon	Moustached Warbler	Temp	Yes
	A. vaughani	Pitcairn Reed-warbler	Subtrop	Yes
	Thraupidae			
	Neothraupis fasciata	White-banded Tanager	Subtrop	No
	Tangara larvata	Golden-hooded Tanager	Trop	No
	T. mexicana	Turquoise Tanager	Trop	No
	Timaliidae			
	Chaetops frenatus	Cape Rockjumper	Subtrop	No
	Yuhina brunneiceps	Taiwan Yuhina	Subtrop	No
	Turdidae			
	Catharus bicknelli	Bicknell's Thrush	Temp	Yes
	Erythropygia coryphaeus	Karoo Scrub-robin	Subtrop	Yes
	Phoenicurus ochruros	Black Redstart	Temp	No
	Sialia mexicana	Western Bluebird	Temp	Yes
	S. sialis	Eastern Bluebird	Temp/Subtrop	Yes
	Troglodytidae			
	Campylorhynchus griseus	Bicoloured Wren	Trop	Yes
	C. nuchalis	Stripe-backed Wren	Trop	Yes
	C. rufinucha	Rufous-naped Wren	Trop	No
	C. yucatanicus	Yucatan Wren	Trop	No
	Donacobius atricapillus	Donacobius	Trop/Subtrop	No
	Thryothorus pleurostictus	Banded Wren	Trop	Yes
	Thryothorus leucotis	Buff-breasted Wren	Trop/Subtrop	Yes
	Tyrannidae			
	Phelpsia inornata	White-bearded Flycatcher	Trop	No
	Vangidae			
	Schetba rufa	Rufous Vanga	Subtrop	No
	Zosteropidae			
	Zosterops modestus	Seychelles Grey White-eye	Trop	No